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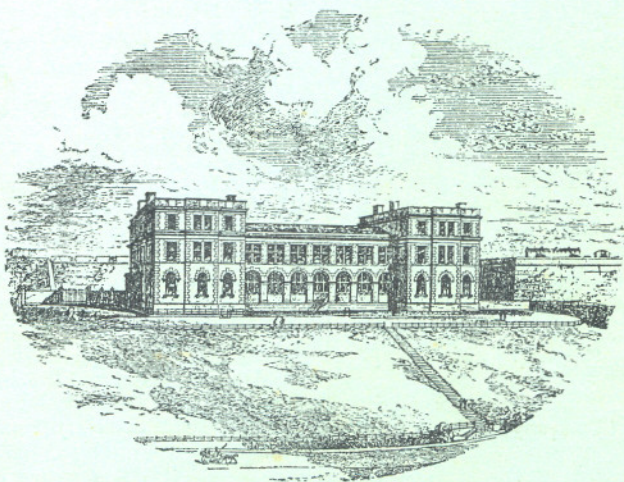
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# The Euphausiidæ in the Neighbourhood of Plymouth.

## III. *Thysanoessa inermis*.

By

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With Plates I-V.

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In a former paper (Lebour, 1924) attention was called to the eggs, Calyp-topsis and first Furcilia stages of *Thysanoessa inermis* together with the form *neglecta*, which was regarded as a different species, mainly on account of the size of the eggs shed by the females in glass jars in the aquarium, those of the *neglecta* form being much smaller than those of the *inermis* form. Certain differences were also found between the males of the two forms.

Having through the kindness of Mr. C. F. Hickling obtained a number of *Thysanoessa* from the Atlantic Slope, chiefly in the region of the Smalls trawling ground, I found both forms present, which were usually much larger than those from the Channel, and presented certain other differences. Specimens of the two forms from both localities were sent to Dr. H. J. Hansen, of Copenhagen, who has kindly examined them and pronounced them all to belong to the same species, e.g. *Thysanoessa inermis*. It is an interesting fact that the specimens from the Smalls district are usually much larger than those from the Channel, and the *neglecta* form has the long legs much longer and stouter. Specimens from Iceland, for which I am indebted to Dr. Hansen, are also of a large size.

As Hansen has already pointed out (1911, 1915), *Thysanoessa inermis* which has a wide range of distribution has two forms, a short-legged form, formerly known as *Rhoda inermis* and a long-legged form, formerly known as *Thysanoessa neglecta*; these may be referred to respectively as the *inermis* and *neglecta* forms. Both enter the English Channel and breed there, but are very small, the females breeding at 13-14 mm., the adult males barely reaching 14 mm. in length. The only records from the Channel are those found in the Plymouth district and off the Dodman. Adults occur in spring, when they are breeding, larvæ occurring through the summer and gradually disappearing. It is a curious fact that although there are many males of the *inermis* form, those of the *neglecta* form are exceedingly rare, only three from the Channel having

been seen, two young and one fully grown. These males, however, agree with the *inermis* form with regard to the modification of the pleopods and general armature of the antennule, a slight difference being seen in the number of setæ on the lobe of the first peduncular segment and in the hooks on the second peduncular segment, which are fewer in the *neglecta* form. This difference was also seen in specimens from Aberdeen and from Trondjem, Norway, kindly sent by Dr. A. Bowman and Dr. Nordhaus respectively. It is possible that these differences are due to age. Slight differences in the pleopods of the male are probably to be accounted for as variations within the species.

Bearing in mind these differences besides the legs the two forms are here regarded as one species.

The Atlantic specimens procured by Mr. Hickling are usually very large with the long legs of the *neglecta* form much stouter and longer than in those from the Channel. They reach a length of 17-19 mm., and may be still immature although adult females with spermatophores similar to the Channel specimens also occur in the same locality. Again there are very few males. Indeed, males are scarce here in both forms, and large catches of females only were made in the autumn and winter. It is thus probable that the females go about in swarms by themselves until joined by the males in the breeding season, and they apparently come into shallower from deeper water to breed. Large males occurred in both forms, but the pleopods and antennules differed from the adults, so much so that I was inclined to regard them as a different species until advised by Dr. Hansen that they were immature. The immature Atlantic forms are thus frequently larger than adults from the Channel.

In some Atlantic samples procured by Mr. Hickling in March, 1925, from near the coast both *Meganyctiphanes norvegica* and *Thysanoessa inermis* were breeding. Females with spermatophores of the latter species, *inermis* form, occurred, and its eggs as well as those of *Meganyctiphanes* were also present. The latter were rather smaller than those from the Channel, but those of *T. inermis* were the same size as the eggs shed by the *inermis* form brought in from the Channel and shed in glass jars in the aquarium. No very small eggs were seen similar to those shed by the *neglecta* form. Nauplii of both *Meganyctiphanes* and *Thysanoessa* were to be seen emerging from these Atlantic eggs, and could be quite easily distinguished. The nauplius of *Meganyctiphanes norvegica* is described and figured by myself in an earlier paper (1924), that of *Thysanoessa inermis* is described here for the first time as are also the following larval stages.

The nauplii are slightly more slender than those of *Meganyctiphanes* and more pointed anteriorly and posteriorly, otherwise they are very similar and they are typical nauplii.

The first nauplius (Plate I, 1) measures 0.48 mm. long, without posterior setæ and with three pairs of biramous swimming appendages.

The second nauplius (Plate I, 2) measures 0.51 mm. long and has two posterior setæ with the limbs more developed.

The metanauplius (Plate I, 3-5) measures 0.58 mm. long, and is again more slender than *Meganyctiphanes* and slightly larger, the carapace being bordered with regular short spines except at the extreme posterior end, thus differing from *Meganyctiphanes* who has irregular spines. The carapace is folded under the body at the sides and in front projects over the lobe bearing the eye. The antennules project forwards, the antennæ forwards and laterally, whilst the mandibles are now uniramous stumps. Behind the mandibles can be seen the rudiments of the fourth, fifth and sixth limbs. The abdomen projects behind the carapace, and is armed with twelve spines.

From the metanauplius comes the first Calyptopis, and both this and the second Calyptopis occurred in the samples with the eggs and nauplii. These are essentially the same as those found in plankton from round about Plymouth, the only difference being that they were slightly smaller.

It has already been shown (1924) that the Calyptopis stages of *Thysanoessa* from the Channel when alive is perfectly transparent and colourless except for conspicuous crimson chromatophores on the telson, one pair in the first, two pairs in the second and third Calyptopis. No colour showed in the preserved specimens from the Atlantic.

The last Calyptopis was not found among the Atlantic samples, neither were the early *Furcilia* stages, although later on in the year many later *Furcilia* stage and *Cyrtopia* stages occurred. The only early *Furcilia* was one (the first stage) from over deep water, which was exceedingly small and almost certainly belonged to *Thysanoessa longicaudata*, a few later larval stages of (presumably) this species were also found. These, although recognisable as separate species, differed only slightly from *T. inermis*.

A short description will now be given of the various stages in the life history of *Thysanoessa inermis*. In working this out special care was taken to find out whether any difference existed in the larval stages of the two forms, and whether the Atlantic larvæ were the same as those from the Channel. There is, in fact, very little difference between the larvæ of the two forms, which can only be distinguished with certainty in about the eleventh *Furcilia* stage, and then only by their legs. A very slight difference in the telson was usually seen in the younger stages, but it was occasionally variable. This was the comparative straightness or roundness of the hind margin of the telson, which in the *neglecta* form was straighter and more oblong than in the *inermis* form which was more rounded. I have called these two forms of telson A and B (Plate II,

9 and 10). This difference was noticeable in the later Furcilia stages with seven terminal spines, but seems to apply to the younger stages too, even showing in the last Calyptopis stages which could presumably be separated in this way. All the late Furcilia stages and the Cyrtopia stages are easily separated by their legs, but otherwise the larvæ cannot be distinguished with certainty, so that if, as is frequently the case, the legs are broken, it is practically impossible to distinguish the form.

As regards the Atlantic material the larvæ cannot usually be separated, except by the legs, from the Channel specimens. A slight difference was seen in some of the early Cyrtopia stages which were developing more rapidly than those from the Channel, the first Cyrtopia in some cases having five terminal spines on the telson instead of seven, the second having three instead of five. A slight difference was also seen in the size of the larvæ, which were often smaller than the Channel specimens in the same stage. This is rather strange as the adults are usually larger. With the exceptions mentioned above the larvæ are alike. In the following survey of the various stages the figures are taken from both Atlantic and Channel material.

#### THE LIFE HISTORY OF THYSANOESSA INERMIS (KROYER).

The eggs, nauplii, and metanauplius have already been described in the present paper (p. 3). The three Calyptopis stages have been briefly described before (1924), but a few more notes are given here.

#### THE CALYPTOPIS STAGES.

The Calyptopis stages are all characteristically slender and easily distinguishable from those of Nyctiphanes and Meganectiphanes, the only other euphausiids found to occur in the Channel, and the only other common forms in Mr. Hickling's Atlantic material.

*First Calyptopis* (Plate II, 1-6) measures 1.2-1.3 mm. in the Channel specimens. In those from the Atlantic they measure about 1.04-1.05 mm. in length. It is an interesting fact that there are six terminal spines on the telson both in the Metanauplius and first Calyptopis, the central spine being absent and only appearing in the second Calyptopis. Seven terminal spines is the usual number, but in the larvæ of *Stylocheiron Suhmii* recently investigated from Alexandria, Egypt, a description of which will, it is hoped, shortly be published, there are six up to the time when reduction takes place and then there are four; in this case the central spine not being present until the appearance of the single spine of the adolescent form. There is thus shown to be a tendency to suppress the central spine which brings the euphausiid larvæ into closer line with the Caridean larva in which the central spine is always lacking. (See

Gurney, 1925.) It is to be noted that the first larval stage of *Upogebia* has no central spine (Webb, 1919).

The appendages of the first *Calyptopis* (Plate II, 3-6) have no special features, and are much like those of *Nyctiphanes* and *Meganectiphanes*. The endopodite of the first maxilla is, however, in one piece and not two jointed, as in a figure of a *Calyptopis* figured by Hansen (1925) which he regards as a *Thysanoessa*, and which, he says, becomes unjointed in a later stage.

*Second Calyptopis* (Plate II, 7, 8) measures about 2 mm. in length from the Channel, and about 1.6 mm. from the Atlantic, otherwise they are essentially the same. The telson (Fig. 8) is now armed with seven terminal spines besides the four pairs of laterals, the laterals being arranged in the usual way, one pair behind the centre of the telson, one short pair just above the corners and two pairs of long laterals at the corners. The compound eyes are beginning to form. The carapace which has no trace of a lateral denticle (and this is the same in all stages) has a slight protuberance dorsally near the centre, which is often hardly or not at all discernible. The abdomen consists of five segments. The thoracic segments show as minute divisions, and the first thoracic limb is well developed.

*Third Calyptopis* (Plate II, 9, 10, and Plate III, 1, 2) measures 2.4-2.7 mm. in length from the Channel. It has six abdominal segments and the uropods are present. There are no more thoracic limbs behind the first. The eye is more developed, but still uncovered. In preserved specimens, however, it has a tendency to come out from the covering carapace and is so figured in Fig. 1, Plate III.

#### THE FURCILIA STAGES.

Twelve Furcilia stages have been found, but there are almost certainly fourteen, for one may infer that there is a stage, the seventh, between the form with five pairs of non-setose pleopods and the form with two pairs of setose and three pairs of non-setose pleopods, and also that there is one, the tenth, with four pairs of setose and one pair of non-setose pleopods. This latter stage was found in *Thysanoessa longicaudata*, and almost certainly exists in other species.

All are very transparent when alive with little pigment except on the telson, although a diffuse pinkish colour may be present, especially near the mouth parts. The Furcilia stages measure 3 mm. to 5.3 mm. in length, the first having no pleopods, the four last having all the pleopods biramous and setose. They correspond in a general way with the Furcilia stages of *Nyctiphanes* and *Meganectiphanes*, but there is an essential difference in the development of the pleopods, there being a stage (the sixth) in which all five pairs of pleopods

are simple and non-setose, whereas in *Nyctiphanes* and *Meganyctiphanes* the first pair becomes setose before the development of the fifth pair. The order of appearance of the pleopods appears to be of importance, and all the species of a genus probably develop in the same way, as do also closely related genera. Thus *Nyctiphanes* and *Meganyctiphanes* develop similarly, *Thysanoessa* differently and *Stylocheiron* differently from all others so far as is known. No lateral denticle is present in any stage, which is interesting, as it occurs in other species of different genera when lacking in the adult, but here it agrees with *Stylocheiron*, which has no lateral denticle in any stage. The dorsal carination of the carapace is only faintly marked, and in preserved specimens the small prominence which lies almost centrally is often indistinguishable. The rostrum is at first cut off straight, but gradually tapers from the sides and is not square as in *Nyctiphanes* and *Meganyctiphanes*. In the later stages it becomes more pointed.

The antennules are of the usual larval form, but the flagella remain very short, even in the last *Furcilia* stage. The antennæ hardly alter at all, but remain as conspicuous swimming organs. The mandibles have scarcely a trace of the palp even in the last stage. The first and second maxillæ have no special characters. The first thoracic limb is well developed, and is much like the adult in the first stage. The second thoracic limb which is only a small bud in the first stage is long, and shows definitely the *neglecta* or *inermis* form from at least the eleventh stage, sometimes earlier. The eleventh stage has the third thoracic limb well developed and slightly bent, the fourth small and straight, the fifth rudimentary. The twelfth, thirteenth and fourteenth are similar to the eleventh, but slightly larger and with the limbs more developed, the sixth thoracic limb still very rudimentary in the last stage.

*First Furcilia* (Plate III, 3, 4), 3.2 mm. long. No pleopods. Seven terminal spines to telson (there are seven in all the *Furcilia* stages).

*Second Furcilia* (Plate III, 5), 3.2 mm. long. One pair of simple pleopods.

*Third Furcilia* (Plate III, 6), 3.5 mm. long. Two pairs of simple pleopods.

*Fourth Furcilia* (Plate III, 7, 8), 3.6 mm. long. Three pairs of simple pleopods.

*Fifth Furcilia* (Plate III, 9), 3.6 mm. long. Four pairs of simple pleopods.

*Sixth Furcilia* (Plate III, 10), 3.6 mm. long. Five pairs of simple pleopods.

*Seventh Furcilia*, not found. Should have one pair of setose and four pairs of simple pleopods.

*Eighth Furcilia* (Plate III, 11), 3.8 mm. long. Two pairs of setose pleopods, three pairs simple.

*Ninth Furcilia* (Plate III, 12), 4 mm. long. Three pairs of setose pleopods, two pairs simple. Rudiment of the second thoracic limb in the *neglecta* form longer than in the *inermis* form, so that from now onwards they can be distinguished.

*Tenth Furcilia* (Plate III, 13), *Thysanoessa longicaudata* was found in this stage (3.5 mm. in length). Almost certainly a corresponding stage exists in *T. inermis*, but has not yet been found. Four pairs of setose pleopods, one pair simple.

*Eleventh Furcilia* (Plate III, 14), 4.2 mm. long. All pleopods setose. Fifth thoracic limb rudimentary. Second thoracic limb long in the *neglecta* form, reaching to beyond the corner of the carapace, third not bent, fourth very short.

*Twelfth Furcilia* (Plate III, 15; Plate IV, 1), 4.5 mm. long. Bend of second thoracic limb in the *neglecta* form, reaching to about the first third of the eye; fourth and fifth thoracic legs longer than in the eleventh stage, fifth not segmented.

*Thirteenth Furcilia* (Plate IV, 2), 4.9-5 mm. long. Similar to eleventh and twelfth, fifth thoracic leg still unjointed but with rudimentary exopodite and gill, fourth longer but not bent.

*Fourteenth Furcilia* (Plate III, 16; Plate IV, 3, 11), 5-5.3 mm. long. Similar to eleventh, twelfth, and thirteenth, but with legs more developed, fifth jointed, sixth rudimentary with one seta, fourth bent.

In all these four *Furcilia* stages with pleopods all setose the two forms can be easily separated by the legs, and from now onwards there is no difficulty at all in separating them.

#### THE CYRTOPIA STAGES.

The *Cyrtopia* stages gradually lead up to the mature form, the first stage measuring 5-6 mm. in length, the adult measuring from 13-19 mm. or more. It is to be noted that the small mature forms are fully developed, unlike *Nyctiphanes* which breeds before its appendages are completely formed. It is an interesting fact that in the development of the seventh thoracic leg in *Thysanoessa inermis* the endopodite is formed last, unlike the legs in front of it and unlike the same leg in *Nyctiphanes* and *Meganyctiphanes*, in which it is formed first, and it is not cut off from the base until late, not apparently until maturity is reached (Plate V, 6, 8). Young stages show the leg very like the male with no separate endopodite. Thus in the larger specimens from the Atlantic the seventh leg in the female may be at 18 mm., still like the male and without an endopodite, whereas in the Channel mature females of 13 mm. have a well-developed endopodite. The reason is presumably the fact



that in *Thysanoessa* the endopodite of the seventh leg being always rudimentary its early development is not essential, as it is in the long and useful leg in *Nyctiphanes* and *Meganyctiphanes*. The pleopods and antennules of the male are apparently modified late in the development, for no sexual differences can be made out in specimens up to 10 mm. or more from the Atlantic. This may, of course, mean that no young males were present, but in the Channel specimens of 11 mm. were nearly mature. It is probable that external sexual differentiation takes place late. In the Atlantic specimens immature males up to 18 and 19 mm. in length had very different antennules and pleopods from the adult, the antennules being about half-way between females and males, the pleopods being more like those of a different species, having sharp, short processes and more setæ round the setiferous lobe (Plate V, 1). The telson in the first *Cyrtopia* usually still has seven terminal spines (Plate IV, 6), those from the Atlantic sometimes having five. The second *Cyrtopia* has five (Plate IV, 7), the third three (Plate IV, 8), and the fourth one (Plate IV, 9). The fifth (Plate IV, 10) is without the outer pair of long lateral spines, so that from the fifth to the adult the spines only undergo a change of form. The antennules at first have the flagella very short, and the spine on the outside of the first peduncular segment large, these gradually attaining the adult form. The antennæ although differentiated into scale and flagellum are in the first stage much like the swimming antennæ of the *Furcilia*, but the flagellum soon elongates (Plate IV, 11, 12). The mandible has at first only the vestige of a very small palp, which gradually develops. The spine above the telson is present in the second *Cyrtopia*, the spine below having appeared in the eleventh *Furcilia*. The sixth thoracic legs are rudimentary in the first *Cyrtopia*, the seventh leg beginning with its luminous organ in the second *Cyrtopia*. The rudimentary eighth thoracic leg soon follows, and from now onwards the antennular flagella elongate and the species is easily recognisable, although as stated above the sexes are difficult to separate until later.

*First Cyrtopia* (Plate IV, 4, 5, 6, 12, 14, 15, 16), 5-6.3 mm. long, the smaller specimens occurring from the Atlantic. Seven terminal spines to telson, occasionally five in the Atlantic specimens. In these with seven and five spines there seems to be no other difference except in length. The sixth thoracic leg is rudimentary with rudimentary exopodite, legs one to four bent, fifth jointed but not bent. Antennular flagella still short. Flagella of antennæ short, but three jointed.

*Second Cyrtopia* (Plate IV, 7, 13), 6-6.5 mm. long. Five terminal spines to telson, predecessors of three spines which can be seen underneath the cuticle in some specimens. There are occasionally three terminal spines in this stage from the Atlantic. Seventh thoracic leg rudimentary with gill and luminous organ, eighth a small bud. Bend of long leg in

the *neglecta* form reaches nearly to the end of the second peduncular joint of the antennule. Flagellum of antenna projects well beyond the scale and beyond the third peduncular joint of the antennule.

*Third Cyrtopia* (Plate IV, 8), 6.5 mm. long. Three terminal spines to telson. Seventh thoracic leg short with three-lobed gill.

*Fourth Cyrtopia* (Plate IV, 9), 6.75–7 mm. long. One spine to telson with two pairs of long laterals. Seventh leg slightly longer.

*Fifth Cyrtopia* (Plate IV, 10), 7.25–7.5 mm. long. Outer pair of long lateral spines of telson gone. Seventh leg slightly longer.

*Sixth Cyrtopia*, 8 mm. long. Seventh leg beginning to form exopodite, four-lobed gill.

*Seventh Cyrtopia*, 8.5 mm. long. Base and exopodite of seventh leg each with one seta. Eighth leg very short.

*Eighth Cyrtopia*, 9 mm. long. Exopodite of seventh leg longer.

*Ninth Cyrtopia*, 9.5 mm. long. Exopodite and base of seventh leg each with two setæ.

*Tenth Cyrtopia*, 10 mm. long. Exopodite of seventh leg with three setæ, quite distinct from base.

*Eleventh Cyrtopia*, 10.5 mm. long. Exopodite of seventh leg divided into two, with three terminal setæ and one lateral. No endopodite in female at present.

*Twelfth Cyrtopia* (Plate V, 2), 11 mm. long. Very like the eleventh, still no endopodite to seventh leg in female. The male from the Channel may have its antennules and pleopods modified, so that it is nearly like the adult. In the Atlantic specimens not nearly so far advanced.

From now onwards the *Cyrtopia* gradually merges into the adult, fully mature specimens occurring in the Channel at 13–14 mm., the females carrying spermatophores at 13 mm., the males being fully modified at 14 mm. (In specimens from Aberdeen mature males measured 15 mm.) It is, therefore, certain that *Thysanoessa inermis* can breed at that size although apparently the Atlantic specimens of the same size are not nearly mature. All the females with spermatophores had the endopodite of the seventh thoracic leg fully formed, the antennules and pleopods of the males from the Channel being fully formed at 14 mm. There is a very distinct difference in the size of breeding individuals on the one hand from the Channel, Aberdeen, and parts of Norway, and on the other hand from the Atlantic in the region of the Smalls Trawling Ground and from Iceland. The difference in size in the Atlantic specimens is correlated with a distinct difference in the length and stoutness of the long legs in the *neglecta* form.

We see from these notes that the life history of *Thysanoessa inermis* corresponds closely with that of *Nyctiphanes Couchii* and *Meganyctiphanes norvegica*, although it is always distinguishable at any stage. The young

are all more slender, the rostrum more pointed in the *Furcilia* and *Cyrtopia*, and there is no lateral denticle to the carapace at any stage. The colouring differs slightly. The pleopods are developed in a different order. The endopodite of the seventh thoracic leg of the female is developed long after the exopodite which is unlike the development of the legs in front and unlike *Nyctiphanes* and *Meganyctiphanes*. Apparently all legs are complete before breeding, which is unlike *Nyctiphanes* which may breed before the legs and gills are fully formed.

We have now completed the life histories of all the euphausiids known up to the present time in the English Channel, e.g. *Nyctiphanes Couchii*, *Meganyctiphanes norvegica*, and *Thysanoessa inermis* (both *inermis* and *neglecta* forms). Of these the only species which apparently live all the year round in the Channel itself is *Nyctiphanes Couchii*, the others seem to enter the Channel for breeding in the late winter and spring, and adults are not to be found there at other times of year.

*Meganyctiphanes* and *Thysanoessa* are oceanic and approach the coast to breed, *Nyctiphanes* is truly neritic, and it is of great interest to find that with the shallow water habit is correlated a hurrying up of the development. Thus *Nyctiphanes* carries her eggs which are set free from the egg sac in an advanced stage, the nauplius being only found within the sac and having its mandibles uniramous and not developed as swimming organs, whereas the eggs of *Meganyctiphanes* and *Thysanoessa* are shed in the one-celled stage, and the first nauplius having three pairs of biramous swimming appendages is hatched into the sea. The development of *Nyctiphanes* continues to be abbreviated, and we have the late *Furcilia* and *Cyrtopia* stages all further advanced than similar stages in the other two species, until finally we have *Nyctiphanes* breeding before it is fully developed.

*Nyctiphanes* seems to breed all the year round both in the Atlantic and in the Channel, but its maximum breeding time seems to be the spring. In the autumn, winter, and spring it is usually present in the Plymouth district in large quantities, usually dwindling in the summer. *Meganyctiphanes* and *Thysanoessa* seem only to breed in the late winter and spring.

The elucidation of these life histories is of importance from the point of view of the food of fishes. Euphausiids are much eaten by Hake, Mackerel, Herring, Pilchards and many other fishes. Hickling (1925) finds that *Meganyctiphanes* is a very important food of the Hake. Herrings feed on euphausiids to a large extent (Hardy, 1924; Lebour, 1924, and many others), especially *Nyctiphanes*, and the period of maximum numbers of *Nyctiphanes* corresponds to the time of the Herring fishery in Devon and Cornwall. Although Herring do not usually eat much at the breeding season, still they undoubtedly sometimes have their stomachs

full of *Nyctiphanes*, both before and after and even occasionally during the breeding season.

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## EXPLANATION OF PLATES.

PLATES I and II are drawn to the same scale as Plates I to V in the first paper (Nov., 1924), and Plates III to V are drawn to the same scales as Plates I to IX in the second paper (Oct., 1925).

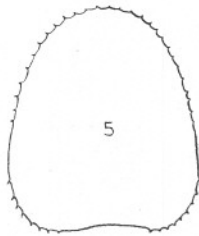
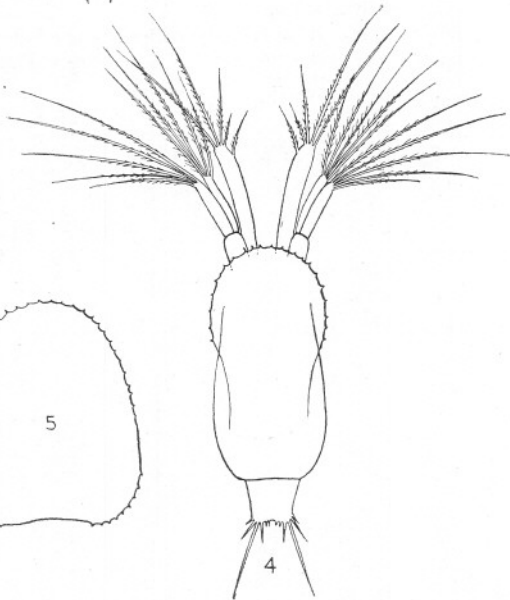
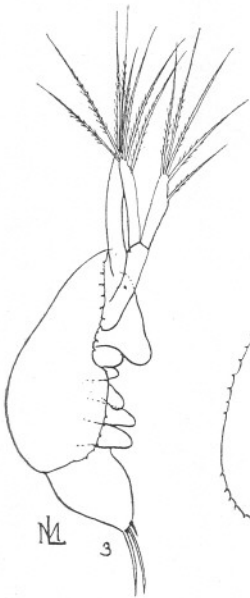
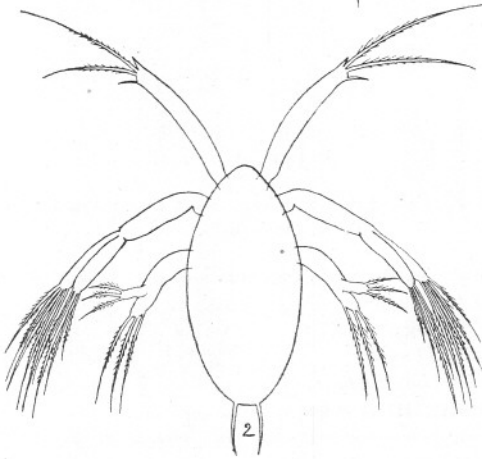
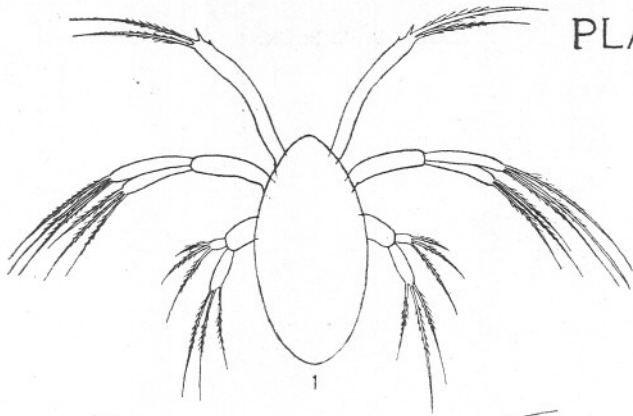
## PLATE I.

Nauplii and Metanauplius of *Thysanoessa inermis*, from the Atlantic.

## FIG.

1. First Nauplius, 0.048 mm. long.
2. Second Nauplius, 0.51 mm. long.
- 3-5. Metanauplius, 0.58 mm. long.
  3. Side view.
  4. Dorsal view.
  5. Carapace spread out.

PLATE I.



*Thysanoessa inermis.*

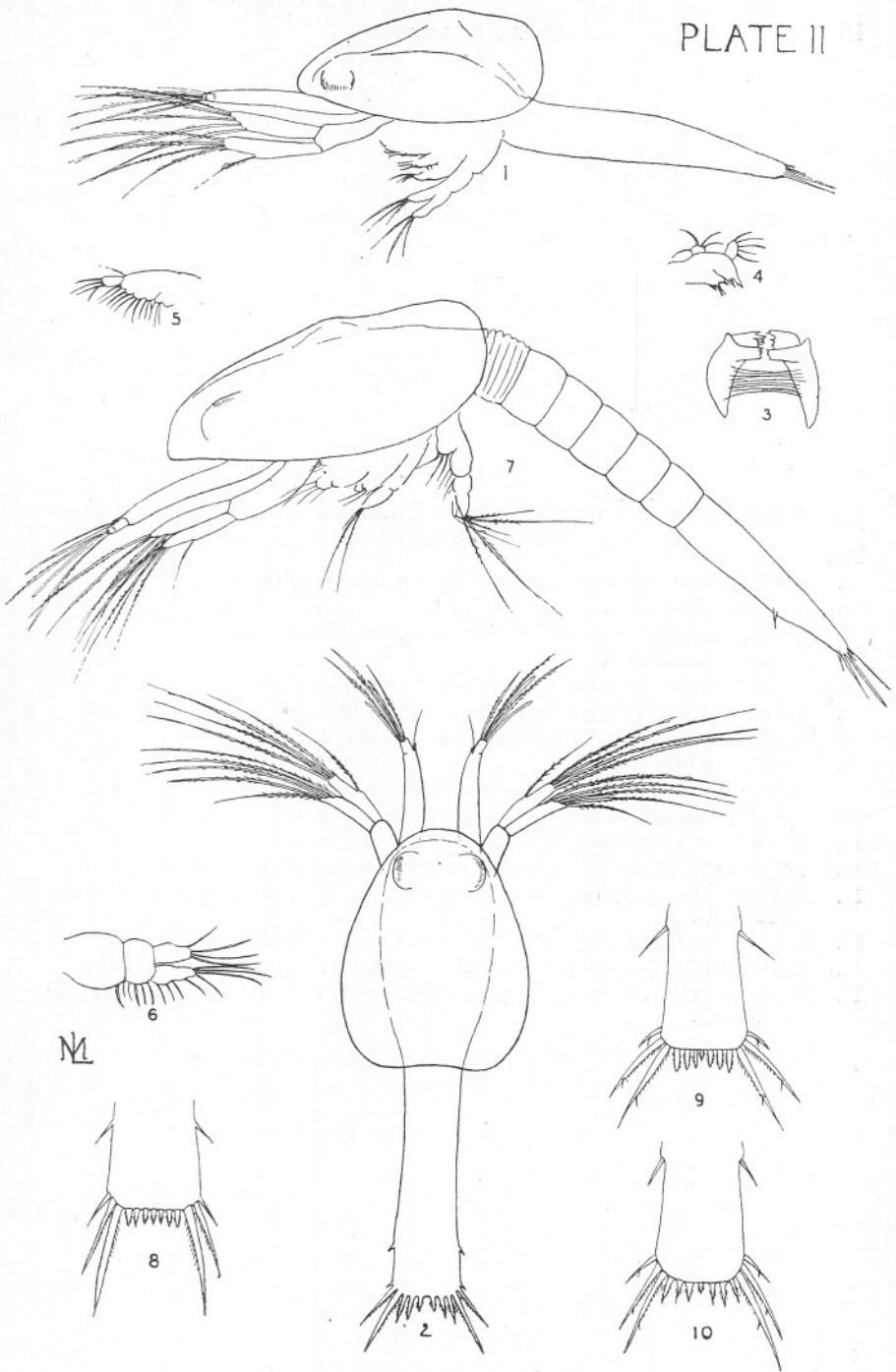
## PLATE II.

First and Second Calyptopis of *Thysanoessa inermis* and telson of Third Calyptopis.

FIG.

1. First Calyptopis, side view, 1.04 mm. long, from the Atlantic.
2. The same dorsal view.
3. Mandible of same.
4. First Maxilla of same.
5. Second Maxilla of same.
6. First Thoracic Leg of same.
7. Second Calyptopis, side view, 1.6 mm. long, from the Atlantic.
8. Telson of same.
9. Telson of third Calyptopis, form A (probably *neglecta*).
10. Telson of third Calyptopis, form B (probably *inermis*).

PLATE II



*Thysanoessa inermis.*

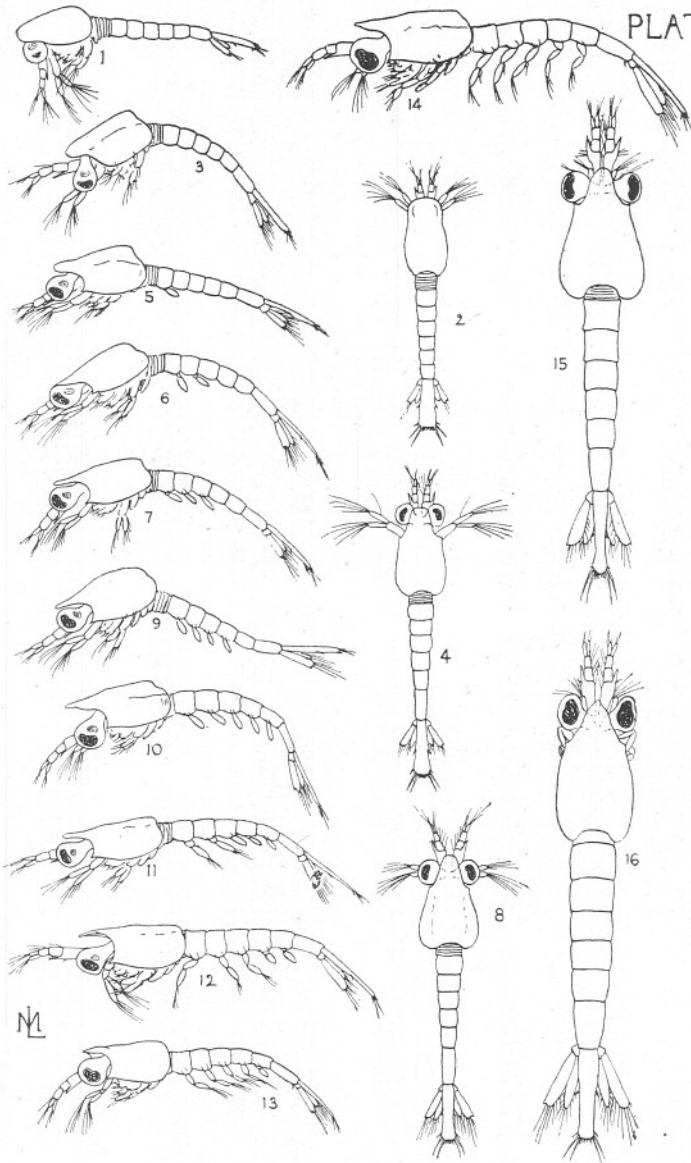


## PLATE III.

Last Calyptopis, first to eleventh Furcilia of *Thysanoessa inermis* (except the tenth, which is *T. longicaudata*).

FIG.

1. Last Calyptopis, side view, 2.4 mm. long, from the Channel.
2. The same, dorsal view.
3. First Furcilia, side view, 3.2 mm. long, from the Channel.
4. The same, dorsal view.
5. Second Furcilia, side view, 3.2 mm. long, from the Channel.
6. Third Furcilia, side view, 3.5 mm. long, from the Channel.
7. Fourth Furcilia, side view, 3.6 mm. long, from the Channel.
8. The same, dorsal view.
9. Fifth Furcilia, side view, 3.6 mm. long, from the Channel.
10. Sixth Furcilia, side view, 3.6 mm. long, from the Channel.
11. Eighth Furcilia, side view, 3.8 mm. long, from the Channel.
12. Ninth Furcilia (*neglecta* form), side view, 4 mm. long, from the Channel.
13. Tenth Furcilia of *Thysanoessa longicaudata*, side view, 3.5 mm. long, from the Atlantic.
14. Eleventh Furcilia (*neglecta* form), side view, 4.2 mm. long, from the Channel.
15. Twelfth Furcilia (*neglecta* form), dorsal view, 4.5 mm. long, from the Channel.
16. Fourteenth and last Furcilia (*neglecta* form), dorsal view, 5.2 mm. long, from the Atlantic.



*Thysanoessa inermis* and *T. longicaudata*.

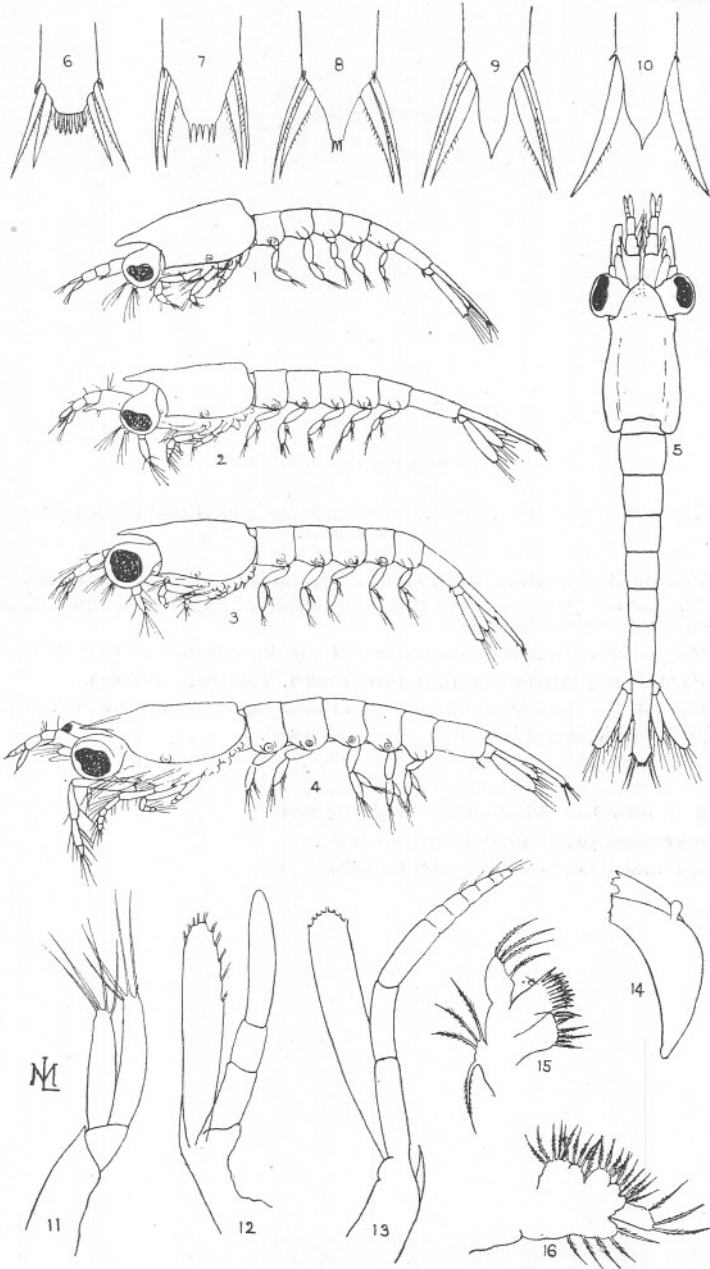
## PLATE IV.

Later Furcilia and Cyrtopia stages of *Thysanoessa inermis*.

FIG.

1. Twelfth Furcilia (*neglecta* form), side view, 4.5 mm. long, from the Channel.
2. Thirteenth Furcilia (*neglecta* form), side view, 4.9 mm. long, from the Atlantic.
3. Fourteenth and last Furcilia (*neglecta* form), side view, 5.2 mm. long, from the Atlantic.
4. First Cyrtopia (*neglecta* form), side view, 6 mm. long, from the Channel.
5. The same, dorsal view.
6. Telson of same.
7. Telson of second Cyrtopia.
8. Telson of third Cyrtopia.
9. Telson of fourth Cyrtopia.
10. Telson of fifth Cyrtopia.
11. Antenna of last Furcilia.
12. Antenna of first Cyrtopia.
13. Antenna of second Furcilia.
14. Mandible of first Cyrtopia.
15. First Maxilla of Cyrtopia.
16. Second Maxilla of Cyrtopia.

PLATE IV



*Thysanoessa inermis.*

## PLATE V.

Development of male pleopods and of seventh and eighth thoracic legs in  
*Thysanoessa inermis*.

FIG.

1. First Pleopod of ♂ (*neglecta* form), 17 mm. long, immature, from the Atlantic.
2. First Pleopod of ♂, 11 mm. long (form not certain as legs were broken off), immature, from off the Dodman.
3. First Pleopod of ♂ (*inermis* form), mature, 14 mm. long, from the Channel.
4. First Pleopod of ♂ (*neglecta* form), mature, 13 mm. long from Aberdeen.
5. First Pleopod of ♂ (*neglecta* form), mature, 14 mm. long, from the Channel.
6. Seventh Thoracic Leg of immature ♀ (*neglecta* form).
7. Seventh Thoracic Leg of adult ♂ (*neglecta* form).
8. Seventh Thoracic Leg of adult ♀ (*neglecta* form).
9. Eighth Thoracic Leg of immature ♀ (*neglecta* form).
10. Eighth Thoracic Leg of adult ♂ (*neglecta* form).
11. Eighth Thoracic Leg of adult ♀ (*neglecta* form).



*Thysanocessa inermis.*



## Further Observations on Marine Ciliates Living in the Laboratory Tanks at Plymouth.

By  
W. De Morgan.

With 28 Figures in the Text.

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#### TRACHELOCERCA PHÆNICOPTERUS Cohn.

ALWAYS to be found in Drake's Island Tank.\* Very abundant during the summer, but diminishing in number during the winter months. It has been described by O. Müller (22), Ehrenberg (6), Stein (31), Dujardin (5), Claparède and Lachmann (3), under various names, but their descriptions may be regarded as only of historic interest. The later observations of Gruber (13), Cohn (4), and Entz (8) are more detailed, and Lebedew (17) has given the fullest account of the animal. Kent (16), Bütschli (1), and Schewiakoff (27) have only short notices.

*Trachelocerca* is found in all the European seas, principally in the still water of bays and inlets, among decaying algæ.

It thrives in aquaria, so long as the saline concentration of the water does not vary too widely. Taking the salinity of Drake's Island Tank as 35<sup>0</sup>/<sub>00</sub>, I have reduced it at intervals of six hours to 8<sup>0</sup>/<sub>00</sub> without affecting the animals; below 8<sup>0</sup>/<sub>00</sub> they begin to deteriorate, and at 7·5<sup>0</sup>/<sub>00</sub> cytolysis sets in. They will not survive much increase of the normal salinity. Probably had the animals been allowed a longer time

\* A large shallow tank standing in front of a south window in the Laboratory.



to adapt themselves to the reduced salinities they would have survived longer.

They feed freely on green algæ, flagellates, eggs of annelids, and Lebedew states that they can ingest even annelids themselves. Masses of ingested bacteria, in the form of small spherules, and thread-like masses, which stain readily with borax carmine may be seen distributed through the body plasma, particularly in the case of individuals taken from cultures containing decaying matter. Lebedew does not believe that *Trachelocerca*, like *Vorticella*, feeds on free-swimming bacteria, but entirely on masses collected in the scum on the cultures.

The general appearance (Fig. 1) and extraordinary contractility of *Trachelocerca* make it impossible to mistake it for any other Infusorian.

When lying quiet, the body appears oval or spindle-shaped, opaque, and tapering gradually anteriorly into a narrow neck, which is not so opaque as the body, and terminating in the cytostome. When the animal is extended the anterior end containing the cytostome is slightly enlarged.

The posterior end of the body is sometimes rounded, sometimes pointed, and generally forms a kind of tail ending in a sharp-pointed hook. The length of this tail is very variable, and Lebedew considers that there are two varieties of *Trachelocerca*, "tailed" and "tailless." In Plymouth the tailless variety is rare. In transverse section the body is round, oval or bent so as to form a furrow. When greatly extended it forms a flat ribband.

There is much included matter in the body plasma which Schewiakoff believed to consist of inorganic matter, such as calcium phosphate remaining from the digested food. Lebedew points out that after treatment with alcohol this included matter disappears, while the balance stains with different stains, and is probably of organic origin. He thinks, therefore, that it is the reserve material so often present in Protozoa. Vacuoles of various sizes are also present in the endoplasm.

When contracted the animal may measure only .1 mm. in length, and when extended 1.5 mm. Van Beneden mentions having seen a specimen even 3 mm. long. I think this quite possible, as I have a specimen fixed in boiling sublimate, of 1.25 mm. length; and with the use even of boiling sublimate as a fixative, the animal's extraordinary power of sudden contraction is only slightly checked. Lebedew states that when swimming rapidly the animal can contract  $\frac{1}{2}$  of its length in a flash.

When fully extended, and swimming rapidly *Trachelocerca* resembles a long, narrow rod, there being little appreciable difference of diameter throughout its length.

*Trachelocerca* is generally sluggish, and lies with the neck slightly extended, twisting it in different directions, and darting it forward and withdrawing it with great rapidity.

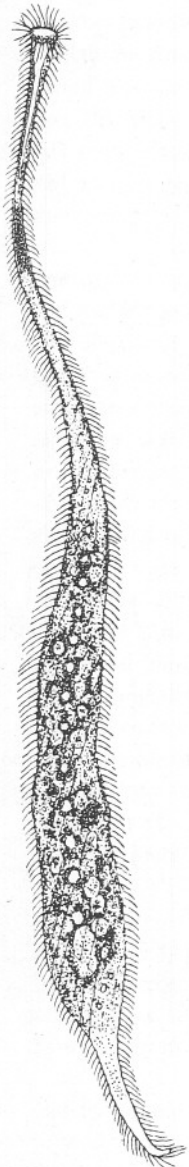
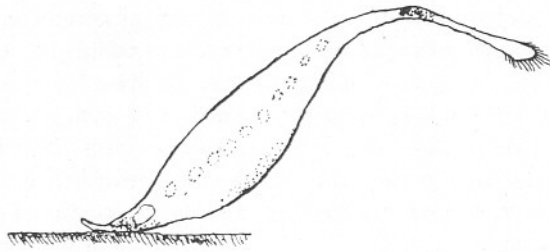
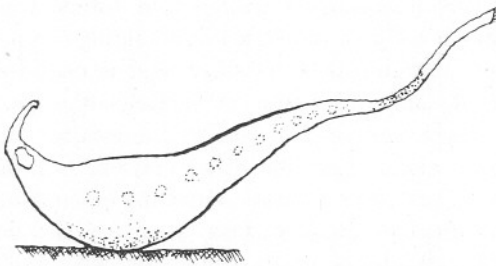


FIG. 1. *Trachelocerca phœnicopterus* in a state of ordinary extension. The 13 light spheres are nuclei.



A



B

FIG. 2. *Trachelocerca phœnicopterus*, adherent to the surface on which it is lying.

A. Near tail end. B. At a point higher up the body.

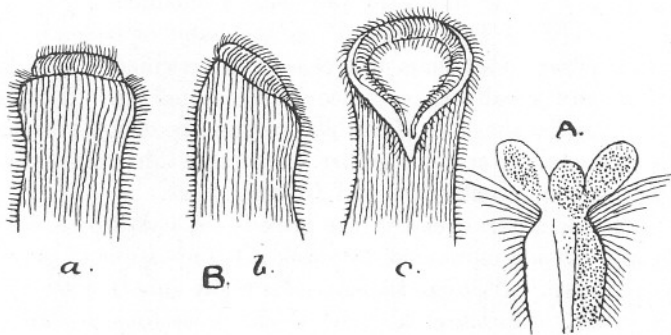


FIG. 3. Cytostome of *Trachelocerca phœnicopterus*.  
B. After Lebedew. (a) Dorsal view. (b) Profile. (c) Ventral.  
A. After Entz.

It adheres to the surface on which it is lying with considerable tenacity, and is often difficult to remove by the pipette (Fig. 2). On occasions it swims with great rapidity, and is then extended to a maximum length.

A peculiar crease or furrow may be observed running along the body. It is more or less strongly defined, and occupies various parts of, and positions on the body. Occasionally it runs the whole length from the anterior end to the tail. It was first described by Cohn (4). Entz (8), however, denied its existence, and suggested that Cohn's specimens were abnormal.

Lebedew observed it exclusively in the tailed forms. I have examined many Plymouth specimens and always found it present, except when the animal is at maximum extension, and forms a narrow ribband. It appears that it is due to a longitudinal folding of the body, so as to bring the opposite margins close together, and is possibly connected in some way with the animal's power of surface adhesion. Lebedew remarks that the presence of such a furrow (Längsfalte) might be expected on exconjugants along their line of separation, but that after careful examination he has never observed anything of the kind, nor do individuals having the crease show any signs of antecedent conjugation. He also suggests the possibility of its connexion with the power of adhesion, and compares it with C. Hamburger's (15) observations on *Trachelius ovum*, of what she calls a suction-cup (Saugknopf). Lebedew, however, always alludes to the posterior extremity as the point of adhesion. This is not exactly correct. Attachment is effected slightly above the extreme posterior end, generally at the point where the tail may be said to join the body. Often, however, it occurs much higher up, near the middle of the body, and in the tailless as well as the tailed variety. It may also be noticed that the crease does not extend to the extreme posterior end. Fig. 2, A and B, shows the two usual attachments.

In cultures *Trachelocerca* has the habit of collecting into masses, in which the individuals are closely intertwined. Lebedew thinks that syngamy usually takes place in this condition. I have not observed that such is the case. Possibly the presence of some favourite food causes the animals to crowd together. The same thing takes place in cultures of *Spirostomum ambiguum* and *Dileptus gigas*.

At the anterior end of the neck is the Cytostome. By reason of the rapid darting motions of the neck it is impossible to get a steady view of this organ. Although the animal is easily anæsthetised by 1% Eurythane solution, the marginal rim of the cytostome is always withdrawn. Observers consequently differ in their accounts of the structure. When the neck is extended the anterior end is slightly enlarged, and in the middle of this area is the cytostome, which is thus described by Entz (8). "The nearly central mouth-opening leads directly to a cytopharynx

of somewhat remarkable size. Outside around the mouth lie four lobes arranged in a cross, and between them four somewhat smaller lobes. The lobes are of varying degrees of sharpness and sometimes disappear altogether" (Fig. 3A).

Schewiakoff's (28) description is similar.

Even if the margin of the cytostome is slightly lobular, which I think is the case, Entz's drawing is much exaggerated. Lebedew's description is as follows: "The anterior end of the body seen in profile is sharply truncated (Fig. 3B b). The mouth opening occupies the anterior end, and runs as a furrow of varying length on one side of the body. The side towards which the anterior end is truncated, and in which the mouth-opening is situated, may be, as with other Infusoria, called the ventral side. (Fig. 3B c of the present paper is a reproduction of Lebedew's figure.) A peculiar cytoplasmic ring surrounds the whole cytostome. This rim is striated, and carries a wreath of cilia. It can be protruded or withdrawn in varying degrees. In fixed specimens it is always withdrawn. It is in no sense a closed rim, but runs along the cytostome, and terminates lower down on the ventral side in two small angles (Kante)."

My own observations generally agree with those of Lebedew. The anterior end of the neck is obliquely truncated, and a rim with cilia longer than those on the rest of the body is apparent; but I am unable to say whether this rim terminates ventrally in two angles, or whether the two ends are joined.

Entz's figure certainly does not represent the fully extruded cytostome accurately; but I have observed that in fixed specimens the withdrawn margin is invariably lobular, and possibly Entz made his drawing from a fixed specimen.

I have never been able to make out the four smaller lobes he describes. It seems possible that the expanded rim when withdrawn would of necessity be divided into lobes so as to fit the reduced diameter of the neck.

Lebedew compares the cytostome of *Trachelocerca* with that of *Dileptus* as described by Schewiakoff (27), which it resembles, except that the rim of the cytostome runs anteriorly in *Dileptus*, and the reverse in *Trachelocerca*. *Dileptus*, moreover, has a cytopharynx, and striations which have been interpreted as supporting-rods, but which Schewiakoff suggests may be really the striation of the rim as in *Trachelocerca*.

The *cytopyge*, according to Lebedew, is situated at the posterior end, opening in tailless forms directly at the posterior end, but in tailed forms at the side.

The whole body is enveloped in a fairly thick, transparent and homogeneous pellicle. On the pellicle are rows of papillæ running longitudinally

parallel to one another. The papillæ are close together and on each is a pretty long, very fine cilium. These cilia throughout the body are of the same length, but at the anterior and posterior ends, and on the cytostomial rim are rather longer. Each cilium rises from a basal corpuscle. These are easily seen in compressed and stained specimens. Fixation in boiling sublimate or Bouin Duboscq's solution, and staining with iron hæmatoxylin give good results.

When the animal is fully extended the margin of the pellicle is quite straight and smooth. As it contracts the margin becomes wrinkled, and these wrinkles appear as fine cross striæ on the body.

Lebedew describes the process of wrinkling as follows: "If the animal contracts slightly a number of fine cross striations appear on the pellicle (Fig. 5). With stronger contraction the outer surface arches itself outwards, between the rows of cilia, so that the cilia run in furrows along the body (Fig. 4). At the same time the cross striations become fewer in

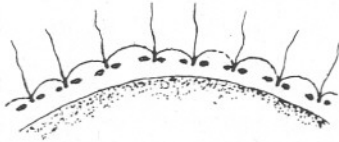


FIG. 4. Section of A form of *T. phænicopterus*, showing the cilia arising between the wrinkles of the pellicle. Their basal corpuscles and sections of two myofibrillæ on either side of them are seen. After Lebedew.

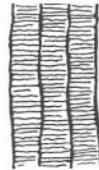


FIG. 5. Striations on pellicle of *T. phænicopterus*, when animal is slightly contracted. After Lebedew.

number, but much more strongly marked, so that the space between two rows of cilia resembles a column of small quadrangular figures, something like boxes, lying one above the other. (See Fig. 6A, after Lebedew.) These columns appear to be individual, and lie between the muscle fibrillæ. If a fibrilla gets loose or destroyed the columns present an irregular or toothed outline." (See Fig. 6B, after Lebedew.)

I have noticed something of this appearance in compressed living specimens. Lebedew's drawings were made from specimens fixed in Picroacetic acid and crushed under the coverslip. My crushed and stained specimens do not appear so.

As might be expected from the extreme contractility of *Trachelocerca*, the myofibrillæ are well developed. They may be seen in whole preparations and in longitudinal and transverse sections. They run close and parallel to the lines of cilia, which are marked by the basal corpuscles (Fig. 7A). They stain more deeply than the surrounding plasma. They do not appear to run in canals as is the case with *Stentor*, *Condylostoma* and some other Infusorians.

The thickness of the fibrillæ varies, occasionally distinct nodosities are present. It is reasonable to conjecture that this is the result of contraction. In some cases Lebedew has seen fibrillæ of the rose-wreath form, and always in individuals closely contracted, and at points where the contraction was greatest (Fig. 7B).

Occasionally one or more rows of cilia may be unaccompanied by myofibrillæ, or a portion of a myofibrilla may be absent. Lebedew says that he has seen cases where all the myofibrillæ were absent. Lying on the opposite side of the basal corpuscles to the myofibrillæ above described, Lebedew states that he has seen another fibrilla (Fig 7B c). He conjectures that these may be either nerve-elements, "Neurophanea"

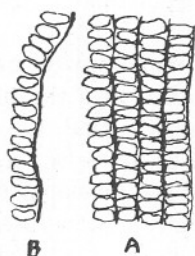


FIG. 6. (A) Appearance of pile of quadrangular figures produced by contraction of pellicle of *T. phœnicopterus*; (B) The same after loosening of a myofibrilla. After Lebedew.

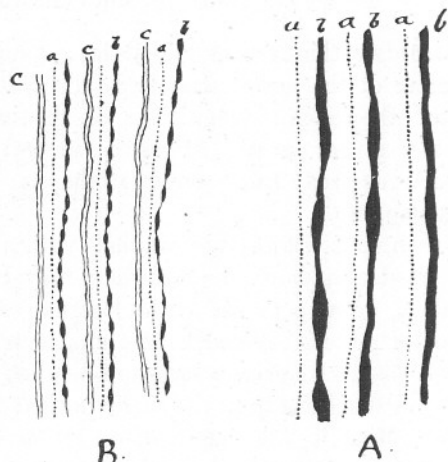


FIG. 7. (A) Sagittal section of *T. phœnicopterus*, showing (a) basal corpuscles of cilia, (b) myofibrillæ; (B) The same showing (a) basal corpuscles, (b) myofibrillæ in rose wreath form, (c) the fibrilla which does not stain so deeply. After Lebedew.

described by Neresheimer as occurring in *Stentor*, but denied by Schröder (26), or that they are true fibrillæ; in which case their number and distribution might be regarded as inconstant. I have failed to locate these fibrillæ in my preparations.

I have found no Trichocysts in the Plymouth *Trachelocercæ*, nor has Lebedew seen them in his individuals; but Schewiakoff states that he has observed them under the pellicle.

The contractile vacuole is rarely present. It lies at the posterior end, and functions very slowly. Lebedew says that it is not rare in the tailless variety, but absent in the tailed.

Previous to Lebedew's paper (17) accounts of the nucleus of *Trachelocerca* are scanty and contradictory. Entz describes it as single, oval,

uniformly coarsely granular and lying about the middle of the body. Gruber, on the contrary, describes numerous small nuclei scattered irregularly through the body plasma, and opines that if a *Trachelocerca* does exist it must belong to a different species. Gruber found an animal with only one nucleus, and called it *Trachelocerca minor*. Lebedew has observed all three forms, and believes that he can prove them all to belong to one and the same species, and to be genetically related. He distinguishes them as follows:—

- A. The form with a single nucleus.
- B. With a number of nuclei arranged in one or two rows.
- C. Those which according to Gruber have no nuclei, but in which nuclei are really present, but their structure very irregular.

Lebedew thinks that the diverse opinions regarding the nature and number of the nuclei arise from the fact that in any given sample of water the nuclear conditions of the animals therein are the same at any given period. He gives several examples in support of this theory derived from observations at Moscow, Sevastopol, Trieste, Rovigno, etc.

In Drake's Island Tank animals with a single or double row of nuclei are most abundant; among them may be found a few with the single nucleus, or with nuclei of the irregular or indeterminate kind, C. For want of material Lebedew was unable to complete his observations on the A class. He gives a long and detailed account of the development of the multinucleate from the single nuclear form, which cannot be inserted here. Minchin (20) summarises his account as follows: "A simple instance of direct multiple division of a nucleus, in which apparently no centrioles are present has been described by Lebedew in *Trachelocerca*. In this case partitions are formed within the nucleus, between the grains and masses of chromatin, and finally the nucleus becomes segmented into a mulberry-like mass of daughter nuclei which separate from one another" (Figs. 8A and B).

In fixed and stained preparations of animals from Drake's Island Tank, I have been able to follow all the stages of nuclear multiplication described by Lebedew.

The nucleus lies generally dorsally, and Lebedew compares it to that of the *Acinetæ* (*Dendrocometes*), where chromatin is embedded in the nuclear stroma in the form of small granules. The number of nuclei observable is generally from 4 to 20, which may subsequently be increased to 50, or even 80, according to Lebedew.

As regards the nuclear division of the A form with one nucleus, Lebedew thinks that after the first division of the nucleus into two, the animal itself divides into two daughter products, each with a single nucleus,

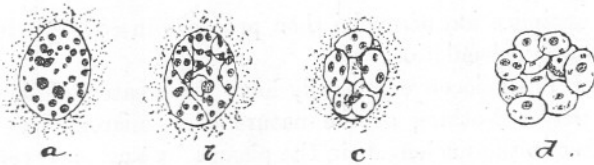


FIG. 8A. Four stages of direct multiple fission of nucleus.  
 (a) Nucleus of an A form animal. No differentiation visible.  
 (b, c, d). Stages resulting in the formation of a morula-like mass. After Lebedew.

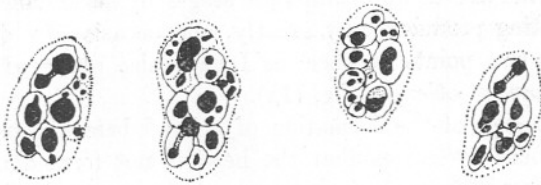


FIG. 8B. Nuclei from specimen fixed Bouin Duboscq solution stained Iron Hæmatoxylin  $\times 630$ . This individual contained thirty nuclei.

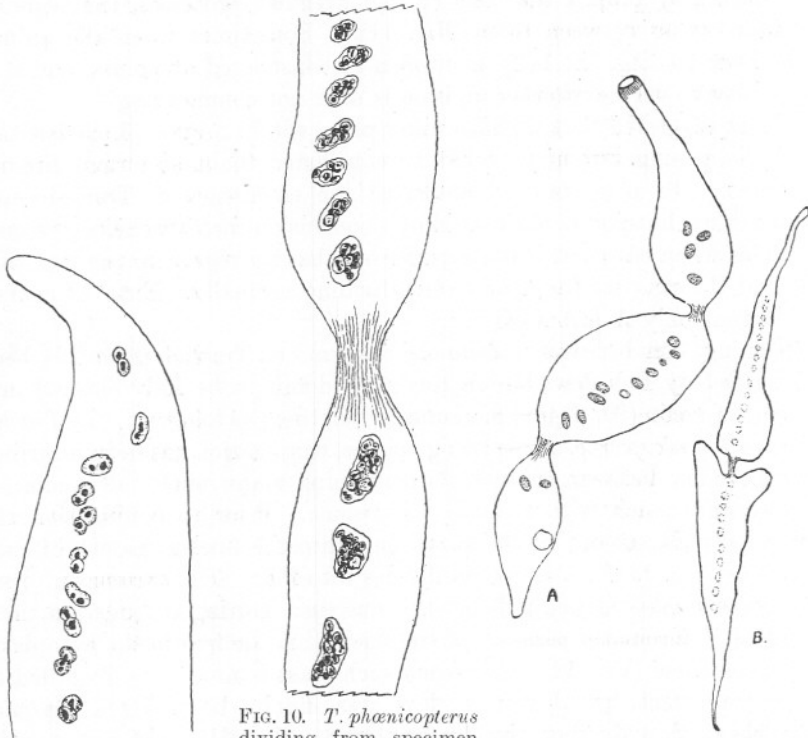


FIG. 10. *T. phænicopterus* dividing from specimen with thirty nuclei. Fixed Bouin Duboscq solution, stained Iron hæmatox.  $\times 315$ . More advanced than Fig. 9.

FIG. 9. Posterior division product of *T. phænicopterus* fixed corrosive sub., stained Iron alum  $\times 315$ , early formation of morulae.

FIG. 11. (A) *T. phænicopterus*, fixed Bouin Duboscq, stained Iron hæmatox.  $\times 300$ . Nuclei diagrammatic; (B) *T. phænicopterus*. Irregular division.



and that multiplication of nuclei then proceeds in each product. This, however, is only speculation.

The larger *Trachelocercæ* generally have the greater number of nuclei and conversely. Nothing of the nature of a micronucleus has been noticed either in the nucleus or in the plasma by any observer.

Division takes place very irregularly. The number, size, and condition of the nuclei do not appear to have any connexion with division of the animal itself. Figs. 9 and 10 represent products of two individuals in which the nuclei are in quite different stages of development. In size also the resulting products vary greatly, and occasionally division may take place at two points at once, as I have also observed in *Dileptus gigas* and *Holophrya oblonga* (Fig. 11A).

There is no sign of the formation of a head before division is fully completed. Lebedew states that the head is not formed until two or three hours after division.

Sometimes division is not so regular; the anterior end of the posterior product may project into one or two irregular processes, the point of rupture lying between them (Fig. 11B). Sometimes when the animal has been feeding, the body is swollen or constricted at points, and it is not easy to decide whether division is or is not commencing.

Entz suggested that division takes place within a cyst. Lebedew saw this happening, but under what he considered to be abnormal circumstances. He also saw and described the emergence of *Trachelocerca* from cysts, but points out that Entz's conclusion that *Trachelocerca* only divides when encysted is quite erroneous, having regard to the fact that B and C forms are frequently seen dividing normally. Entz, of course, held that only A forms existed.

Conjugation between multinucleate forms of *Trachelocerca* has been described by Lebedew, but in too great detail to be fully entered into here. Minchin (20, p. 449) has summarised them as follows: "In *Trachelocerca phœnicopterus*, a free living species, conjugation has been described by Lebedew between individuals containing many nuclei all similar in appearance, each with a large karyosome. Prior to conjugation the chromatin passes out of the karyosome into the nuclear cavity of each nucleus (Fig. 12A\* B), and then divides into four. The chromatin forms a compact mass at one pole of each nucleus. During conjugation these masses of chromatin pass out of the nuclei, and lie free in the cytoplasm between them (Fig. 12, C-G); each such mass is now to be regarded as a micronucleus, and lies in a clear area, finally becoming a vesicular nucleus with a distinct alveolar structure; the old nuclei can now be considered as macronuclei. All the nuclei now collect in a mass near the middle of the body. The macronuclei ultimately degenerate; the

\* Minchin's figure is reproduced in this paper under this number.

miconuclei multiply by fission, but ultimately, according to Lebedew, they all degenerate with the exception of one in each conjugant; the persistent micronucleus divides into two pronuclei which conjugate in the usual way; unfortunately the author's observations contain so many gaps that this statement cannot be considered established so decisively as could be desired. The exconjugants contain each a single synkaryon

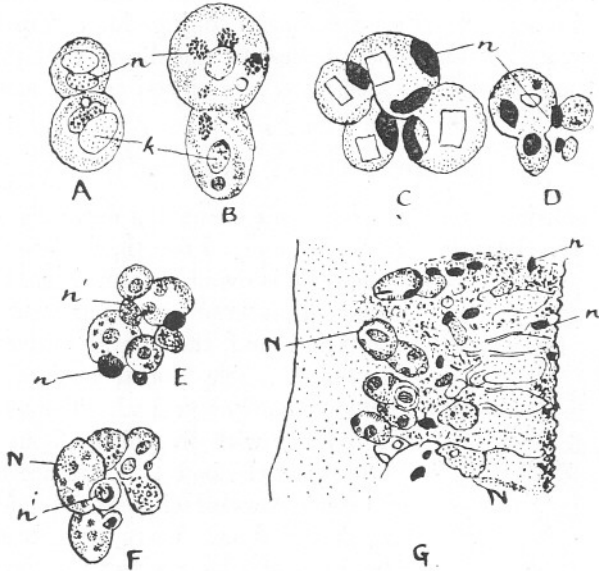


FIG. 12.

Formation of micronuclei in *T. phœnicopterus*. A, B: a nucleus has divided into two, and from the karyosome (k) of each daughter nucleus masses of chromatin are being given off into the nuclear cavity. C, D: the two nuclei of the preceding stage have divided again, to form a group of four, and the chromatin masses (n) have acquired a compact structure and are passing out of the nuclei to form the micronuclei. In C crystals are seen in the cavity of the old nuclei, probably a sign of degeneration. E, F: two groups of nuclei, both from the same specimen: the micronuclei given off from the old nuclei become surrounded by a vacuole ( $n^1$  in F) and then acquire an alveolar structure ( $n^1$  in E). G, portion of a preparation of the body of a conjugant, the wavy contour on the right being the surface of the body which is in contact with the other conjugant; numerous micronuclei (n) are seen, and also macronuclei, some of which still appear normal (N), others degenerating ( $N^1$ ). Minchin, after Lebedew.

which divides by successive divisions into a number of nuclei not differentiated into micronuclei and macronuclei.

“The case of *Trachelocerca*, as it is described, furnishes an important clue to understanding the origin of the heterokaryote condition of Infusoria, from that found in other Protozoa. In this case, during the ordinary vegetative condition, the generative chromatin representing the micronucleus of other Infusoria, and the vegetative chromatin

representing the macronucleus are contained in one and the same nucleus, and become separate only when syngamy is about to take place. The first sign of the separation is the formation of chromidia from the karyosome within the nucleus, resulting in the formation of a secondary nucleus which becomes separate, and which behaves exactly as an ordinary micronucleus; thus indicating a clear homology between the micronuclei of Infusoria and the secondary generative nuclei of Sarcodina. The production of numerous micronuclei in the conjugation of *Trachelocerca* is noteworthy, and would appear to favour the theory that primitively numerous gametes (swarm-spores) were produced in the conjugation of Infusoria."

#### URONEMA MARINA Dujardin.

A small holotrichous ciliate very common among decaying algæ, and organic matter. Length,  $\cdot 025$  to  $\cdot 04$  mm. Breadth,  $\cdot 015$  to  $\cdot 028$  mm.

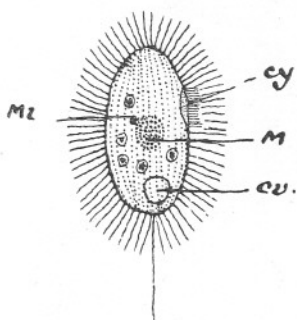


FIG. 13. *Uronema marina*. cy.: Cytostome. M.: Macronucleus. Mi.: Micronucleus. cv.: Contractile vacuole.

The body is ovoid in form (Fig. 13); sometimes the anterior end is narrower than the posterior, and the lateral outline slightly flattened. The dorsal surface is more convex than the ventral. The whole body is covered with fine cilia, about half the breadth of the body. There are twelve to fourteen rows of cilia on the dorsal and ventral surfaces. There is no striation, but the lines of cilia may give the appearance of it. At the posterior end is a long bristle-like cilium which Schewiakoff (28) thinks is sensory. I have never observed anything in the animal's behaviour when the bristle

is irritated to confirm this. Smith (30) also says that he could not agree with Schewiakoff's statement, as the animal lies quiet when the bristle is bent over to one side or the other. The body is colourless and elastic.

The cytostome is a pretty large oval opening in the upper half of the body on the ventral surface. Schewiakoff (28) says that the left margin of the cytostome carries a fairly large flapper-like (Klapperartig) undulatory membrane—that it is clearly striated, and appears as if it consisted of an agglutination of single cilia. On the right margin there are single cilia only. Smith's (30) description is similar to Schewiakoff's.

I observe that both margins are fringed with very fine cilia shorter than those of the body closely packed together, and that the cilia of either side when erected appear to form a striated undulating membrane, just as in the case of *Lembus elongatus*. Thus either margin may be said

to carry an undulating membrane really resolvable under suitable magnification into very fine cilia. This is easily verifiable when the animal is lying perfectly quiescent with the cilia around the cytostome erected. The spherical macronucleus and a small spherical micronucleus close to it lie about the centre of the body. Smith (30) states that in a large percentage of cases, the macronucleus is found to be double, and thinks that this may be interpreted as a sign of precocious division long before division of the cytoplasm commences. I have not observed this peculiarity of the nucleus. The contractile vacuole lies at the posterior end, in front of the bristle.

The endoplasm is clear and contains vacuoles, and small refringent granules especially in the posterior part. Bacteria form the principal food of the animal. It moves rapidly, revolving on the longitudinal axis of the body.

The genus *Uronema* was founded by Dujardin (5), and *Uronema marina* has been described by him, by Cohn (4), Quennerstedt (24), Mereschkowsky (19), Smith (30), Kent, and by Gourret and Roeser (12) as *Cryptochilum nigricans*. Dujardin believed that the animal was mouthless, while Cohn recognised its position, but did not make out the so-called undulatory membrane, which Kent figures as sack-like. *Uronema* is probably identical with Maupas' *Cryptochilum* and Fabre-Domergue's *Philaster*.

#### CYCLIDIUM GLAUCOMA O. F. Müller.

A very small holotrichous ciliate resembling *Pleuronema chrysalis*. Found among putrid organic matter, decaying algæ, and in the film formed by bacteria and Zoogloea. Generally in company with *Lembus*, *Uronema*, *Chaenea*, etc. One of the commonest and most widely distributed ciliates. It seems to feed principally on Bacteria.

Length, .018 to .024 mm. Breadth, .01 to .016 mm.

The body is fairly elastic, but constant in shape and colourless.

In shape longish oval, or egg-shaped, and generally narrower at the extremities, but this is variable, and occasionally they are slightly flattened.

The dorsal surface is convex, the ventral flat, but hollowed out to form a peristomial area which occupies about two-thirds of the ventral area. In the anterior one-third of its length the peristome is narrower, and then widens out to form an area included by its borders, of which the left forms a deep curve while the right is flatter. It thus much resembles the peristome of *Pleuronema chrysalis*.

The body is clothed with long fine cilia, which when the animal is at rest appear stiff and bristle-like. They are spaced fairly widely apart, except at the anterior extremity, where they are more numerous and

more close set. The cilia arise from small papillæ, which viewed together suggest striation. From the posterior end projects a very long pointed bristle-like cilium, which is characteristic of the genus (Figs. 15, 16).

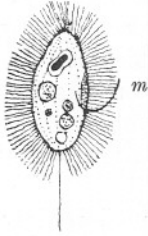


FIG. 14. *Cyclidium citrullus* after Möbius.  $\times 480$ . m. The line formed by ends of cilia which he believed to be a bristle.

The pellicle is very thin and homogeneous, and difficult to make out. The endoplasm is transparent and slightly granular.

The orifice of the cytostome is very minute, and lies within the wide depression of the peristomial area. Schewiakoff (28) says that it is continued into a short, pipe-like cytopharynx, running dorsally towards the left. This I have not observed.

A long undulating membrane runs along the whole of the left peristome margin, turns round the end, and extends for a short distance up the right margin; but not so far as in *Pleuronema*, in which nearly one-third of the right margin is occupied by it.

The membrane thus forms a kind of bag round the posterior end of the peristome. This undulatory membrane consists of very fine cilia, and when the animal is lying in a suitable position its outline under

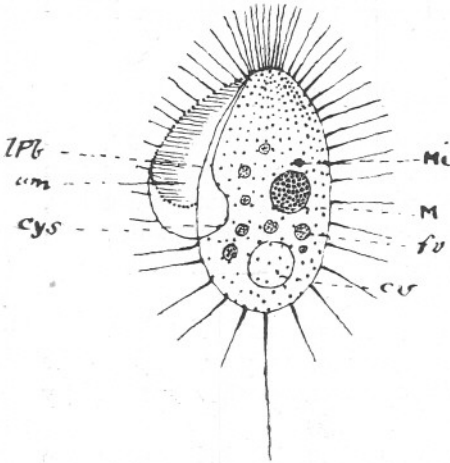


FIG. 15. *Cyclidium glaucoma*. Left side. um.: Undulating membrane formed by fine cilia. rPb., lPb.: Right and left peristomial borders. M.: Macronucleus. Mi.: Micronucleus. fv.: Food vacuoles. cv.: Contractile vacuole. cys.: Cytostome.

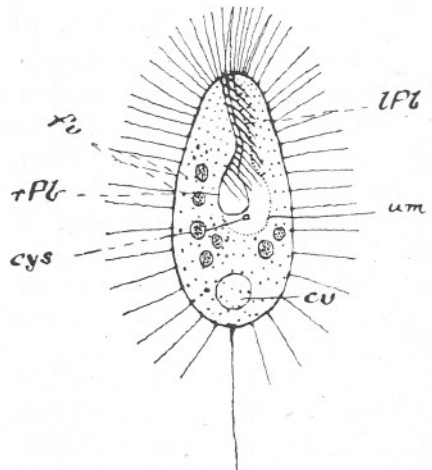


FIG. 16. *Cyclidium glaucoma*. Ventral view. Lettering the same as in Fig. 15.

high magnification shows as a line of dots, formed by the ends of the cilia, as in the case of other ciliates, e.g. *Lembus elongatus*. Under low magnifications the dots appear as a continuous line; and this led some

of the earlier observers to describe it as a long flagellum or bristle. Möbius also (21) in describing a *C. citrullus* compares it to a long flagellum (Geissel) with its extremity bent towards the anterior end. Möbius' figure (reproduced here as Fig. 14) is an excellent representation of this appearance. Cohn (4) compares it to a stiff, hook-shaped bristle bent backwards, and correctly conjectures that it may be a sail made of agglutinated cilia. The membrane or rather the cilia composing it can be withdrawn wholly or partially within the peristomial area.

Along the right peristomial margin is a row of cilia equal in length to the body cilia, and directed obliquely towards the posterior end.

I have not seen the cytopyge. Schewiakoff (28) says that it opens on the ventral surface near the origin of the terminal bristle. The contractile vacuole lies close to it.

The macronucleus (Figs. 14, 15) lies near the middle of the body; it is spherical and finely granular. It is always accompanied by a small spherical micronucleus.

*Cyclidium glaucoma* has the habit of lying quite still, with all the cilia rigid and outspread, the contractile vacuole only continuing to pulsate. After a short interval, but long enough for observation, the animal disappears with a sudden jump, to be found again a short distance away. For this reason probably Fromentel and Dujardin gave it the specific name of *saltans*. The sudden motion appears to be effected by the terminal bristle which Gourret and Roeser (11) call the "Soie saltatrice."

Schewiakoff (28) describes another species of *Cyclidium* under the name *citrullus*, which appears to differ little from *glaucoma* except in size, and Gourret and Roeser state that at Marseilles they found two slightly different types of *glaucoma*: one in which the terminal bristle is not so highly developed and the cilia are shorter; and the other more elongated in shape, slightly rose-coloured, and with an exceptionally long terminal bristle.

*Cyclidium glaucoma* has been described by numerous authors: Schewiakoff (28), Müller (22), Ehrenberg (6), Claparède and Lachmann (3), Stein (31), Kent (16), Gourret and Roeser (11), Bütschli (1).

Schewiakoff (28) gives the following as synonymous with *C. glaucoma*:—

*C. nigrescans* and *C. saltans* Fromentel.

*Pleuronema cyclidium* Claparède and Lachmann.

*Alyscum saltans* Dujardin.

*Euchelys nodulosa* Dujardin.

*Disticha hirsuta* Fromentel.

Stein believed it to be a spore-product (Schwärmsprössling) of *Chilodon*.

## BLEPHAROSTOMA FIGERRIMA (Cohn).

A very small holotrichous ciliate, abundant in decaying organic matter, in company with *Lembus*, *Uronema*, *Chaenea*, etc.

The body (Fig. 17A) is rather spindle-shaped, and varies in length from .03 to .06 mm. The length is rather more than twice the breadth, except when the animal is full of food (Fig. 17B) when it is almost spherical. The anterior extremity ends in a sharp slightly curved, beak-like pro-

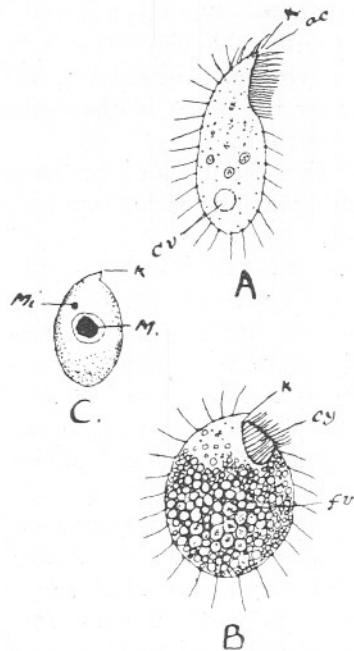


FIG. 17. *Blepharostoma pigerrima*.

- A. In ordinary condition.  
 B. Distended with food.  
 C. Fixed and stained  $\times 630$ .

k.: Beak. ac.: Anterior stiff cilia. cy.: Enlarged cytostome. cv.: Contractile vacuole. fv.: Food vacuoles. M.: Macronucleus. Mi.: Micronucleus.

jection. This point persists under all conditions even when the animal is greatly distended (Fig. 17B). It is not deformed in any degree after fixation, and appears to consist of a denser substance than the rest of the body plasma. It takes a bluish stain from picronigrosin, and probably contains Chitin.

The dorsal surface of the body is slightly convex and the ventral nearly flat. There is a deep hollow in the anterior third of one of the sides, and from the apex runs a peristomial groove for about one-third of the

body length, terminating in the large oval cytostome. There is no cytopharynx. The margins of the peristomial groove carry cilia, which vibrate but slowly. Three or four of the anterior of these cilia are stouter than the others and resemble cirri. They maintain a slow, twitching motion, while the other cilia are still. The body cilia are fairly long, slightly less than half the breadth of the body, and disposed in about ten rows. They move stiffly. There is no terminal bristle and no surface striation. The endoplasm is clear with only a few refringent granules.

The body is not very contractile, but the posterior portion is extremely plastic, and can suffer great deformation, when the animal is moving about and feeding. While so doing it is quickly filled with food vacuoles and becomes nearly spherical. The anterior beak, however, is always visible, but the cytostome is forced upwards and forms a large opening nearly at the anterior extremity, and just below the beak.

The macronucleus is spherical (Fig. 17c), and lies just behind the mouth. A small spherical micronucleus lies near it.

The contractile vacuole is generally at the posterior end.

The animal moves slowly among decaying matter.

*Blepharostoma pigerrima* was described by Cohn (4), in 1866, as *Colpoda pigerrima*. In 1888 Gourret and Roeser (12) described as *Cryptochilum fusiforme* a new species which resembles the Plymouth ciliate in every particular except in the presence of a micronucleus. The persistence of the anterior beak after the enlargement of the posterior part of the body is referred to by them. Gourret and Roeser do not refer to Cohn's *Colpoda pigerrima*, although they debated whether their new species should be included in the genus *Colpoda*. The genus *Cryptochilum* was founded by Maupas in 1888, and Gourret and Roeser were doubtful at first whether to include the new species in it, having particular regard to the absence of the posterior bristle and of longitudinal striation, both of which are characteristic of Maupas' genus, *Cryptochilum*.

They finally decided that particular points of resemblance, such as the position of the peristomial groove and cytostome, the hollowing out of one of the lateral faces and the absence of a cytopharynx, overbalance the negative characters; more particularly as Maupas in his description of *Cryptochilum nigricans* remarks that striation is not always very clearly defined (la striation n'est pas toujours très nettement accusée).

The genus *Blepharostoma* was formed by Schewiakoff in 1893. I have not seen his work, but the generic description is given in *Nord. Plankton*, XIII, p. 64, as *Blepharostoma* Schewiak., 1893: "Very small, oval to spindle-shaped. Body covered with longitudinal rows of fairly long, close-packed cilia. Mouth opening large, oval. The whole border of mouth with the exception of the hindmost portion studded with long,



strong cilia. Undulating membrane wanting. Nucleus central. Contractile vacuole terminal."

*HOLOSTICHA RUBRA* (Ehrenberg) var. *FLAVA*.

A hypotrichous ciliate generally found in Drake's Island Tank. Abundant in the summer.

Body very flexible and elastic, but slightly contractile longitudinally. Length, .18 to .37 mm., and four or five times the breadth. The greatest width is about the middle of the body. The anterior end is narrowed and rounded, forming a kind of lobe, which is divided so as to form two lips of which the ventral one is transparent and projects slightly beyond the dorsal (Fig. 18 l). These two lips thus enclose a groove which is continued to right and left, and along it the anterior crown of cilia runs. The posterior extremity is wider than the anterior, but narrower than the

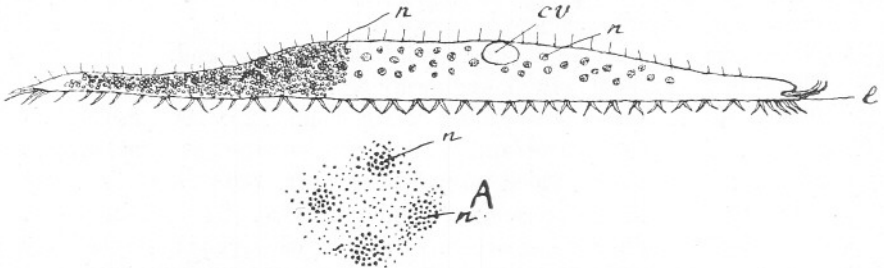


FIG. 18. *Holosticha rubra* var. *flava*, viewed from the right side. The posterior portion shows the closely pressed corpuscles.

A. Chromatin granules aggregating to form nuclei,  
n. : Nuclei. l. : Clear under lip. cv. : Contractile vacuole.

middle body width. It is obtusely rounded, and rarely I have seen it prolonged into a tail-like appendage. The median region of the body is thicker than the anterior and posterior, so that the dorsal outline is convex (Fig. 19).

The ventral surface is generally flat, but the margins of the body can be contracted inwards, so that there is a ventral hollow. The dorsal surface is studded with very fine short cilia, placed a considerable distance apart. There is no sign of striation.

The colour is dusky yellow, and during 1925 I have not observed much variation in it. Sometimes dark-brown pigment masses lie near the base of the cirri, comparable to the red pigment in *Holosticha rubra*, but this is not usual. In the ectoplasm a number of very small spherules of equal size lie in direct contact with one another. These do not stain *intra vitam*, and require high magnification to make out.

There are four rows of ventral cirri. The two central rows start from

the anterior end, and run the whole length of the body to the posterior end. The left (ventral) row begins at the point where the anterior row of cilia commences, and extends to the posterior end. The right (ventral) row, from about the middle of the peristomial right (ventral) margin to the posterior end. These cirri are fine, and all of the same size. There is a solitary cirrus, which lies on the left margin of the peristomial area.

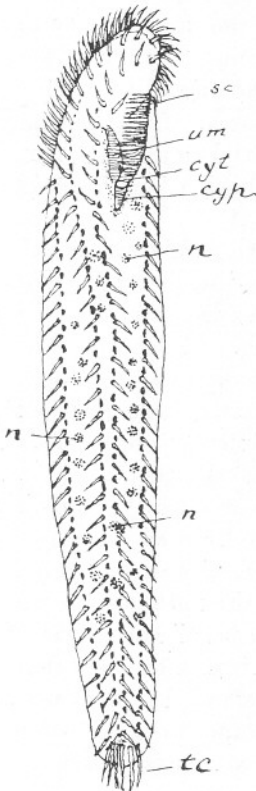


FIG. 19. *Holosticha rubra* var. *flava*, ventral view. cyt.: Cytostome. cyp.: Cytopharynx. um.: Undulating membrane. n.: Nuclei. tc.: Terminal cirri. sc.: Solitary cirrus.

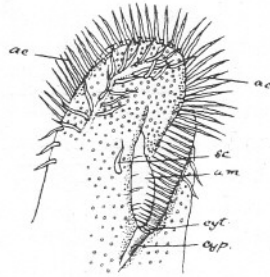


FIG. 20. Peristomial area of *Holosticha rubra* var. *flava* enlarged. ac.: Anterior stout cilia. sc.: Solitary cirrus. um.: Undulating membrane. cyt.: Cytostome. cyp.: Cytopharynx.

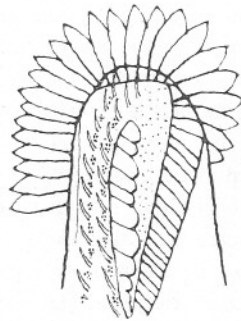


FIG. 21. Maupas' drawing of peristomial area of *Uroleptus Roscovianus*.

The cilia of the anterior crown start from a point within the anterior one-fifth of the body, on the left, and run round the anterior end following the groove between the dorsal and ventral lips, and terminate with the dorsal lobe.

There are six to eight cirri at the posterior end, which project about half their length beyond the extremity (Fig. 19).

The peristomial area (Fig. 20) occupies nearly the whole of the right (ventral) half of the anterior one-fifth of the body. It forms approximately an isosceles triangle with the base at the anterior end. At the posterior end is the cytostome, which is continued into a short cytopharynx, the walls of which are ciliated. The membrane covering the cytopharynx is very transparent, and its course very distinct.

A row of stout cilia or cirri run along the right (ventral) margin of the peristomial area. They are continuous with the cilia of the cytopharynx, and extend along the right margin until they meet the cilia of the anterior crown. It should be noted that viewing the animal ventrally they are based on the right margin of the peristomial area. The figures of Maupas, Entz, and Gourret and Roeser leave it doubtful from which margin they arise, but Wallengren's (32) admirable drawings of *Holosticha rubra* leave no doubt on this point.

There is a small vibratile membrane which readily breaks up into fine cilia, lying along the left peristomial margin just above the cytostome.

*Holosticha flava* affords a good example of the structure of cirri and membranes usually described as undulating. Under the coverslip the cirri and membranes may often be seen breaking down into their component cilia. It is, therefore, possible that the same species of ciliate may display cirri or membranes under different conditions. I have frequently observed cilia interposed among the peristomial cirri, and the undulating membrane in *Holosticha* is frequently very difficult to detect on account of its having broken down into exceedingly fine cilia.

Maupas, in his drawing of *Uroleptus Roscovianus*, probably identical with *Holosticha rubra* (Fig. 21), represents the anterior and peristomial margins as surrounded with large membranellæ. I have never seen such an extreme case in *Holosticha*, but, of course, it might occur if the synthesis of the cilia were extended. It seems, therefore, that the foundation of species on the possession of cirri or membranes in particular positions, should be adopted with caution, and only after examination of a very large number of specimens from different localities.

It may be mentioned here that immersion of the animal in 1% solution of Eurythane in sea-water much facilitates observation. The effect of the anæsthetic is almost immediate, and the animal is not damaged. I have used solution of cherry tree gum with good results. But the structure of the peristome is best observed when the animal is in sea-water under the coverslip, taking advantage of the comparatively short time between the retardation of the animal under the slip and its disintegration. The contractile vacuole generally appears about the middle of the body towards one side near the dorsal surface. In *Uroleptus Roscovianus* Maupas (18) describes two canals. I have observed neither these nor the cytopye.

*Nucleus.* Staining *intra vitam* with congo-red or methyl-green, the nuclei appear as small spherical masses, distributed irregularly through the endoplasm. Fixed with sublimate or Bouin Duboscq's solution and stained with any of the ordinary stains, these masses are seen to be aggregates of small, deeply staining granules. These granules are scattered

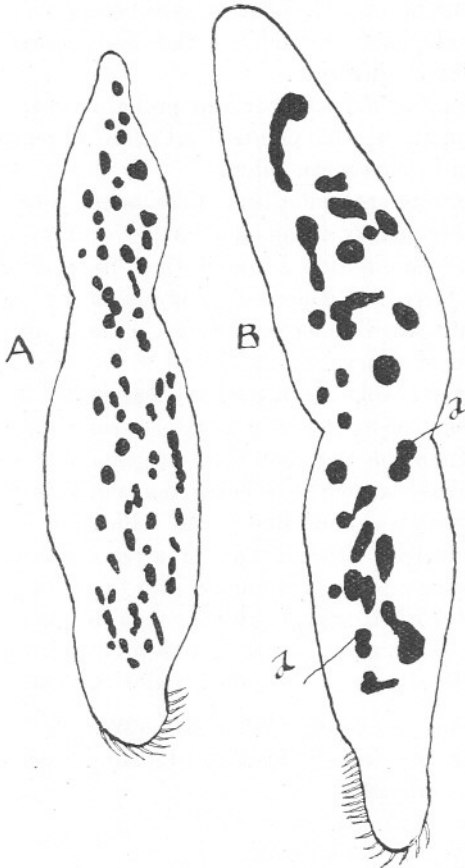


FIG. 22. Two views of *Holosticha rubra* var. *flava* in process of division.

- A. Showing the numerous small nuclear aggregates.  
 B. Larger aggregates and smaller number. d.: Dumb-bell shaped masses formed by aggregation of two spheres.

throughout the endoplasm, and collect to form masses, according to Maupas  $\cdot 003$  to  $\cdot 004$  mm. diameter. Maupas (18) thinks that there is a homogeneous central substance round which the granules collect.

The existence of a micronucleus is doubtful. Gourret and Roeser (12) observe that there are two ovoid nuclei lying near together in the posterior

part of the body ; but that they are difficult to see, even after fixation by osmic acid and staining with aniline stains.

Entz (8) describes two well-developed nuclei and micronuclei—one lying at the posterior end of the peristome between the adoral band and the left body margin, and the other near the left margin of the body above the middle.

Gruber (13) maintained that the nucleus consists of granules scattered through the endoplasm, resembling the well-known disintegration of the nucleus after conjugation.

Entz (8) suggested that Gruber had probably only examined animals just after conjugation, and pointed out that Ehrenberg had observed two large nuclei in *Holosticha rubra*.

In 1911 there were great numbers of *Holosticha rubra* in Drake's Island Tank, and I subsequently obtained a further supply from dredgings, etc. On microscopic examination I found that in every case the nuclear matter was scattered or collected in granular masses of varying size, exactly as occurs with *Holosticha flava*. I have also examined many cases of division of which Fig. 22, A and B, are typical examples.

In each case the granular spheres have aggregated into larger masses—the dumb-bell-shaped figures in B evidently resulting from the union of two spheres. In B the aggregates are larger and fewer than in A, but in each case the nuclear matter is being distributed to the future products as separate aggregates, and there is no indication of the formation of a single large nucleus either before or after division. Probably after division the aggregates break up again into their component granules.

*Holosticha rubra* Ehrb. may, I think, be regarded as the type species and *Holosticha flava* as a variety, differing only in colour and possibly in size.

*Holosticha rubra* has been described under the following names :—

*Holosticha rubra* Kent (16), Wallengren (32).

*Oxytricha rubra* Ehrenberg (6), Dujardin (5), Fresenius (9A), Cohn (4), Quennerstedt (24).

*Oxytricha flava* Cohn (4).

*Oxytricha flava* var. *carnea* Cohn (4).

*Holosticha flava* Rees (25), Gruber (14), Kent (16), Fabre-Domergue (9), Smith (30).

*Holosticha flavorubra* Entz (8), Gourret and Roeser (12).

*Uroleptus Roscovianus* Maupas (18).

The only point in which these varieties differ is the colour, which is very variable. Maupas describes *Uroleptus Roscovianus* as rose-red ; the specimens in Drake's Island Tank were more the colour of Paracarmine, and the scale runs through brick-red, reddish yellow, down to the ochreish yellow of the individuals which are now most abundant in the Tank.

## HOLOSTICHA MULTINUCLEATA Maupas.

A hypotrichous ciliate found throughout the year in Drake's Island Tank, and abundant in the summer months (Fig. 23). It is described by Maupas (18), but his figures are not good representations of the Plymouth animal, because the anterior and peristomial cirri are aggregated into membranellæ, as is also the case with *Holosticha rubra* var. *flava*.

Wallengren (32) describes as *Holosticha multinucleata* var. *decolor* a variety which except in one or two minor points is identical with the Plymouth variety. His paper is in Swedish, but the figures are excellent.

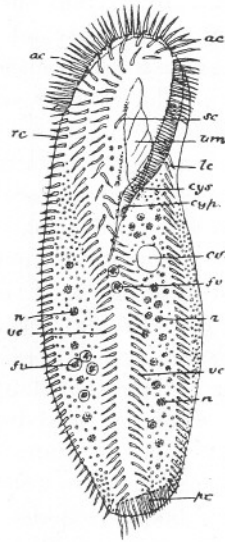


FIG. 23. *Holosticha multinucleata*, ventral view.

ac. : Anterior cirri. rc. : Right cirri. lc. : Left cirri. sc. : Solitary cirrus.  
 ve. : Ventral cirri. pc. : Posterior cirri. cys. : Cytostome. cyp. : Cytopharynx.  
 um. : Undulating membrane. fv. : Food vacuoles. vc. : Contractile vacuole.  
 n. : Masses of aggregated nuclear material. The areas of closely packed yellow corpuscles are not shown.

His views are summarised in *Nord. Plankton*, XIII, 88, as follows: "Apart from certain variations in the arrangement of the rows of cirri, differs chiefly from the type form in the absence of pigment."

*Holosticha multinucleata* resembles *Holosticha flava* in many respects, differing principally in its general shape and proportions; and is very easy to identify (Fig. 23).

It varies in length from .120 mm. to .270 mm., and occasionally reaches .3 mm. The length is generally about three times, but occasionally only twice the breadth. Maupas states that the ratio is less in the larger,

than in the smaller individuals, but my observations show that large and small vary indifferently. The body is not very contractile longitudinally, but is very elastic. The anterior extremity is boldly curved, and viewed dorsally appears as a lobe, turned towards the left. The posterior end is variable, sometimes forming a regular curve slightly less than the anterior, sometimes truncated, but never forming a tail. Occasionally it is wider than the anterior extremity. The right border of the body generally forms a long, fairly regular curve, while the left is more convex, especially in the middle region. These curves are, however, often broken, giving a more or less undulating outline. The ventral surface is flat; the dorsal arched, its highest point being about the middle of the body, and gradually flattens out towards each end. The ventral surface projects very slightly beyond the dorsal, and between them runs a groove which extends along either side, and along which runs the row of anterior cirri. The lower or ventral lip is, however, not transparent as in *Holosticha flava*. Maupas does not describe or figure this groove. It is shown in Wallengren's drawing.

The peristomial area resembles a large isosceles triangle with the base anterior, and occupies about one-third of the length of the body, and one-half of the width. I have frequently seen cases in which it occupied one-half the length. The left-hand border of the peristome carries a row of cirri, and the right a large, well-developed undulating membrane. Cross-striation is faintly visible, and it does not break up easily into its component cilia, although by constant flapping, its margin becomes frayed. It is easily removed entire by microdissection.

The cytostome is at the apex of the triangle forming the peristomial area, and is continued into a long narrow cytopharynx, which is ciliated.

In colour and structure the body resembles the Plymouth *Holosticha flava*, the former being greyish yellow, and the latter full of small spherical corpuscles of equal size, equally distributed through the body, but more closely packed in two areas equidistant from each other and from the right and left body margins. These areas are often nearly pure yellow in colour.

Maupas describes large irregular pigment granules, and other very small ones of brick-red colour. These very small granules he has seen arranged in five longitudinal rows on the dorsal surface.

The ventral cirri run in two rows from the anterior to the posterior end. Below the level of the mouth they curve slightly towards the left. They are all of the same dimensions, but Maupas states that in some of his specimens those of the left row just at the point where it commences to curve were longer than the others.

Posteriorly there is a row of transverse cirri directed obliquely from left to right. There are twelve or thirteen of them, and the longest project

beyond the margin of the body. Maupas says that their ends are curved towards the right. This I have not seen.

The left-hand row of marginal cirri commences considerably above the cytostome, and lies well within the left body margin. The right commences at, or slightly above the point where the anterior vibratile cirri arise and runs to the posterior end, gradually approaching the body margin, so that the ends of many of the cirri are visible when the animal is viewed dorsally.

There is a solitary cirrus to the right of the right peristomial border. On the dorsal surface are fine short cilia as in *Holosticha flava*.

The contractile vacuole is situated slightly behind the cytostome, and

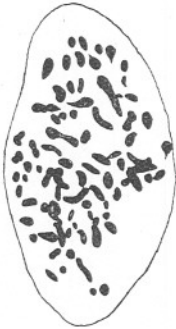


FIG. 24A.

Fixed and stained preparations of *Holosticha multinucleata*,  $\times 240$ , showing aggregates of nuclear matter. Compare Figs. 22A and 22B.

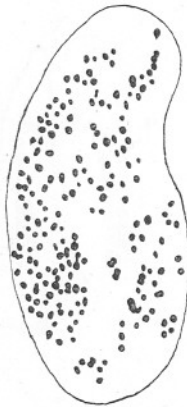


FIG. 24B.

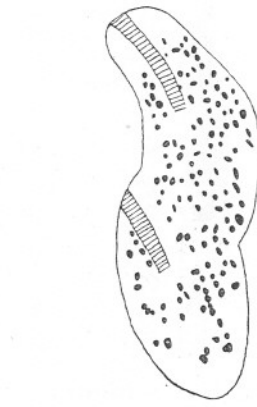


FIG. 25.

*Holosticha multinucleata* dividing from fixed and stained specimen  $\times 240$ , showing irregular distribution of aggregates of nuclear matter to division products.

towards the left border. Maupas thinks that it lies in the dorsal wall, as in other Oxytrichids.

As regards the nucleus *H. multinucleata* resembles *H. flava*. The nuclear matter is distributed throughout the endoplasm in the form of small irregular spherical masses consisting of aggregated granules (Figs. 24A, 24B). They stain readily after fixation with Iron Hæmatoxylin, Hæmalum, Paracarmine, and Delafield's Hæmatoxylin. The figures show their similarity to those of *Holosticha rubra* var. *flava*.

Fig. 25 shows *H. multinucleata* dividing. The nuclear masses are distributed irregularly, as in *H. flava*.

I have not seen a micronucleus, nor any account of one by other observers. Its existence must be regarded as uncertain.

*H. multinucleata* is a restless ciliate, always creeping along the bottom



and twisting among algæ, debris, etc. Occasionally it takes short flights, revolving on its longitudinal axis. It is very easy to examine in a 1% solution of Eurythane.

*LEMBUS ELONGATUS* (Clap. and Lachmann).

A very small holotrichous ciliate, abundant in putrifying cultures in company with other species of *Lembus*, *Uronema*, *Chaenea*, etc.

The body (Fig. 26) somewhat resembles an elongated flask, which tapers from a little above the middle to form a narrow anterior portion, which sometimes inclines very slightly backward. Both anterior and posterior ends are rounded off.

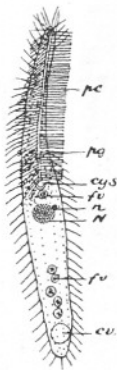


FIG. 26. *Lembus elongatus*.  
pc.: Cilia along one margin  
of peristomial groove erected  
pg.: Peristomial groove.  
cys.: Cytostome. N.: Macro-  
nucleus. n.: micronucleus.  
fv.: Food vacuole. cv.:  
Contractile vacuole.

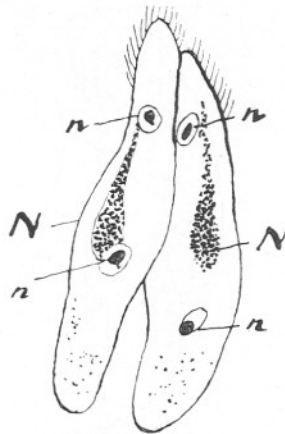


FIG. 27. *Lembus elongatus*. Con-  
jugation from fixed and stained  
specimen  $\times 630$ . N.: Macro-  
nucleus degenerating. n.: Miconuclei.



FIG. 28. *Lembus elongatus*. Stained  
*intra vitam* with  
orange-red.

It varies in length from about  $\cdot 03$  to  $\cdot 13$  mm., and in breadth at the widest part from  $\cdot 01$  to  $\cdot 017$  mm.

It is very elastic and flexible, but not markedly contractile. It hardly changes under fixation.

The endoplasm is exceedingly clear, and contains only a few refringent granules, principally confined to the anterior portion, and food vacuoles.

The body is clothed with about ten rows of fine flexible cilia, based on small papillæ, and thus appearing as faint lines of striation. There is no cross striation.

At the posterior end there is a fine bristle-like cilium, about twice as long as the body cilia.

The cytostome lies about the middle of the body, forming a shallow depression, communicating directly with the endoplasm. It is semi-

circular in shape, and its margins appear to be slightly thickened. I cannot make out the cytopharynx. Fabre-Domergue (9) states that there is a short tubular one, leading directly into the endoplasm. Gourret and Roeser (11), however, deny its presence.

From the cytostome a very narrow channel runs slightly obliquely to the anterior end. Both margins carry a row of exceedingly fine, closely set cilia rather longer than those of the body. These cilia can be erected so as to stand out rigidly, on either side of the channel or simultaneously. Under low magnification they appear like membranes, and have been described as such. Under an immersion objective they are resolved into the component cilia; the distal ends of the cilia appearing as a line of dots, owing to their vibration.

The views of observers on the cuticular striation and the structure of the peristome vary.

Cohn (4) states that the body surface is marked by clear, parallel, horizontal furrows.

Quennerstedt (24) believed that longitudinal striation existed, but that it was feeble, widely separated, and difficult to see. He was unable to detect any cross-striation, but pointed out that the appearance of the body outline, particularly at the posterior end, suggested it.

Fabre-Domergue (9) writes: "The tegument carries a system of longitudinal striation, and a system of transverse striation, which cross one another at right angles, and make the surface appear as if it were divided into small squares."

Similarly Gourret and Roeser (11) describe the striation.

Wallengren (33) made out only longitudinal striations, very faint, and widely separated. He considered that there is no transverse striation, but that under a low power an impression was conveyed that they did exist.

As regards the peristome, Cohn (4) writes that a mouth cleft extends from the anterior end to the second third of the body, and that from this a sail-like membrane can be more or less extended.

Kent and Rees (16 and 25) agree that the membrane consists of cilia, and Rees states that there are two such pseudomembranes, one along the left and the other along the right margin of the peristomial channel.

Quennerstedt (24) says that there is no real peristome; at the most a small narrow cleft is present; that Cohn's "mouthsail" is a finely striated undulating membrane stretching along one side over the oval mouth-opening. Later he adds that he observed another membrane, within Cohn's "mouthsail."

Fabre-Domergue (9) describes a finely striated undulating membrane. Gourret and Roeser (11) describe such a membrane attached to the

left margin of the peristome, and within this adoral membrane a row of finer cilia on the peristomial groove.

Wallengren (33) describes a well-developed undulating membrane running along the right margin of the peristome; this membrane is distinctly cross-striated. This membrane Wallengren believed to be a true membrane, and not a row of free aggregated cilia, since he never saw it resolved into its component cilia. Wallengren, however, noticed that when the membrane was erected, its free margin appeared as a line of dots. He thinks that the impression that there are two membranes, is due to a wrong interpretation of what is seen when the row of peristomial cilia is not erect. In this case the striated basal portion of the membrane would appear along one margin, and the gently undulating distal margin would appear to run along the left margin of the peristomial channel. When the membrane was erected, the illusion of there being two membranes would disappear. Of course, Wallengren's interpretation fails because he had never seen the membrane resolved into separate cilia, and reaggregated. Wallengren, however, admits that there is a slightly narrower undulating membrane along the right peristomial border, within the larger membrane, and that when the latter is extended, the inner membrane may be seen gently undulating. Probably what Wallengren saw was the lips of the cilia along the left margin moving gently. Had he waited he might have seen them erected so as to form the second membrane.

The contractile vacuole is at the posterior end of the body.

The macronucleus is situated about the middle of the body, spherical or ovoid in shape and of finely granular structure. It is accompanied by a small spherical micronucleus, also of granular structure. When the animal is about to divide, the micronucleus elongates and becomes constricted, and divides into two spherical portions which move apart to opposite poles of the macronucleus, meanwhile the macronucleus becomes constricted and divides, followed by the cytoplasm of the body. I am unable to decide whether the micronucleus divides mitotically or not. Some of my preparations suggest that it does so.

I have several times observed conjugation, in every case the process was in the same stage. The micronucleus had divided into two, and the macronucleus was breaking down. Probably conjugation follows the course observed in *Paramœcium*, where the micronucleus divides twice, giving four micronuclei in each conjugant. Of these three disappear, and the persisting one divides, forming two pronuclei. From the condition of the macronucleus (Fig. 27), which appears to be breaking down, the first division of the micronuclei is suggested.

*Lembus elongatus* can swim pretty swiftly, with an oscillating motion, describing a wide spiral round the direction of motion. It remains

quiescent for long periods, erecting the cilia along the margins of the peristomial groove sometimes together, sometimes alternately, at the same time slowly revolving on its longitudinal axis.

Staining *intra vitam* with neutral red has a singular result. The whole body of the animal becomes covered with fairly regular figures arranged in longitudinal rows, giving the animal a resemblance to a painted vase (Fig. 28). The surface of the figures is raised like a blister above the surface of the body. Similar patterns arise when *Lembus sarcophagus* and *Lembus pusillus* are stained *intra vitam* with neutral red. Whatever be the nature of the substance that takes the stain it is destroyed by fixation—I have never observed a similar phenomenon, in any case of fixation and staining by usual reagents.

This ciliate has been described as *Lembus elongatus* by Kent (16) and Wallengen (33); as *Cyclidium elongatum* by Claparède and Lachmann (3) and Rees (25); as *Lembus retifer* by Cohn (4), Quennerstedt (24), Kent (16), Maupas (18), Entz (8), Gruber (14), Gourret and Rœser (11); as *Lembus striatus* by Fabre-Domergue (9); as *Lembus intermedius* by Gourret and Rœser (11); as *Lembus infusionum* by Calkins (2); and as *Proboscella vermina* by Kent (16).

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## The Nitrite Content of Sea-Water.

By

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With 1 Figure in the Text.

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THE estimation of chemically bound nitrogen compounds in sea-water has, in the past, been a matter of considerable difficulty because of the small quantities of these substances involved. They are present in the form of free and saline ammonia, nitrites, nitrates and organically bound nitrogen. The ammonia has usually been estimated by distilling it off in alkaline solution and determining colorimetrically in the slightly acid distillate by means of Nessler's reagent. The nitrites and nitrates are first of all reduced to ammonia, which is then distilled off in alkaline solution and estimated as before. The organic nitrogen compounds are first converted to ammonia by the Kjeldahl method or a modification thereof which is estimated as before.

Even when comparatively large quantities of sea-water are used, the error of these methods is considerable, as is admitted by the investigators themselves. In making a series of analyses of the nitrogen compounds in sea-water by these methods I found the chief difficulty to be in the use of the Nessler reagent. In such dilute solutions of ammonia the addition of even a slight excess of Nessler reagent produced a greenish tint which interfered with the matching of the colours. In addition the process is long and requires considerable quantities of sea-water.

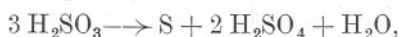
Recently Gad-Andresen (5) has described a method for the estimation of nitrogen compounds in sea-water which, as it is volumetric, is a great advance on previous methods. The process consists of a preliminary conversion of nitrites, nitrates, and organic nitrogen to ammonia and subsequent decomposition of this with alkaline hypobromite in Barcroft's differential manometer. The nitrogen gas liberated is measured by the difference of pressure, and, the constants of the apparatus being known, the ammonia, and thus the other compounds, can be estimated. The free and saline ammonia are estimated by distilling off in alkaline solution after concentration of the sample, and measuring the liberated nitrogen as before.

A series of test analyses were made, using this method, and it was



found that with solutions of artificial sea-water containing known amounts of nitrates and ammonia, the agreement between theoretical and calculated results was good, the error being about  $\pm 5$  per cent, which is the accuracy claimed by Gad-Andresen. The only disadvantage of the method for these compounds seems to be the length of time required to complete a series of analyses. Its advantages lie in its accuracy and the comparatively small quantities of sea-water required.

With regard to nitrites it was found that the method was unsuitable. The samples are preserved by adding 1 c.c. per litre of a saturated solution of sulphur dioxide or concentrated sulphuric acid. Solutions of sulphur dioxide, *i.e.* sulphurous acid, are unstable and decompose on standing to give sulphur and sulphuric acid,



and sulphuric acid even in the cold in dilute solutions, decomposes nitrites to give nitric acid and nitric oxide.



To find whether this would take place in sea-water in the great dilution in which nitrite is known to be present, 500 c.c. sea-water were treated with 0.5 c.c. sulphuric acid as described and distilled. A sample of the original sea-water tested with Ilosvay's modification of Griess' reagent gave in thirty minutes a faint pink coloration indicating the presence of a small quantity of nitrite. The first 100 c.c. of the distillate gave a slightly stronger reaction than the original sea-water, showing that all the nitrite had not been decomposed by the sulphuric acid. As distillation was started a few minutes after adding the sulphuric acid, and other samples which had been preserved with sulphuric acid gave negative results, it must be concluded that it is unsafe to use sulphuric acid for the preservation of nitrites in sea-water. No reaction was obtained with subsequent portions of the distillate, nor did the residue in the flask give a positive result as would be necessary for estimation by Gad-Andresen's method. Unfortunately also, the nitrite on decomposing gives rise to nitrates which will then affect the nitrate estimation in the sample.

To estimate the nitrite in sea-water, it seemed worth attempting to use a colorimetric method as there are several of great delicacy. Eventually the Griess method as modified by Ilosvay (6) and applied to sea-water by Buch (3) was adopted. It has the advantage over other methods in that it is sufficiently sensitive to enable the nitrite in sea-water to be estimated directly without any preliminary concentration of the nitrite as is necessary with the *m*-phenylenediamine method or the Trommsdorff method. The reaction depends on the formation of a pink azo dye by the action of the nitrite in acid solution on a mixture of *o*-naphthylamine and sulphanilic acid.

The two following solutions are required :—

*Sulphanilic acid.* One gram of sulphanilic acid is dissolved with the aid of heat in 14.7 grams of glacial acetic acid mixed with an equal bulk of water. More water is gradually added to the warmed liquid with constant stirring till 285 c.c. have been used altogether.

*$\alpha$ -Naphthylamine.* 0.2 gram of  $\alpha$ -naphthylamine is dissolved with the aid of heat in 14.7 grams of glacial acetic acid mixed with twice its bulk of water. More water is added till 325 c.c. have been used altogether.

These solutions are kept separately and mixed in equal proportions just before they are required. The solution of  $\alpha$ -naphthylamine tends to become pink on keeping owing to the development of nitrite in the solution from ammonia in the air. Should this occur a fresh solution must be prepared. These solutions are not affected by light.

The quantitative application of the method to sea-water has been described by Buch (3), who showed that the effect of varying salinity was negligible, and that the effect of varying temperature could be avoided by having standard and unknown at the same temperature during colour development. One or two modifications of his method have been adopted for ease of colour reading and for convenience at sea.

Standard solutions are prepared containing 0.01 mg. nitrite nitrogen per litre and 0.005 mg. nitrite nitrogen per litre and 100 c.c. of each placed in separate beakers. 100 c.c. of the sea-water sample to be examined are placed in another beaker and 4 c.c. of the mixed Griess-Ilosvay reagent added to each. After standing for a length of time corresponding to the amount of nitrite present the colours are compared in Hehner tubes in an apparatus such as is described by Atkins (2) for the colorimetric estimation of phosphates in sea-water. The tubes are rested on a thin glass plate, through which light is reflected by an opal glass plate, the light being cut off from the remainder of the cylinders by a black case. The height of the liquid in the stronger solution is adjusted till the colours are of equal intensity. From the relative heights the amount of nitrite in the sea-water sample can be estimated. For 0.01 mg. nitrite N. per litre, fifteen minutes at room temperature gives a readable colour. If the sample is more dilute the time should be increased to half an hour or one hour. As the colour development goes on for at least two hours comparisons must only be made on samples to which the reagent has been added simultaneously.

The dilute standard solutions change their nitrite content readily, and, to ensure accuracy, dilution from a strong solution of nitrite must be made; this strong solution must be replaced frequently. A suitable standard for dilution may be prepared by dissolving 0.6075 gram pure crystalline potassium nitrite in a litre of distilled water free from nitrite.

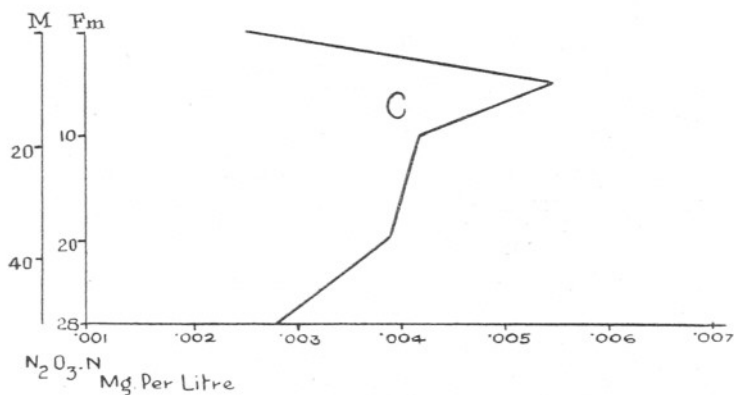
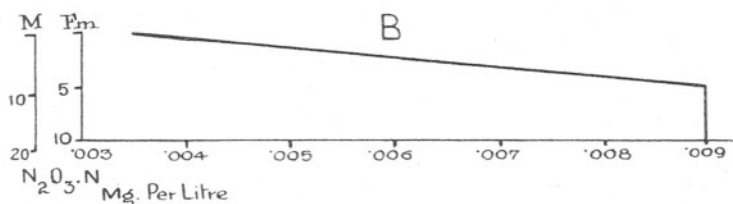
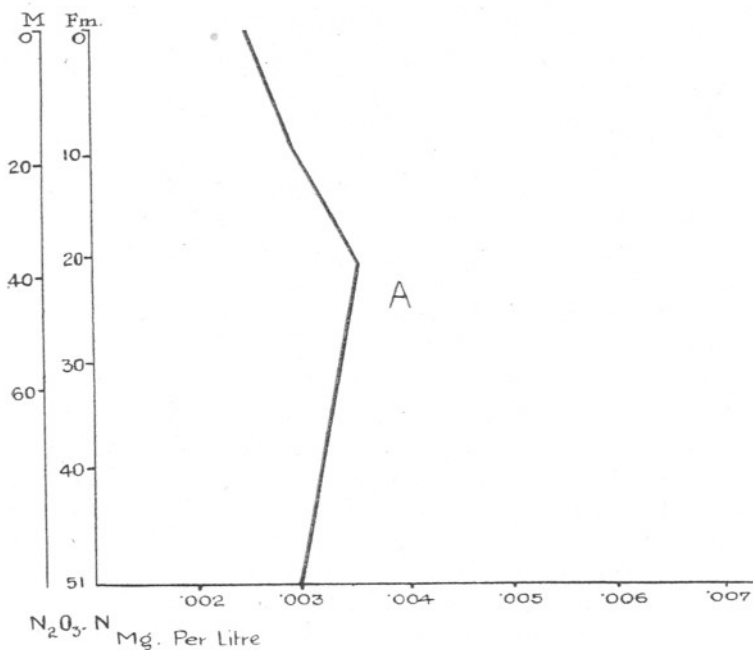
This solution contains 100 mg. nitrite N. per litre. All dilutions must be made with nitrite free distilled water.

A series of samples containing quantities of nitrite nitrogen, varying from 0.01 mg. to 0.002 mg. per litre treated as above, could be easily distinguished, and a closer approximation to their real value obtained by comparing in *Hehner* tubes. For example, a sample containing 0.01 mg. per litre compared with a sample containing 0.005 mg. per litre gave a reading of 96 against 42, *i.e.* 0.0046 mg. per litre; a sample containing 0.002 mg. per litre compared with the sample containing 0.005 mg. per litre gave a reading of 95 against 35, *i.e.* 0.0018 mg. per litre.

An examination of the nitrite content of sea-water at different places and at different depths in the Clyde Sea Area was made. The samples were collected in Winchester or half Winchester quart bottles, and the analysis of the samples carried out within a few hours of their collection and generally at sea. The reason for this is that the nitrite values change readily on keeping, as will be shown later. A few of the results are shown in text Fig. 1: (*a*) is a station in the estuary, (*b*) is a station at the head of Loch Long, and (*c*) is a station half-way down the same loch. The figures for temperature, salinity, and nitrite content are shown below.

	Depth in fm.	Temp. °C.	Salinity.	Nitrite N. mg. per litre.
<i>(a)</i> Gantock Station. 23.6.25.	0	13.73	29.86	0.0025
	5	8.56	31.78	0.0027
	10	8.25	32.01	0.0029
	20	8.29	32.18	0.0035
	35	8.36	32.37	0.0033
	51	8.37	32.26	0.0030
<i>(b)</i> Arrochar Station. 17.6.25.	0	14.43	26.31	0.0035
	5	9.41	32.26	0.0090
	10	7.53	33.54	0.0090
<i>(c)</i> Thornbank Station. 26.6.25.	0	11.29	31.14	0.0025
	5	7.73	31.91	0.0056
	10	7.98	32.04	0.0042
	20	8.07	32.18	0.0039
	28	8.10	33.52	0.0028

Over practically the whole of the Clyde Sea Area during June and August the nitrite decreased from bottom to top, the values obtained during that time rarely exceeding 0.01 mg. per litre. Occasionally values were lower than 0.001 mg. per litre.



TEXT FIG. 1. Graphs showing the nitrite content of sea-water at various depths, at A. Gantock Station. B. Arrochar Station. C. Thornbank Station. The ordinates are depths in fathoms and metres, the abscissæ denote milligrams of nitrite nitrogen per litre.

Recently Domogalla, Juday and Peterson (4) have made a study of the different forms of nitrogen in Lake Mendota, a fresh-water lake. The nitrite nitrogen, which approaches its minimum in June, is of the same order of size as the amounts found in the sea. Their results show in general during the summer, a greater percentage of nitrite in the lower layers than in the surface layers in agreement with the results found so far in the sea.

To find the effect of algal plankton on the nitrite content, diatom cultures, a series which Miss Marshall kindly supplied, prepared as described by Allen and Nelson (1), were tested for nitrite. The original enriched sea-water contained from 0.001 mg. to 0.003 mg. per litre, and as the cultures developed the nitrite content increased rapidly. The nitrite content continued to increase long after the diatoms had ceased increasing. The relation of the nitrite increase to the diatom growth is complicated by many factors, notably the strength of the light, the quantity of nitrate present, and the nature of the flask. It is proposed to investigate this further.

The cause of the change of nitrite in the sea is probably complex. According to Buch samples kept in the dark may increase their nitrite content rapidly, *e.g.* from 0.004 mg. to 0.028 mg. per litre in two days. Kept in a clear glass bottle the nitrite content did not change. There seem to be at least five different ways in which the nitrite content of the sea may be changed.

1. By bacterial action.

This has been a much disputed source. The presence of the necessary bacteria has been demonstrated, but there is still doubt as regards their place in the nitrogen metabolism of the sea.

2. By ultra-violet light.

It was first observed by Thiele (8) that solutions of nitrates on exposure to ultra-violet light give an increasingly strong reaction for nitrites. Moore and Webster (7) later showed that the same happened in sunlight, and that more effect was produced in solutions in quartz vessels than in solutions in glass vessels, thus demonstrating that the shorter wavelength rays were responsible.

3. By the algal plankton.

Moore and Webster showed that plants absorb the nitrite produced by the action of the ultra-violet light acting on the nitrate.

4. By influx from rivers and from the atmosphere.

Moore and Webster showed that night air contains less nitrite than day air, and that this is precipitated from the atmosphere. Uncontaminated rivers have only a small percentage of nitrite.

5. Finally the nitrite may be decreased by oxidation to nitrate.

There is no increase of nitrite directly due to animal life as it is not a normal product of animal metabolism. Both nitrates and ammonia are produced which may indirectly give rise to nitrites.

#### SUMMARY.

1. The method of water sample preservation used by Gad-Andresen is not suitable for nitrite or nitrate estimation.

2. Using Buch's method it has been shown that the variation in nitrite during the summer is from less than 0.001 mg. to about 0.01 mg. per litre and that the deeper water layers have more than the surface layers.

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## Notes on the Preservation of Fishing Nets by means of Copper Soaps.

By

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With 1 Figure in the Text.

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PROCEEDING on the hypothesis that the deterioration of nets is due mainly to bacterial action and the action of sunlight, some attempts were made to prolong the serviceable life of silk plankton tow-nets and hemp "stramin" young fish trawl-nets by periodical treatment with formalin, which had been neutralised with borax to avoid the injurious action of the acid always present in the commercial product. It was, however, found (1923) that formalin treatment was positively harmful, as was also rinsing out the silk nets with fresh water. It was further shown that sunlight is extremely destructive to silk nets. These should therefore be dried after use and stored in the shade, or given the minimum exposure to sunlight during drying. Sunlight is in fact harmful to all fabrics, and the thinner and more transparent the fabric the greater is the resulting damage.

Valuable results were obtained by Taylor and Wells (1923) using copper oleate dissolved in petrol or benzol as a preservative for nets immersed in salt water. To avoid the creeping out of the soap to the surface on drying, the 10 per cent oleate solution receives 1 per cent of mineral oil or of creosote. In fresh water less satisfactory results were obtained unless a considerable amount of tar was added as a binder.

Since silk tow-nets are costly, about £11 for a set of four, and become considerably weakened in about three months, varying according to the amount of wear, trials were made first on fine and coarse tow-net silk. Silk netting treated with 10 per cent copper oleate was kept in sea-water for five months, the water being changed every other day, and though in two or three months all noticeable signs of the soap had vanished the netting remained sound. In about seven months the fine mesh (100 to the inch) netting had become much weakened, and the coarse mesh (26 to the inch) had also deteriorated, though still good enough to use as a net. Controls were much weakened inside five weeks and shortly after that could be torn like wet paper.



Owing to the favourable results obtained all silk nets taken into use by the Marine Biological Association or issued to other institutions have been treated with copper oleate or with a mixed copper soap specially prepared by Messrs. Lever Bros. This, being less soluble than oleate, was used in 5 per cent solution in petrol, which is, however, far from being a saturated solution in warm weather. When tried on stout stramin (hemp) netting good results were obtained, but less striking, for this material is vastly more resistant than silk. It may be added that the fine mesh silk is clogged by a film of soap after treatment, but when towed in the water this soon comes away. Particles of the green copper soap may be found in the tow-nettings for several days.

Stout stramin netting was placed in three jars, with sea-water from the aquarium tanks, which was changed three times a week and examined at intervals. They contained respectively an untreated control, a piece treated with 10 per cent oleate and one treated with 5 per cent mixed soaps.

The behaviour of the stramin and silk nets is shown in the accompanying figure. The serviceable life of the net is considered to be at an end when it is possible to tear it by hand, using considerable effort. This occurs about one month after the time when single threads can be broken by hand.

It may be pointed out that the soaps dissolve only when the nets are in water, but bacterial action goes on as long as the net is damp, so the immersion tests are in this respect unduly severe on the preservative as regards its use on seine nets, though not severe enough as regards pound nets, which are not only continuously immersed, but are also subjected to the action of currents of water.

Light linen and cotton fabrics were exposed in an horizontal position upon the flat roof of the Laboratory, being mounted on wooden frames after treatment with oleate or mixed copper soaps. After exposure for two very rainy months much of the soap on the outer sides was washed away, though after twelve months the stoutest of the cottons still retained a large amount of soap on the under surface, the mixed soap being retained considerably better than the pure oleate. This indicates that the action of rain upon nets heaped on the deck or hung up to dry may be far more rapid in removing copper soap than is that of sea-water. Cotton nets, however, retain the soap far better than stramin.

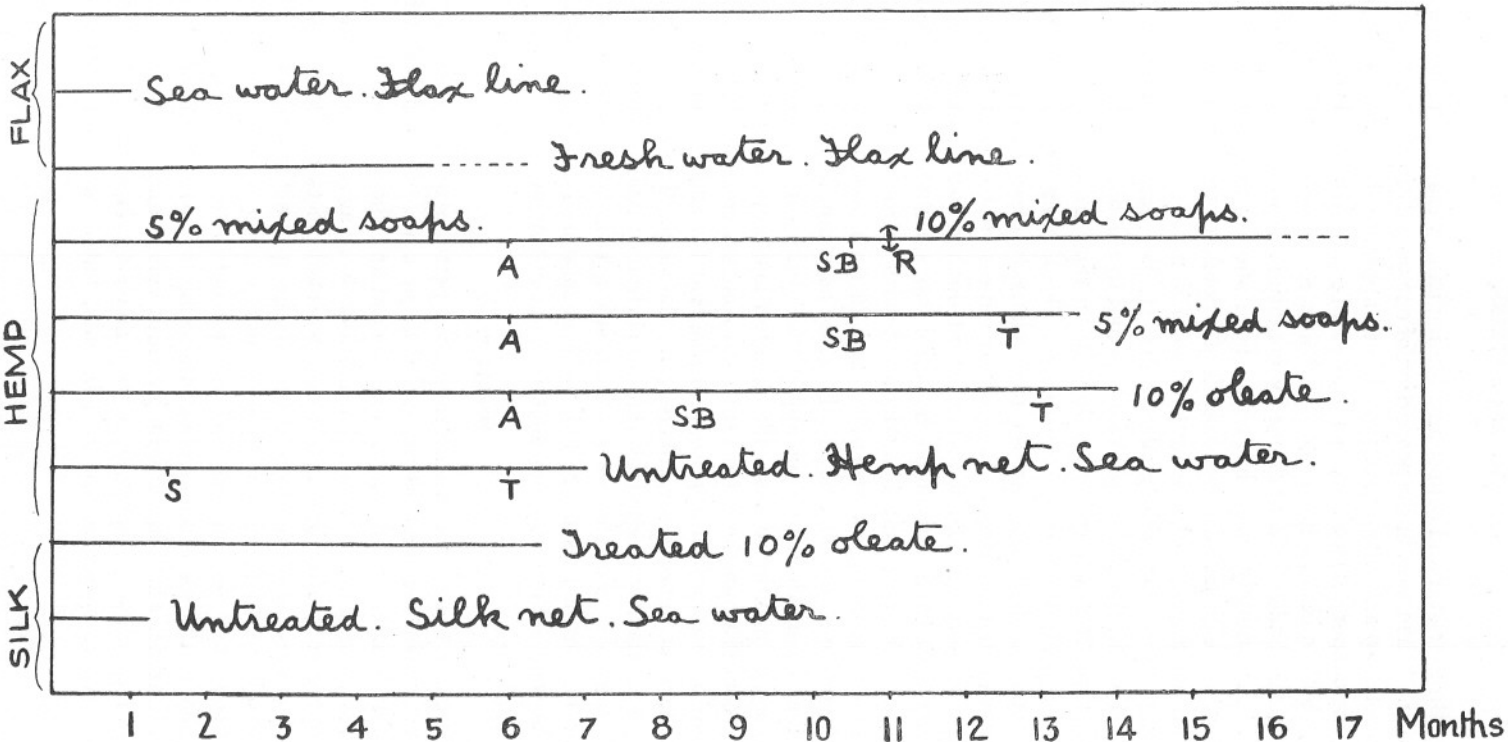
#### USE OF BINDING AGENTS WITH COPPER SOAP.

Taylor and Wells found that the addition of a certain proportion of tar was advantageous in binding the soaps more firmly, and for heavy gear such mixtures are probably very useful. Following the receipt of further information from the U.S. Dept. of Fisheries, through Messrs.

PRESERVATIVE ACTION OF COPPER SOAPS.

NEW SERIES.—VOL. XIV. NO. 1. MARCH, 1926.

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A=not now noticeably green. B=black spots began to appear. R=treated again. S=stink. T=single threads could be broken by hand. --- =still sound. The lines end when the nets or lines are judged to be unserviceable by tearing test.

Lever Brothers, tar and copper anti-fouling paint were tried as binders for the soap. When used in the proportion of one pound of paint or tar to one pound of soap and a gallon of petrol both appear to be far more durable than the copper soaps alone, as far as can be judged from three months' trial; both mixtures have the disadvantage—possibly only initial—of leaving the hands in a very messy condition, especially the one with paint. Accordingly trials have also been started using one-half, one-quarter, one-eighth and one-sixteenth of a pound of paint to one of soap; all dilutions appear to be better than soap alone.

Acting on a suggestion made by Mr. H. W. Harvey resin was also tried. Used in the proportion of one pound to one of soap, to a gallon of petrol, three months' immersion has shown that the addition of resin is a great improvement over soap alone. The netting dries readily after treatment and handling the net is a relatively clean business—a very important point for users. It is as yet impossible to say whether resin mixture is more durable than tar or anti-fouling paint mixtures. The difficulty that resin is insoluble in petrol was surmounted by melting it with the copper soap and then stirring up with petrol, when it was found to give a mixture of low viscosity which in time becomes thicker. For this the writer is indebted to his laboratory assistant, Mr. F. E. Radcliffe, as well as for much help in the application of the various preservatives.

It may be mentioned that silk plankton nets appear to be more uniformly coated when the 5 per cent soap solution contains also one-half per cent of resin, and it appears probable that the small amount of resin will somewhat improve the adherence of the soap. The finest mesh silk is not permanently clogged by this proportion of resin, though it is by larger amounts. For the coarser mesh silk nets it is permissible to use more resin, but at present the half per cent mixture has been substituted here for soap alone in the routine treatment of tow-nets.

#### SOLVENT.

As regards the solvent used, commercial petrol is quite satisfactory in summer, when the temperature is 15° C. or over. In colder weather, 10° C. or less, more difficulty is experienced and the soap solution soon becomes gelatinous. Under all conditions it is advantageous to melt the copper soap after breaking it up into small pieces by immersing the tin in hot water and then to remove it to the open air and to add a little of the solvent to it with stirring, finally pouring it into the solvent. "Water white" benzene was tried as a solvent instead of petrol, but the solubility of the soaps seems about the same in both. Commercial gas-works benzene, which has a light brownish colour and a very noticeable odour of pyridine, is, however, a very much better solvent. It is also cheaper where it can be obtained in bulk, but as it is not universally

obtainable in readily handled quantities, as is petrol, cost of carriage and of drums add considerably to the expense, so that it may become less economical than petrol. For any large scale treatment of nets it is, however, quite the best solvent. Solvent naphtha is more expensive and does not dissolve the soaps so readily.

#### TREATMENT AND ITS COST.

It may be mentioned the herring nets treated with copper soaps gave trouble when taken into use by the meshes slipping. In the usual treatment with cutch the nets shrink, so the knots tighten up, whereas in the soap treatment there is no shrinking. It is, however, customary in this district to pull new nets by hand to tighten up the knots before treating with cutch or creosote, and it seems advisable that such nets should be thus tightened up before treatment with copper soap.

As regards the cost of this treatment, for a 35-lb. herring net about seven gallons of the mixture is required, thus for :

10% benzol solution.

7 gallons benzol at 1s. 3d. per gallon .. ..	8	9
6 lbs. copper soap at, say, 9d. per lb. .. ..	4	6
	<hr/>	
	13	3
5% benzol solution, deduct 3 lbs. of soap ..	2	3
	<hr/>	
	11	0

Using kerosene (paraffin oil) at 9d. per gallon the cost would be 7s. 6d.

Where petrol has to be used the cost of solvent is greater, 1s. 6d. to 1s. 9d. per gallon. In any case the cost of the solvent is far greater than that of the soap, so that evaporation losses should be minimised. No estimate has been included for the cost of labour in handling the nets. The treatment can be carried out by anybody, and a pound of soap to a gallon of solvent is a convenient formula, which gives about a 12 per cent solution. One pound of mineral lubricating oil is added to ten of soap.

#### FISHING-LINES.

Some tests have been carried out upon lines such as used for rod fishing in fresh water mainly, but the results are being held over as nothing very definite has been obtained, owing it seems to the poor adherence of the copper soaps to their highly glossy surface. It may be mentioned, however, that a pure flax line remained sound in a soft fresh water for five months, and is still sound, whereas it became absolutely

rotten in sea-water in one month in summer and in less than two in cooler weather.

Further trials are in progress upon the effect of tar, Japan black, anti-fouling paint and resin as binders to improve the adherence of the soap to the lines and nets.

#### PREPARATION OF SOAP MIXTURE FOR ISSUE IN LIQUID FORM TO BE USED WITH PARAFFIN OIL.

There are obvious advantages to the user if the soap can be obtained in liquid form so that it does not need melting to dissolve in cold weather. Paraffin is also much less inflammable than petrol or benzol, and already has a good name among fishermen, as it is used in washing down newly built boats as a preservative for the wood. It was suggested by Mr. H. W. Harvey that an attempt should be made to produce a soap mixture which would only have to be poured into the paraffin. Among the possible liquids in which the soaps and resin might be brought into solution readily, tetrachlorethane was ruled out on account of its poisonous properties, also methylethyl ketone, butyl alcohol, and turpentine on account of their cost. Carbon tetrachloride appears to be both cheap and suitable. It has also the advantage that it is non-inflammable, being, in fact, the principal constituent of a fire extinguisher for combating oil fires. A pound of copper soap (as supplied ready mixed with one-tenth its weight of mineral oil) is melted and a pound of powdered resin is stirred in—or a pound of tar may be used instead. To the mixture a pound and a half of carbon tetrachloride is added. The result is a mobile solution which becomes thicker when cold. This can be poured into paraffin oil to give roughly a 12 per cent soap solution, using three and a half pounds of the mixture to a gallon of paraffin oil, which weighs about eight and a half pounds and is much cheaper than petrol. A very useful 5–6 per cent solution may be prepared, using half the amount of soap mixture. In the proportions mentioned a mixture allowed to stand in the open on a cold night becomes gelatinous, but in a warm room it becomes liquid again. Being non-inflammable there is no risk of fire, but it should be remembered that carbon tetrachloride is volatile and gives off a very heavy vapour similar to chloroform in its action when inhaled. Pieces of stramin thus treated have been placed in sea-water for a durability test, but as carbon tetrachloride is volatile and Taylor and Wells found paraffin satisfactory where its solvent action was sufficiently good, viz. where it was not desired to mix it with a large volume of tar, it seems that no trouble need be anticipated on this score. We find the adherence is inferior with paraffin.

## SUMMARY.

The use of a mixture of copper soap, 5 or 10 per cent, with 1 per cent mineral oil, dissolved in petrol or benzol, increases the life of silk plankton nets by about four or five hundred per cent, and roughly doubles that of a hemp net for a single treatment. The beneficial effects last far longer than does the green colour. Re-treatment at suitable intervals is recommended.

The use of 5 or 10 per cent of resin\* with an equal percentage of the soap improves its adherence to the fabric, as does also the addition of tar or anti-fouling paint. For silk nets, to avoid clogging, only one-half per cent of resin should be used with 5 per cent of soap.

A liquid soap mixture, which may be used with paraffin oil, can be obtained by adding one pound of resin to one pound of melted copper soap, and then dissolving in one and a half pounds of carbon tetrachloride. When wanted, this is used to make up a paraffin oil soap solution of the desired concentration, but adherence is less than with petrol.

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## NOTE.

When the foregoing paper was almost completed M. Fillon's valuable memoir came to hand. It contains a comparison of results obtained with copper oleate, and with various methods of tanning; it also describes the new method of treatment, with rubber latex, devised by Dr. J. Olie of Utrecht. A treatment with boiling cutch solution (from *Acacia catechu*) followed by the application of ammoniacal copper sulphate, the process being then repeated, was found to be superior to treatment with copper oleate solution in benzol mixed with an equal volume of coal-tar. A previous treatment with cutch brought the latter method nearly up to the level of the ammoniacal copper fixation, the details of which were carried out according to Dr. Olie's instructions.

\* Tensile tests on strands of stramin after four months' immersion show that resin does not improve the soap mixture, though it is retained better than the soaps alone.



## Nitrate in the Sea.

By

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With 3 Figures in the Text.

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IN view of the need of nitrates for the growth of vegetable plankton, it was desired to evolve a more or less rapid method of estimating the minute trace of nitrate which occurs in sea-water, preferably one which would have its greatest accuracy in dealing with waters almost entirely depleted of nitrate. The existing methods were lengthy and subject to a systematic error which lowered their value, if it did not render them useless, in comparing the nitrate content of such almost entirely depleted waters.

Denigès (2) found that an acid solution of strychnine reduced by warming with amalgamated zinc produced a compound which gives a bright red colour with nitrites, and that a similar colour was given with nitrates on the addition of strong sulphuric acid. Kolthoff (3) examined this reaction and found that the colour was given with chlorates, chromates and ferricyanides, as well as by nitrites, with or without strong sulphuric acid, and by ferric iron as well as by nitrates with strong sulphuric acid. He noted further that more consistent results were obtained by using amalgamated zinc, than by zinc or magnesium as had been suggested by Scales and Harrison.

The colour fades on exposure to strong light.

Preliminary experiments showed that this qualitative "test" for nitrates was the most delicate of many examined and that under particular conditions it was capable of giving quantitative results.

### NITRITES.

In a number of water samples from the English Channel, examined either on board ship or immediately after landing, no definitely detectable traces of nitrites could be found either by the Greiss-Ilosvay reagent or with the strychnine reagent without sulphuric acid, except in the case of inshore water subject to pollution. After storage an appreciable quantity of nitrite has been detected in several instances. In water from 830 metres in the Bay of Biscay, preserved with mercuric chloride when collected, and in water at various depths up to 3000 metres, similarly preserved, collected by the R.R.S. *Discovery* some 200 miles west of Portugal, no nitrite could be definitely detected.



## IRON.

Sea-water has been repeatedly found to contain iron in solution. No trace of ferric iron could be detected in a number of samples of sea-water by adding either sulphocyanide or ferrocyanide. Nor could ferric iron be detected after addition to unfiltered sea-water of iron free hydrogen peroxide and acid, by which treatment ferrous iron is converted into ferric. It is only after the water, whether unfiltered or filtered, has been subjected to strong oxidation, such as by boiling with acid bromine water (4) or nitric acid (5) that a reaction for ferric iron is given. There is evidence that the iron in sea-water is present in organic compounds (5).

## THE REAGENT.

When a solution of about 0.5 gram of strychnine sulphate in 25 c.c. of water is warmed with 2 c.c. of hydrochloric acid and 4 square inches of zinc foil, previously wetted with acid mercuric chloride solution to form amalgam on the surface, the less soluble "reduced strychnine" separates out. On continued heating for two or three hours on a water-bath, with the addition of more water from time to time to keep the volume between 10 and 25 c.c. and the addition of a few drops of sulphuric acid towards the end, an active compound is formed. The operation should be carried out away from the gases given off by a naked flame. The yield and time taken is somewhat capricious. By adding a drop of the liquid to a very dilute solution of nitrite, the reaction may be stopped when a satisfactory yield of the active compound has been obtained. After removing the zinc, about 300 c.c. of strong sulphuric acid are added. The reagent so prepared gives a red colour on addition to an equal volume of very dilute nitrate solution; the colour develops more rapidly after the reagent has been stored for several days.

It is essential that pure chemicals, free from nitrate and iron be used, otherwise the reagent gives a pink colour on addition to an equal volume of distilled water, due to the contained impurities. The "pure" zinc foil and "nitrogen free" sulphuric acid supplied by Messrs. British Drug Houses proved satisfactory.

## THE ESTIMATION.

The depth of colour produced, that is, the amount of red substance, is dependent upon (a) the amount of active compound in the particular batch of reagent employed, and (b) the nitrate (or nitrite) in the sea-water. Equivalent quantities of nitrate and of nitrite give the same, or very nearly the same, depth of colour.

The fact that water from the English Channel in August gave no perceptible colour with the reagent, the nitrate having been completely utilised by diatoms, etc. (p. 82), is strong indirect evidence that the

colour developed with the reagent and sea-water is due to nitrate alone, except in the rather rare instances where nitrite also occurs.

The production of colour by the reagent with ferric iron is not of the same order of delicacy as with nitrates. In an experiment where the addition of 50 milligrams of nitrate-nitrogen per cubic metre to a sea-water, almost depleted of nitrate, gave rise to a decided red coloration on addition of the reagent, no increase in colour could be discerned due to the addition of an equal quantity of ferric iron to the sea-water. The addition of 5000 mg. per cubic metre of ferric iron gave rise to a coloration considerably less than that produced by 50 mg. of nitrate-nitrogen. This evidence, together with the absence of detectable ferric iron in sea-water shows that the estimation of nitrate by this method is not likely to be materially affected by the presence of iron in the sea.

With a strong batch of reagent, that is, one containing a large amount of the active compound, a decided pink colour is given with a sea-water containing 10 milligrams per cubic metre of nitrate-nitrogen, and as little as 2 milligrams per cubic metre gives a detectable tint.

Up to a certain concentration of nitrate, the depth of colour, as measured with a Duboscq colorimeter or pair of glass cylinders, is directly proportional to the nitrate-content of the sea-water.

In an experiment with a sample of water, particularly free from nitrate, collected well off shore in the summer, the following proportional relations were found between the depth of colour given by samples of the water to which 10, 20, and 30 milligrams of nitrate-N<sub>2</sub> had been added per cubic metre.

(a)	(b)	Ratio of colour given by $\frac{(a)}{(b)}$
Sea-water alone	Sea-water +10 mg. nitrate N <sub>2</sub> per m <sup>3</sup> .	$\frac{1}{4.75}$
Sea-water +10 mg. nitrate-N <sub>2</sub> per m <sup>3</sup> .	Sea-water +20 mg. nitrate-N <sub>2</sub> per m <sup>3</sup> .	$\frac{1}{1.9}$
Sea-water +20 mg. nitrate-N <sub>2</sub> per m <sup>3</sup> .	Sea-water +30 mg. nitrate-N <sub>2</sub> per m <sup>3</sup> .	$\frac{1}{1.44}$

By giving the depth of colour produced by the sea-water, to which 20 mg. of nitrate-N<sub>2</sub> per cubic metre had been added, the arbitrary value of 100 units of colour

Sea-water alone	gave 11 units.	$\left. \begin{array}{l} \\ \\ \\ \end{array} \right\} \text{Difference.}$
,, +10 mg. nitrate-N <sub>2</sub> ,,	52.5	
,, +20 ,, ,, ,,	100	
,, +30 ,, ,, ,,	144	

Mean number of units of colour produced by the addition of 1.0 mg. of nitrate-N<sub>2</sub> per cubic metre = 4.4 units.

Hence the sea-water without any addition of nitrate, which gave 11 units of colour contained between 2 and 3 milligrams of nitrate-N<sub>2</sub> per cubic metre.

Above a certain concentration of nitrate, which varies with the batch of reagent employed, the colour falls off for each successive increment of nitrate until an orange and finally a yellow colour is produced.

In an experiment the following proportional relations were observed between the depth of colour given by a sample of sea-water to which varying quantities of nitrate had been added.

(a)	(b)	Ratio of depth of colour produced by (a) to that produced by (b).
Sea-water only	Sea-water + 20 mg. of added nitrate-N <sub>2</sub>	$\frac{1}{2.28}$ *
Sea-water + 20 mg. of added nitrate-N <sub>2</sub>	Sea-water + 40 mg.	$\frac{1}{1.29}$
Sea-water + 40 mg.	„ + 80 mg.	$\frac{1}{1.69}$
„ + 80 mg.	„ + 120 mg.	$\frac{1}{1.35}$
„ + 120 mg.	„ + 160 mg.	$\frac{1}{1.18}$
„ + 160 mg.	„ + 200 mg.	$\frac{1}{1.11}$
„ + 200 mg.	„ + 260 mg.	$\frac{1}{1.15}$

Assigning the value of 100 arbitrary units to the depth of colour developed by the sample to which 80 mg. of nitrate-N<sub>2</sub> had been added, then

Sea-water only gives		20 units of colour.
„ + 20 mg. of added nitrate-N <sub>2</sub> per cubic metre gives		46 „ „
„ + 40 „ „		59 „ „
„ + 80 „ „		100 „ „
„ + 120 „ „		135 „ „
„ + 160 „ „		159 „ „
„ + 200 „ „		176 „ „
„ + 260 „ „		183 „ „

\* Values shown are the mean of several colorimeter readings.

Plotting the units of colour against the nitrate added, Fig. 1 was obtained. By extrapolation the sea-water alone without added nitrate is shown to contain ca. 22 mg. of nitrate-N<sub>2</sub> per cubic metre. Above a total content of about 140 mg. per cubic metre the linear relation with the depth of colour ceases.

It was found that the colour developed by a definite quantity of nitrate dissolved in distilled water is usually less than when it is dissolved in sea-water, which apparently contains some substance which activates the reaction. Differences in salinity such as ordinarily occur have little or no effect on the colour developed; this is shown by plotting

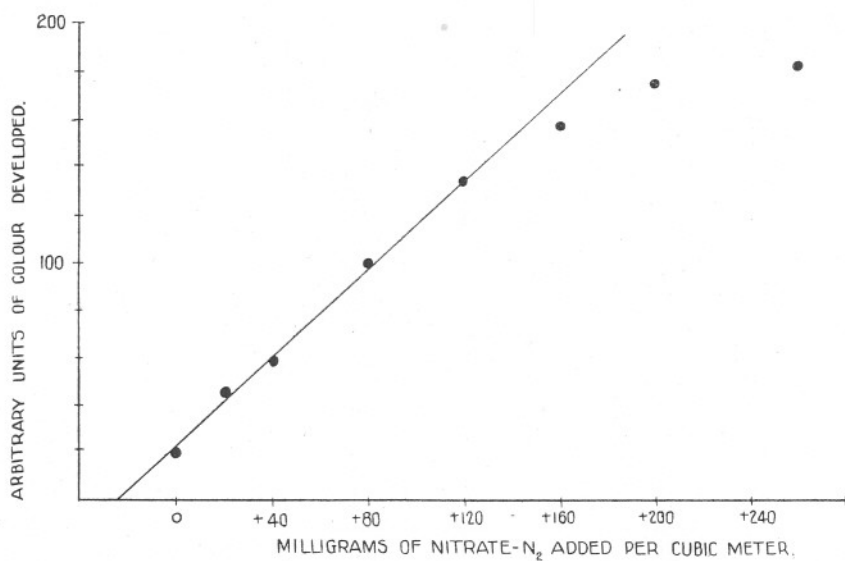


FIG. 1.

the units of colour developed by a sea-water at various dilutions (Fig. 2)

From a number of experiments it appears that the quantity of coloured substance produced due to the addition of the same quantity of nitrate to different sea-waters is very nearly the same, provided, of course, that the batch of reagent used and the conditions under which the reaction proceeds are the same. However, one striking instance has been found where the colour developed due to added nitrate was markedly less than with water from the same position but at lesser depths. This occurred in water collected twenty-two miles south-west of Plymouth on November 11th, 1925, at a depth of 70 metres.

Hence the comparison *inter se* of the depths of colour given by a number of sea-waters does not give the absolute relation of their nitrate contents,

although it does give a very fair approximation. To obtain the absolute relation it is necessary to add a known amount of nitrate to each sample and from the proportional increase in colour developed with the reagent to calculate the nitrate content of the sample. Thus if the colour developed by the sample of sea-water alone is taken as 100 arbitrary units, and after the addition of 50 mg. of nitrate-N<sub>2</sub> per cubic metre it is 170 units, it follows that 50 mg. per cubic metre give rise to 70 units of colour, and the sample contained  $100 \times \frac{50}{70}$  mg. per cubic metre.

Where the sample contains much nitrate so that the depth of colour and the nitrate content are outside the range of the linear relation it is

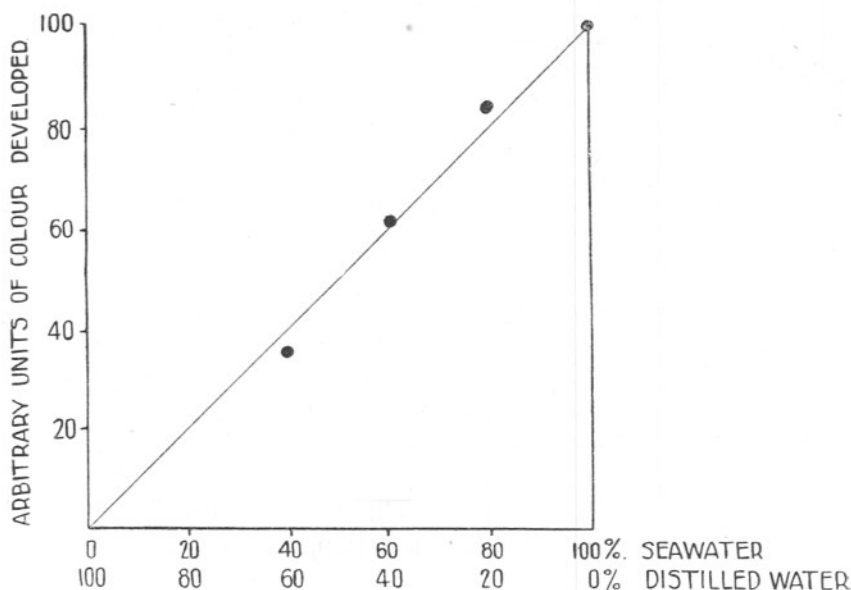


FIG. 2.

necessary to dilute the sample either with distilled water or with sea-water of low and known nitrate content.

Regarding the accuracy of the determinations, it must be borne in mind that 1 mg. per cubic metre is one part in 1000 millions, so a minute speck of nitrate-containing dust or other contamination will lead to a high value. For this reason duplicate determinations and the discarding of any "high" values due to chance contamination are necessary.

From these considerations, the method yields values of the nitrate content of clean water from the open sea which are a very close approximation to the actual content, provided the increment of colour due to the addition of a known amount of nitrate is determined for each sample of sea-water.

With waters polluted with dissolved organic matter in quantity, the method does not give quantitative results, since part of the nitric acid set free nitrates the organic matter. Thus the addition of 170 grams of glucose per cubic metre to a sea-water reduced the nitrate- $N_2$  found by 38%. The presence of much plankton in the sample will therefore affect the results. Hence with estuarine and polluted waters containing organic matter in solution—and in suspension—the values of nitrate content obtained are likely to be somewhat on the low side.

The determinations were mostly carried out by adding 10 c.c. of the reagent to 10 c.c. of sea-water in a stoppered test tube and making the colour comparison with a Duboscq colorimeter by the light of a "Fullo-lite" lamp, after the tubes had stood together for the same period in the dark, generally overnight, in order that the colour might fully develop and a fine precipitate of calcium sulphate, etc., might settle.

#### DISTRIBUTION IN THE SEA.

In 1912 Gran (6) wrote: "The occurrence of dissolved nutritive matter for algæ is on the whole insufficiently known, so we are compelled to estimate its importance by studying the distribution of the water masses, which may be conceived to carry nutritive substances out from the coastal layer or up from the deep water. . . . Where a deep going current is pressed against the coast banks, as off the west coast of Scotland or at the Faero Bank, eddying movements, not only horizontal, but also vertical will necessarily arise, and the water masses from the depths will be carried up to the surface. Nathansohn pointed out that ascending currents may produce a rich phytoplankton."

The only method of estimating nitrates in sea-water up to the present has been to reduce them to ammonia with nascent hydrogen. This method has been employed by Brandt and Raben (15). They found that the deep water of the Atlantic contained more than the surface layers, and that surface water in the North Sea contained less nitrate during the summer than in winter. It appears that the values obtained by this method, for the upper layers at all events, are excessive, being in the order of 60 to 100 milligrams of nitrate-nitrogen per cubic metre. The results of these observers did not suggest that deficiency of nitrate was a limiting factor for plant growth in the sea.

The results obtained in 1925, however, by the method here described, indicate that lack of nitrate does limit plant growth.

#### DISTRIBUTION OF NITRATES DURING 1925.

With one exception, a number of samples from the surface water well away from land or submarine ridges contained a small amount of nitrate (Tables I, II, III, V).

The deep water, on the other hand, was particularly rich in nitrate (Tables III, IV, V).

As land was approached on the south coast of Ireland the upper layers were found to be rich in nitrates in June (Table VI). They abounded in animal and vegetable life.

In the Faero Shetland Channel, where the Atlantic Stream runs into the Norwegian Sea, both deep water and the upper layers are rich in nitrate. In this area and off the south-west of Ireland it is presumed that considerable vertical mixing takes place between the surface and water below about 40 metres during the winter and early summer months. Later in the summer warming of the surface layers is likely to restrain vertical circulation, when a greater difference in the nitrate content of the upper stratum and the water below may be expected. In contrast with the water to the westward of Portugal (Table IV) in these higher latitudes light will penetrate to a lesser depth, and the greater part of the photosynthesis by plants is likely to occur in the upper 30 or 40 metres, as was clearly the case in early summer off Norway (Table V).

TABLE I.

Surface samples collected en route between South America and Europe, and kept in darkness until analysed on September 9th.

Date collected.	Temp. °C.	Lat.	Long.	Nitrate-N <sub>2</sub> mg. per cubic metre.
August 13, 1925 . . .	27.8	0°20'S.	47°16'W.	8
August 16 . . . . .	27.2	9°25'N.	38°48'W.	5
August 18 . . . . .	24.2	19°10'N.	30°15'W.	5
August 21 . . . . .	22.2	28°12'N.	21°20'W.	5
August 24 . . . . .	19.4	37°54'N.	10°16'W.	5
August 26 . . . . .	16.4	48°27'N.	7°10'W.	5

TABLE II.

Surface samples collected en route between Britain and Canada, preserved from bacterial action by mercuric chloride.

Date collected.	Temp. °C.	Salinity parts per thousand.	Lat.	Long.	Nitrate-N <sub>2</sub> mg. per cubic metre.
August 27, 1925 (in Labrador Current)	10.0°	30	51°48'N.	55°00'W.	2
August 27 . . . . .	10.6	35	52°20'N.	50°00'W.	2
August 26 . . . . .	12.8	35	53°00'N.	40°00'W.	7
August 25 . . . . .	14.4	35	53°10'N.	30°00'W.	84

TABLE III.

Bay of Biscay. Lat. 45°50'N., Long. 9°00'W. Collected June 8th, 1925, by H.M.S. *Tomahawk*, preserved with mercuric chloride.

Depth.	Nitrate-N <sub>2</sub> per cubic metre.
360 metres	160 mg.
830 „	ca. 200 „

TABLE IV.

Samples collected by R.R.S. *Discovery*. Preserved against bacterial action by the addition of mercuric chloride.

October 12th, 1925. Lat. 37°44'N., Long. 13°21'W.

Depth in metres.	Temp. °C.	Nitrate-N <sub>2</sub> mg. per cubic metre.
0	21.10	15 ; 11
10	21.10	7
20	21.00	6
30	21.00	—
40	21.00	16
50	20.01	ca. 6
75	17.31	6
100	15.10	55
150	15.06	65
200	13.86	100
300	12.25	178 ; 158
500	10.94	200
1000	9.55	264 ; 262 ; 274
2000	4.81	ca. 265
3000*	3.10	ca. 265

TABLE V.

Samples collected by the S.S. *George Bligh* south-west of Norway, May 16th, 1925. Lat. 57°57'N., Long. 6°45'E. Kept in darkness until analysed on May 25th.

Depth	Nitrate-N <sub>2</sub> mg. per cubic metre.
0 metres.	6, 4
20	16
40	77
100	138, 128
300	160

\* Oct. 16th, 1925, Lat. 29°59'N., Long. 15°03'W.



TABLE VI.

Samples collected off the south coast of Ireland, kept in darkness until analysed on June 6th.

Collected May 14th, 1925. Lat.  $50^{\circ}34'N.$ , Long.  $11^{\circ}17'W.$  in 1040 metres.

Depth.	Nitrate-N <sub>2</sub> mg. per cubic metre.
0 metres.	170 mg.
462	190
1010	190

Collected May 12th, 1925. Lat.  $49^{\circ}21'N.$ , Long.  $8^{\circ}00'W.$  in 138 metres.

Depth.	Nitrate-N <sub>2</sub> mg. per cubic metre.
0 metres.	60 mg.
60	130
133	130

TABLE VII.

Samples collected by the s.s. *Explorer* in July, and kept in darkness until analysed.

Collected in Channel between Faeros and Shetland. Lat.  $61^{\circ}27'N.$ , Long.  $4^{\circ}23'W.$ , July 6th, 1925.

Depth.	Nitrate-N <sub>2</sub> mg. per cubic metre.
10 metres.	67 mg.
60	160
300	160
900	160
1000	160

Lat.  $61^{\circ}02'N.$ , Long.  $3^{\circ}22'W.$ , July 6th, 1925.

Depth.	Nitrate-N <sub>2</sub> mg. per cubic metre.
10 metres.	18 mg.
40	78
100	92
500	106
800	115

North-west of Faero Islands. Lat.  $62^{\circ}53'N.$ , Long.  $9^{\circ}05'W.$ , July 4th, 1925.

Depth.	Nitrate-N <sub>2</sub> mg. per cubic metre.
0 metres.	85 mg.
10	70
30	115
80	over 200
100	" "
300	" "
495	" "

## IN THE ENGLISH CHANNEL.

A growth of diatoms had become apparent after the winter cessation, previous to the analyses being commenced in April, 1925. On April 22nd it is seen from Table VIII that the water at Station E1, twenty-two miles south-west of Plymouth on the line Plymouth-Ushant, was depleted of nitrates in the upper layers. By May 13th the depletion was more marked in the deep water, while farther to the southward at Stations E2 and E3 in water of slightly higher salinity and greater depth the supply of nitrate was considerable.

TABLE VIII.

Nitrate content in milligrams of nitrate-N<sub>2</sub> per cubic metre at various depths (in metres, m.) of water in the English Channel on the line Plymouth-Ushant.

	In Plymouth Sound, Station L <sub>1</sub>	Off west end of Plymouth Breakwater Station L <sub>2</sub>	5 miles S 21° W (true) from Plymouth Hoe Station L <sub>3</sub>	9 miles S 21° W (true) from Plymouth Hoe Station L <sub>4</sub>	22 miles S 21° W (true) from Plymouth Hoe Station E <sub>1</sub>	59½ miles S 21° W (true) from Plymouth Hoe Station E <sub>2</sub>	115½ miles S 21° W (true) from Plymouth Hoe Station E <sub>3</sub>
April 22nd, 1925	—	—	—	—	0 m. 4 5 m. 2 10 m. 2 25 m. 3 50 m. 24 67 m. 24	—	—
May 13th, 1925	—	0 m. 14	—	0 m. 2 — — 40 m. 3 — — —	1 m. 2 10 m. 3 20 m. 5 30 m. 2 50 m. 9 69 m. 8 —	— 10 m. 55 — 30 m. 53 50 m. 15 92 m. 29 —	1 m. 67 10 m. 85 20 m. 85 30 m. 67 50 m. 67 — 105 m. 67
June 3rd, 1925	—	—	—	—	1 m. 3 10 m. 3 — — — 40 m. 8 69 m. 9	—	—
July 8th, 1925	—	—	—	0 m. 4 — — 40 m. 8 — — —	1 m. 4 — 20 m. 4 40 m. 4 70 m. 4 — —	5 m. 3 — 25 m. 24 — 50 m. 29 98 m. 29 —	5 m. 40 — 25 m. 40 — 50 m. 40 — 167 m. 40

TABLE VIII.—*continued.*

	In Plymouth Sound Station L <sub>1</sub>	Off west end of Plymouth Breakwater Station L <sub>2</sub>	5 miles S 21° W (true) from Plymouth Hoe Station L <sub>3</sub>	9 miles S 21° W (true) from Plymouth Hoe Station L <sub>4</sub>	22 miles S 21° W (true) from Plymouth Hoe Station E <sub>1</sub>	59½ miles S 21° W (true) from Plymouth Hoe. Station E <sub>2</sub>	115½ miles S 21° W (true) from Plymouth Hoe Station E <sub>3</sub>
Aug. 5th, 1925	— — — — —	— — — — —	— — — — —	— — — — —	10 m. 0 20 m. 3 — 40 m. 3 69 m. 0	— — — — —	— — — — —
Aug. 31st, 1925	3 m. 9 — — — —	— — — — —	— — — — —	0 m. 0 — 40 m. 7 — —	5 m. 0 — 25 m. 9 — 50 m. 14 69 m. 14	— — — — — —	— — — — — —
Oct. 1st, 1925	0 m. 112 — — — — — —	0 m. 79 — — — — — —	0 m. 37 — — — — — —	0 m. 27 — — — 40 m. 27 — —	0 m. 6 10 m. 6 20 m. 21 30 m. 32 — 50 m. 32 66 m. (19)	— — — — — — —	— — — — — — —
Nov. 11th, 1925	0 m. 176 — — — — — —	0 m. 380 — — — — — —	— — — — — — —	0 m. 76 — — — 40 m. 43 — —	0 m. 68, 10 m. 68 20 m. 65 30 m. 56, — 50 m. 70, 70 m. (25, 30)	66 — — — 41 — — 69 — 30 —	— — — — — — —
Dec. 11th & 15th 1925	— — — — — —	0 m. 120 — — — — —	0 m. 110 — — — — —	0 m. 74 — — 40 m. 50 — —	0 m. 38 10 m. 40 25 m. 43 50 m. 48 70 m. 43 —	— 10 m. 106 25 m. ca120 50 m. ca120 — 90 m. 132	— — — — — —

On this date the water at these stations was still practically isothermal from top to bottom—characteristic of winter conditions—hence vertical mixing by wave motion and tidal streams over an uneven bottom at E3 was not restrained by differences in density.

In July the utilisation of nitrates by diatoms had caused a decrease at Stations E2 and E3. At E2 the decrease was most marked in the upper layers. In the interval between May 13th and July 8th, an increase in salinity had taken place at these two stations, probably due to a movement of more saline Atlantic ocean water into the area.

By August 5th diatoms had utilised all available nitrate at Station E1, and their dying out and lessened activity allowed a re-formation of nitrate in the bottom strata to become apparent by the 31st. During

this period, April to the end of August, the salinity of the water at E1 had remained practically the same, and there is no evidence of any marked movement of the water masses in the area. The rather scanty data indicate a low nitrate content of the inshore water during this period.

It is remarkable that a little nitrate remains in the surface layers of the tropical open ocean (Tables I and IV) where phytoplankton is scanty, while it is able to utilise practically all the nitrate in the English Channel. However, in the Channel, there are plenty of nutrient salts at the end of winter, and with the onset of sunny weather a very dense diatom

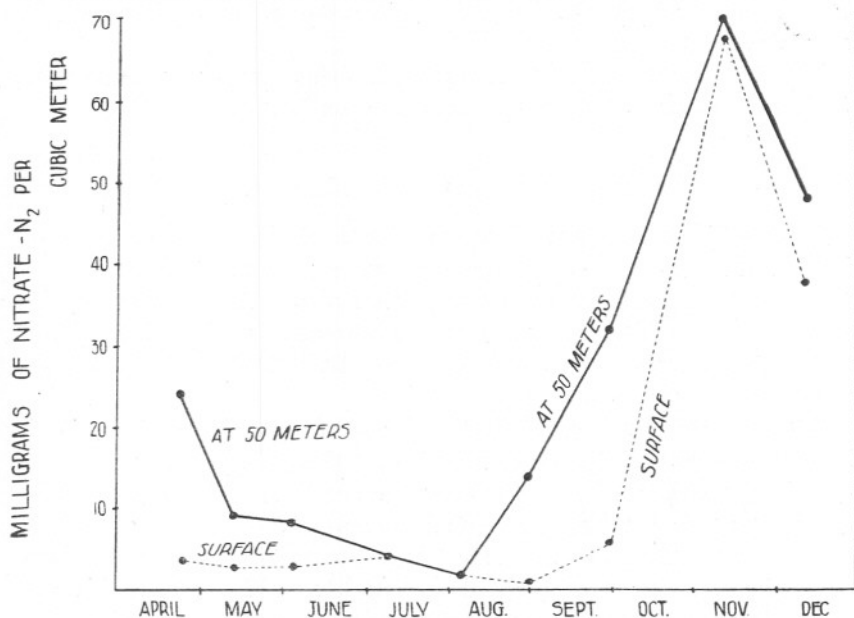


FIG. 3.—Nitrate content of water at Station E1, 22 miles south-west of Plymouth, during 1925 in the surface 5 metres and at 50 metres.

population springs up, gradually to die down during the summer months as the available nutrient salts diminish. In the surface water of the tropical and subtropical ocean there is a sufficiency of light all the year round, but plant growth is limited throughout the year by lack of nutrient salts. There is never a sufficiency to allow a dense vigorous growth to spring up, such as in the English Channel utilises the last traces of nitrate. In the latter area there must also be a greater *continuous* supply of phosphate and nitrate from the denser animal population.

From the end of August onwards the regeneration of nitrate is more rapid than its utilisation by diatoms. The burst of spring growth has died down sometime previously and decaying corpses become numerous.

The utilisation of nitrate in the upper 15 metres by the usual autumn flowering of diatoms is apparent on October 1st.

Between November 11th and December 11th a fall in nitrate occurred at Station E1, and I am indebted to Dr. W. R. G. Atkins for the observation that a fall also occurred in the phosphate, which had started to regenerate more rapidly than it was being utilised by August 5th—earlier than the nitrate. It is noteworthy that there was considerable sunshine during this period, November 11th to December 12th (average 3.6 hours per day).

Reference must be made to the low content of nitrate in the water at 70 metres at E1 on October 1st and November 11th. No reason is suggested for this.

Fig. 3 shows the seasonal variation in nitrate content of the upper 5 metres and of the 50-metre layer at Station E1.

#### THE REGENERATION OF NITRATE.

In 1910 Thomsen found nitrate-forming bacteria in bottom deposits from Kiel Fjord, derived from land washings, but not in sea-water or plankton (7). Lipman was unable to find nitrate forming bacteria in water from near Tortugas, but quotes a statement by Issatchenko that he had found nitrifying bacteria in the Arctic in 1908, but was unable to verify their presence later (8).

Surface water collected at Station E1 on August 5th to which had been added 200 milligrams per cubic metre of ammonium-nitrogen, was kept in the dark for six days at room temperature. At the end of this period no colour developed on adding the reagent. Water from a depth of 69 metres collected on the same day and treated in the same manner was kept in the dark together with a control to which mercuric chloride had been added. After six days a definite colour was obtained with the reagent, while no colour was given by the control.

The depth of colour indicated the formation of nitrate to an amount in the order of 7 milligrams per cubic metre. No nitrite was detectable. On repeating the experiment and keeping for eight days, likewise at room temperature, nitrate was again found in the water, but not in the control, and the amount formed was of the same order.

A further experiment showed that the addition of detritus collected about four miles off shore caused the formation of nitrate to take place in surface water to which a trace of ammonium salt had been added, whereas without the detritus no nitrate was formed. The controls in which bacterial action was stopped by mercuric chloride showed no development of nitrate.

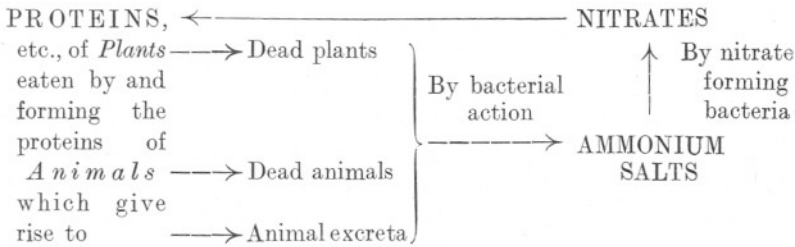
THE NITROGEN CYCLE.

Denitrifying bacteria have been found in water near the shore and in mud of the Baltic (9), but as pointed out by Gran (10) they are not likely to play a part in the economy of the open oceans, since the water almost invariably contains a sufficiency of oxygen for these bacteria, without their having recourse to attack the small quantities of nitrates present.

*Azotobacter*, fixing dissolved nitrogen, has been found in the slime of Baltic algæ (11) and in bottom deposits from near the land (12). There is no evidence as yet that they are general in occurrence or that they add more than a minute fraction to the combined nitrogen in the sea.

As far as we know the inorganic salts necessary for plant life are always present in sea-water in ample amount except phosphates (16) and nitrates. Iron is a possible exception. The nitrates are converted by the algæ into proteins, etc. Some of these algæ die, and from the decay of their corpses ammonium salts are produced. Others nourish marine animals which in turn are fed upon by other animals. These excrete the products of their metabolism and in due course die; ammonium salts are produced from their corpses and excreta by bacterial action.

Thus we have in the sea a closed cycle.



Phosphate is regenerated in a similar manner, and the evidence so far obtained shows that in both cases the cycle is practically a closed one, the increment due to land washings not being very great compared with the amount continually being regenerated from dead marine organisms.

A deficiency of nutrient salts limits both the rate of multiplication of vegetable plankton, and in all probability the rate of carbon assimilation as well (1). All the energy expended in the vital processes of plants and animals in the sea is derived from the energy of light absorbed during the course of carbon assimilation by phytoplankton—the fixed algæ being but a small proportion of the plant life.

Hence a quantitative knowledge of those factors, which control and limit the multiplication of vegetable plankton and which affect its efficiency as an energy absorber, is the first step in any fundamental inquiry concerning the fertility of the sea.

The consideration of this cycle indicates that the fertility of any area

of the open oceans, not subject to considerable inflows of water from other areas, depends upon three main factors. (a) The length of time protein formed by phytoplankton remains part of the plant or nourished animals body. (b) The time which elapses during the decay and formation of ammonium salts and phosphate from corpses and excreta. To this must be added the time taken for nitrate forming bacteria to convert the ammonium into nitrates. (c) The time which elapses before the reformed nitrate and phosphate again reaches the upper layers where there is sufficient light for photosynthesis.

Dealing with these three factors in turn, the first is controlled by the natural length of life of the plants and animals, and by the proportion of the plants which are eaten. This decides the proportion of total living matter to the rate of loss by natural death. The proportion of total living matter to its rate of loss by respiration and excretion is controlled by *temperature*. In a warm sea the loss will be in excess of that taking place under colder conditions, since the rate of metabolism roughly doubles for a rise of  $10^{\circ}\text{C}$ ., and more food will be required by animals to provide for their irreducible metabolism necessary to maintain life.

Of the second factor (b) there is little information. Presumably the breakdown products of proteins and phosphoproteins produced in the course of metabolism are excreted mostly as urea and phosphates, and the decay of corpses is largely brought about by bacterial agency. From the analyses of water collected in the Atlantic during the expedition of the *Planet* it appears that there is rarely less than 25 milligrams per cubic metre of ammonium nitrogen in the waters of the open ocean (15, Tafel 9). The distribution of nitrate forming bacteria, possibly identical with the *nitrobacter* of the land (7) (13) in the open ocean is quite unknown.

The third factor (c), being the length of time that the reformed nitrate lies unusable below the illuminated upper layers, is of great magnitude. A glance at Table IV shows an enormous store of nitrate below the upper 100-metre layer. A rough calculation indicates an amount somewhere in the order of 250 thousand million metric tons of nitrate-nitrogen in the deeper layers of the great oceans, lying dormant until such time as currents bring the deep water into the upper sunlit layers. There is every reason to suppose that this third factor regulates the speed at which nitrogen and phosphorus pass through the complete cycle in the sea *as a whole*, being the slowest in the series of changes.

In particular shallow areas, however, such as where tidal streams and sufficient surface cooling to set up convection currents reaching to the bottom cause vertical circulation, during the whole or part of the year, the regenerated nitrate is subject to no delay before again becoming available. These areas, usually coastal, are very fertile. The North Sea,

English Channel, and the Shallow Shelf between the Grand Banks and Cape Cod are such. Here the conditions are somewhat complicated by a certain amount of inflow of oceanic water, and by the fact that the rate of regeneration of nitrate, and phosphate, from dead organisms overtakes the rate at which plant life utilises it during the autumn and short days of winter. A store of available nitrate and phosphate (16) is thus formed which is rapidly used up as soon as some three hours of sunshine per day occur in the spring in the English Channel. Insufficient illumination becomes the limiting factor during the winter months, delaying for a period the rate at which combined nitrogen and phosphorus passes through the complete cycle.

In the deep open oceans the winter cooling of the surface layers in temperate and arctic regions will set up convection currents. By lessening the density gradient, the convection currents will be assisted by wave motion in bringing about more effectual mixing with the layers below. Hence in such latitudes, as opposed to the subtropical regions, a small store of nutrient salts may be expected in the spring, and in general a richer plankton particularly in the early summer. In the tropical regions of the Atlantic the heated surface water streams away to form the Gulf Stream, etc., to be replaced by water upwelling from below. Hence in these regions richer plankton may be expected than in the subtropical. These expectations are born out by the results of Hensen's Plankton Expedition (14).

It is a remarkable fact that plant growth should be able to strip sea-water of both nitrates and phosphates, and that in the English Channel the store of these nutrient salts formed during autumn and winter should be used up at about the same time.

I am indebted to Dr. W. R. G. Atkins for a number of samples of water which had been collected for him and for several most helpful suggestions, to Dr. Stanley Kemp and the Staff of the R.R.S. *Discovery*, to Dr. L. T. Hogben, and to the Commanding Officer of H.M.S. *Tomahawk* for collecting samples of waters.

#### SUMMARY.

1. A method of estimating nitrates in sea-water is described.
2. A considerable concentration of nitrates occurs in the depths of the ocean and a very low concentration (0 to 10 parts per 1000 million of nitrate-nitrogen) in the surface layers of those areas where there is no upwelling of water from below.
3. The nitrates in the water of the English Channel, twenty-two miles south-west of Plymouth, are almost entirely utilised by phytoplankton in the summer, and commence to be reformed from ammonium salts at a greater rate than they are utilised by the end of the summer. The



nitrate reformed near the bottom mix with the upper layers when the column of water becomes nearly isothermal in the autumn.

4. Sea-water from near the bottom at this position contains nitrate-forming bacteria.

5. Conditions which limit the total plant and animal population of areas of the sea are discussed.

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## Seasonal Changes in the Silica Content of Natural Waters in Relation to the Phytoplankton.

By

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With 3 Figures in the Text.

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IN a previous paper (1923) it was shown that the colorimetric method of Diénert and Wandenbulcke (1923) was suitable for studying silica concentrations down to a limit of 0.2–0.15 mg. per litre without concentrating the solution, the liquid under examination being, after the addition of the reagents, close to pH 2. The method consists of the addition of 2 c.c. of a 10 per cent solution of ammonium molybdate to 100 c.c. of the water to be tested. This is followed by the addition of four drops of a 50 per cent (by volume) solution of sulphuric acid. A yellow colour results, which reaches its maximum in ten to twenty minutes, after which it remains constant for some time. The authors named standardised their solutions against silica, but recommend picric acid as affording permanent standards. They find it convenient to make up a solution containing 36.9 mg. of picric acid per litre as giving a yellow colour corresponding to that given by 50 mg. p.l. of  $\text{SiO}_2$  in solution as silicate, and in this the writer has followed them. The method has since been largely used by Thresh and Beale (1925), who consider it as accurate as the gravimetric method, but use 40 mg. of picric acid as equivalent to 50 mg. of silica. The excessively minute amount of silica present in sea-water renders an even more delicate method desirable, and using 100 c.c. of water compared against a standard corresponding to 0.5 mg. per litre it was previously reported possible to detect silica down to 0.15 mg. p.l., which means a scale reading of 30 c.c. in the Hehner cylinder used for comparison. With increased practice the writer has since been able to match tints down to a scale reading of 8 c.c., which appears to be indistinguishable from pure water; such a reading corresponds to 0.04 mg. p.l., so when this is recorded in a table it must be understood that there may be any lesser quantity; this amount is tabulated as 40 mg. per cubic metre, as the milligram per cubic metre is the most convenient unit to adopt for recording the minor constituents of sea-water; for fresh water these numbers are parts per thousand million, but owing

to the greater density of sea-water the expression is not quite accurate when applied to the latter. Though readings below 8 c.c. cannot be distinguished from pure water, yet above this differences of 4 c.c., or possibly 2 c.c., may be distinguished, namely, 0.02 or 0.01 mg. p.l. Since only 100 c.c. is used the actual amounts distinguished are 0.002 to 0.001 mg. Gravimetric estimations necessarily involve the concentration of filtered sea-water, usually carried out at boiling-point or near it. As previously mentioned, silica, which has escaped filtration, may thus be brought into solution. It depends on how efficiently the finest particles have been removed. That solution may take place was shown by evaporating to dryness, in a nickel dish, sea-water found to contain 0.16 mg. p.l.  $\text{SiO}_2$ ; on cooling and making up to 100 c.c. with distilled water the total soluble silica was found to be 0.54 mg. p.l. Filtration through a single Whatman No. 41 filter paper seems, however, to remove all silica or silicate in suspension, for before filtering, after filtering, after evaporating to dryness in a platinum dish and in a nickel dish and making up again to the original volume, a sample of sea-water was found to give the following values, respectively, 0.33, 0.33, 0.33, 0.32 mg. p.l. In a silica dish, however, 0.84 mg. p.l. was obtained.

It has been established that the presence of phosphate in the water introduces no error into the silicate estimation, for 0.5 mg. p.l. of  $\text{P}_2\text{O}_5$  yields a tint equivalent to 0.08 mg. p.l. silica, whereas only in the deeper ocean water is as much as 0.05 mg. p.l. of  $\text{P}_2\text{O}_5$  found.

When estimating silicate in water near the coast, or in certain fresh waters, a yellowish or brownish tint may be observed. When a blank without the reagents has shown a tint greater than a scale reading of 8 c.c., the limit for pure water, a suitable correction has been applied. Thus were the water alone to match a 0.5 mg. p.l. standard at 24 c.c., using 100 c.c. of the sample, then 0.12 should be deducted for the tint, as the colour is equivalent to that amount of silica. To be strictly accurate the blank reading, 8 c.c., should previously have been deducted, viz.  $24 - 8 = 16$ , therefore deduct 0.08. This, however, was not done as the tint correction is only approximate unless the amount is small and the colour match is seldom exact. Such tints are often met with in fresh water and in the water of Plymouth Sound, but never in the open sea.

#### SILICATE CONTENT OF FRESH WATER.

In general fresh water is far richer in silicate than is the sea. The seasonal changes were studied (Atkins and Harris, 1924 and 1925) during 1923 and 1924 in two fresh water ponds, one pipe supply from a shallow well and in Plymouth tap water. The latter is very constant at around 3.3 mg. p.l., or 3300 mg. per  $\text{m}^3$ . The shallow well supply varied from

about 2 to 6 mg. p.l., the minimum being in February and the maximum in July. These variations were possibly connected with rainfall, and possibly with the increase in temperature favouring the solution of the silicates. Staddon reservoir, in part supplied from this well, fell from about 4 mg. p.l. in March, 1923, to under 2 in June, it then rose sharply to an August maximum of about 8 mg. p.l., reaching a minimum of less than 2 in January. The other pond rose from less than 1 mg. p.l. in September to over 2 in late December, falling to 0.5 in March. The changes are undoubtedly complex, for in addition to temperature and evaporation effects the removal of silica by diatoms must not be neglected. This was probably the explanation of the spring decrease. The hydrogen ion concentration of the water is also, it appears, of importance, since mineral matter in suspension is more likely to have silicates dissolved out from it when the alkalinity is great. The question is in need of further observational and experimental study.

#### SILICATE CONTENT OF SEA-WATER.

A series of analyses of water from the L and E series of stations are shown in Table 1. The exact positions of these may be found in this Journal, 1922, 12, 747 and 755, but it may be explained that the L series are on the line from the Laboratory to the Eddystone, and the E series on the Ushant line from the Eddystone. Inspection of the table shows that silicate diminishes from the Sound to the open sea, and there is also perhaps a slight diminution from E1 to Ushant, E3. A few typical results are shown in Fig. 1.

In addition there is a well-marked seasonal change, at E1 a winter value of 200–240 falls to 40–80 in April to June. This is followed by a rise 100–160 in October, but in both 1923 and 1925–1924 was omitted—the November value is only about 70 mg. per m<sup>3</sup>. The high values for July, 1925, are suspect, as thirteen days elapsed between collection and analysis, the weather, moreover, was hot. There was thus the possibility of matter in suspension and the glass of the bottles being attacked. It was previously shown (1923) that storage in the spring-clip sample bottles of hard green glass did not result in the solution of more than 10 mg. per m<sup>3</sup> in five days. In specially warm weather this may be somewhat increased. It is certainly a cause of error in some of the results recorded in Table 2, in which of necessity analysis was delayed. Their substantial accuracy is, however, unimpaired. In future work an attempt will be made to avoid this error by coating the bottles with paraffin wax. Even if it be allowed that the E1 results for July are high, the error cannot be more than about 40 mg. per m<sup>3</sup> at the most. This July rise is in keeping with Brandt's rise in June.

TABLE 1.

## SILICATE CONTENT OF SEA-WATER AT L AND E STATIONS.

Silicate as  $\text{SiO}_2$  in mg. per  $\text{m}^3$ .

		1923.			1924.				1925.							1926.	
		15/10	7/11	10/12	15/2	8/4	17/6	17/2	14/3	22/4	3/6	9/7	5/8	1/10	11/11	11/12	12/1
L1 } L2 } L3 } L4 }		500	420	600	520	—	80	—	420	—	330	—	—	—	270	—	910
		350		580	—	170		—	—	—	—	210	200	150	280	570	130
		—	70	490	420	—	—	—	—	70	120	170	—	—	180	—	330
		—		360	—	130	—	—	180	—	—	—	140	160	190	90	130
L5 and 6	—	—	280	200	—	—	—	250	—	80	—	—	—	90	90	110	
E1	m 0	100	70	90	200	80	60	240	160	40	40	150	80	160	70	90	—
	„ 40	100	—	150	—	—	100	—	—	—	40	—	70	150	70	90	—
	„ 70	100	—	200	200	80	140	—	160	70	40	150	80	100	70	—	—
E2	„ 0	—	70	—	—	—	—	—	—	—	140	—	—	—	—	130*	—
	„ 80	—	—	—	—	—	—	—	—	—	150	—	—	—	—	100*	—
E3	„ 0	—	—	—	180	—	—	—	—	—	120	—	—	—	—	—	—
	„ 100	—	70	—	180	—	—	—	—	—	120	—	—	—	—	—	—
Analysed		17/10	9/11	11/12	26/2	5/5	20/6	21/2	23/3	23/4	4/6	22/7	7/8	5/10	13/11	18/12	13/1

\* Taken December 15th. The L6 value on 12.i.26 was identical with the L5, and was used as a record for E1 in the graphs, being genuine open sea-water, thoroughly mixed by storms.

Brandt (1920) has recorded a seasonal change in the Baltic, silicate as silica varying from 900 mg. per  $m^3$  in February to 600 in May, followed by a rise in June. Bottom water in February contained 1150 mg. As the Baltic receives large accessions of fresh water and is land-locked, it is to be expected that its water should be richer in silicate than is the English Channel and the Atlantic.

The comparatively shallow water of the English Channel affords no

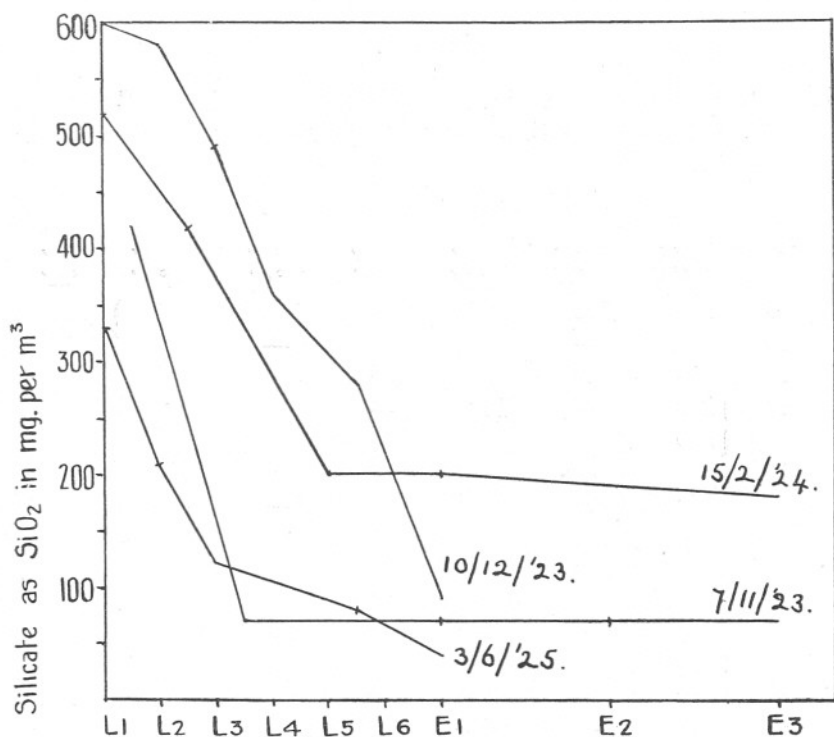


FIG. 1.—Decrease of silicate from Plymouth Sound to open sea of English Channel. The L stations are at approximately equal distances apart and E2 is midway between E1 and E3, but the distances are not shown to scale, that between the E stations being relatively much reduced.

decisive proof of the variation in silicate with increasing depth; though the values for E1 on December 10th, 1923, and June 17th, 1924, show decided differences from surface to bottom, yet in other cases, where phosphate analyses showed depletion at the surface, no such changes were observed as regards silicate. It must, however, be remembered that the matching of the very faint tints shown by such dilute solutions of silicate is always a matter of difficulty. Inspection of Table 2, on the contrary, shows an invariable increase with depth in the deeper waters.

Owing to storage before analysis all the results are probably slightly too high. They agree in affording undoubted evidence of increase in silicate in the deeper waters of the Atlantic, which thus act as reservoirs of this radicle, available only for plant utilisation when brought to illuminated regions along with phosphates and nitrates (Atkins and Harvey, 1925). It may also be noted that the water immediately next the bottom may be considerably richer in silica than that at a relatively slightly lesser depth.

TABLE 2.

SILICATE CONTENT IN THE FAROE-ICELAND AND FAROE-SHETLAND CHANNELS, OFF THE S. OF IRELAND, IN THE BAY OF BISCAY, AND OFF PORTUGAL.

Silicate as SiO <sub>2</sub> in mg. per m <sup>3</sup> .							
Metres.	62°53'N depth.	61°27' 9°05'W 4°23'	61°02' 3°22'	49°20' 8°00'	50°34' 11°17'	45°50' 9°00'	37°44' 13°21'
0	150	100	95	110	140	—	} 220
50	—	—	—	—	—	—	
60	140	150	—	200	—	—	—
80	{ 200	—	160	—	—	—	} 220
		200					
100	250	{ 220	180	—	—	—	} 220
150	—		250	—	*	—	
200	250	250	—	*	—	—	—
300	—	—	210	*	—	—	250
400	—	270	—	*	200	—	—
	{ 270						
500		280	—	310	*	—	—
800	*	—	360	*	—	520	—
900	*	310	*	*	—	—	—
1000	*	360	*	*	380	—	450
2000	*	*	*	*	*	*	480
3000	*	*	*	*	*	*	1200†
Taken	4/7/'25	6/7	6/7	12/5	14/5	8/6	12/10
Analysed	28/7/'25	28/7	28/7	5/6	5/6	13/7	2/11

The writer is indebted to Mr. H. W. Harvey and the crew of the *Salpa* for much assistance in obtaining the local samples, to Dr. Bowman and the staff of the Aberdeen Laboratory for the northern samples, to Mr.

\* Denotes bottom has been passed by this.

† Taken October 16th at 29°59'N., 15°03'W.

G. W. Farran for those off the Irish coast, and to Dr. Stanley Kemp of the R.R.S. *Discovery* for the interesting series down to 3000 metres.

Making all possible allowance for the error due to solution of silicate from the glass, these open ocean samples afford no evidence that silica is ever completely used up at the surface of the sea. Lack of it cannot, therefore, be held to limit diatom growth, provided always that the diatom is able completely to strip the water of silicate and to utilise even the most minute amounts; this it must be emphasised has never been proved directly, and it is conceivable that just as a chemical pre-

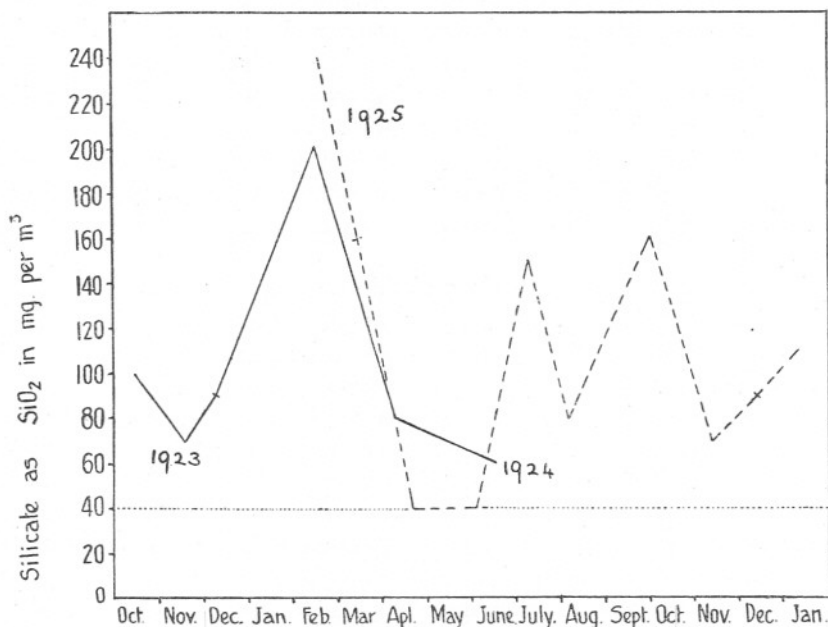


FIG. 2.—Seasonal variations in silicate at Station E1, surface. The dotted horizontal line at 40 mg. per m<sup>3</sup> may be the true position of the base line, for as explained in the text 40 mg. is the limit which can be detected. A value 40 mg. may therefore be any lesser amount.

cipitation may—and usually does—still leave a certain minute amount unprecipitated, so also the quite unknown process by which the diatom forms its siliceous test may result in leaving some silica in solution. The analyses recorded in Table 1 and plotted in Fig. 2 show none the less that this precipitation may be so complete that no detectable silicate is left in shallower water, as on April 22nd and June 3rd, 1925, at E1; for the recorded value, 40 mg. per m<sup>3</sup> is, as already explained, equal to the blank or limiting value. The blank amount has not been subtracted, as since the previous paper practice has reduced it from 150 to 40. The latter value is about the winter maximum value for phosphate as P<sub>2</sub>O<sub>5</sub>, so



it seems that a more delicate analysis would be required definitely to prove that silica was a limiting factor.

The diminution in silicate which occurs in spring and autumn at E1 points to its removal by diatoms. The fall in spring corresponds with that in phosphate, but in November, 1925, a decrease in silicate corresponded with an increase in phosphate (as shown in a forthcoming paper), though in December an unusual decrease in phosphate corresponded with a slight increase in silicate, giving values for both months identical with those of 1923. It must, however, be remembered that the phosphate content at any time is a resultant value, so that an increase may be accompanied by a diatom outburst if down-grade processes, liberating phosphate from other sources, predominate. The water at E1 is rarely affected at all by outflowing river water, so the low rainfall of the late autumn of 1925 cannot be held to account for the low silicate at E1. The season was, however, clear and sunny, so the decrease in phosphate in December and the low silicate values are probably explained by the rather unusual development of phytoplankton at this period.

In Fig. 3 are shown the periods of silicate diminution; these it may be supposed are proportional to diatom production; the values are obtained by subtracting the silica result for each month from that of the previous month of observation, and then representing a loss of silicate in solution as a gain in silica, precipitated in diatoms, as shown by ordinates above the axis. Below the axis the corresponding amounts of silica gained by the water are shown. This it may be assumed is a closed system; if so the annual increase and decrease should on an average of years be equal. Silicate is, however, brought in by rivers and diatomaceous deposits and sponge spicules are found in various places, so it is an open question whether the ocean silicate cycle is to be regarded as an almost closed one, like the phosphate cycle, or one in which the annual silicate addition is precipitated by living organisms. It seems more probable, however, that a portion of the diatom silica again finds its way into the water of the ocean. The point needs experimental investigation.

If we attempt to construct a balance sheet for the silica in the water at E1, the maximum winter value 240 mg. per  $m^3$  minus the minimum shows a utilisation of 200 mg. If, however, all the observations showing depletion are taken it is seen that 360 mg. was used up and 230 mg. regenerated or supplied afresh, the deficit on the turnover being 130 mg. If the analyses are correct this figure should also be given by subtracting the initial and final values for the silica content at E1, viz. 240-110 mg., namely, 130. The exact agreement is somewhat surprising. It is to be noted that for some unknown reason the silica content at E1 is low this

winter even though the phosphate content has now recovered its high winter value.

The writer is indebted to Dr. M. V. Lebour for the information that the late autumn of 1925 was a period when *Rhizosolenia robusta* was specially plentiful in the water off Plymouth. This is a large diatom, just visible to the naked eye, and it reaches approximately its northerly limit of distribution at Plymouth. Other species of this genus, namely, *R. shrubsolei*, *R. styliiformis*, and *R. alata* have been far more abundant

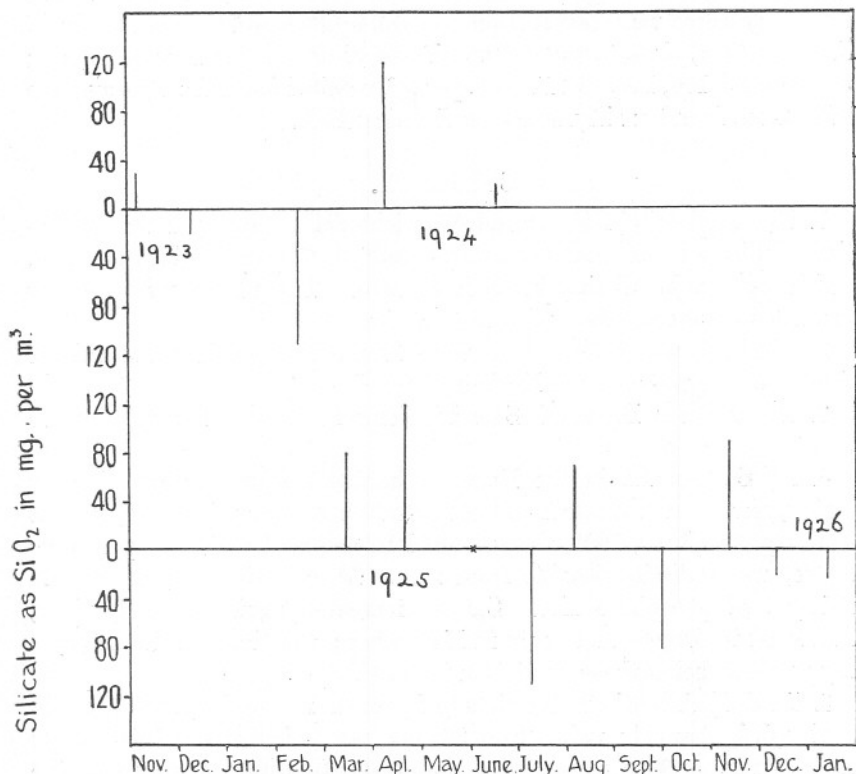


FIG. 3.—Periods of production of diatoms as judged by upward lines, corresponding to mg. per m<sup>3</sup> of silicate, as silica, used up. Downward lines denote enrichment in silicate, due to its regeneration from the decay of diatoms or other sources.

than usual over the same period and took the place of *Biddulphia regia*, *B. sinensis*, and *B. mobiliensis*, which were not as plentiful as usual. The diatom distribution was unlike that of any other year of the last ten. It seems possible that the abundance of *R. robusta* is not unconnected with the fall in silica in November shown in Fig. 3, though the actual value reached was the same as in 1923.

Interesting light is thrown on the silica content of the Atlantic Ocean,

surface water in winter, by a series of samples taken by the s.s. *Hildebrand* between Para and about  $2\frac{1}{2}^{\circ}$  west of Ushant. The most southerly samples were all consumed in phosphate and nitrate determinations, but four between  $6^{\circ}12'$  and  $14^{\circ}15'N$ . and  $41^{\circ}36'$  and  $34^{\circ}40'W$ . respectively, namely, in the open ocean averaged 240 mg. per  $m^3$ , minimum 200, which may be a little too high on account of solution of glass in warm weather. They were taken from December 19th to 21st, analysed January 13th. The next four samples vary from 170–110 mg. per  $m^3$ , average 140. They, too, are from the open ocean, the last being east of Madeira. The remaining three were taken (from December 28th to 30th and analysed January 13th) close to the coast of Portugal and in the Bay of Biscay; they showed 100, 120, and 110 mg. per  $m^3$ , results identical on the average with those found off Plymouth on January 12th.

#### SUMMARY.

1. The method of Diéner and Wandenbulcke permits of the estimation of silicate in solution down to the limit of 0.04 mg. of silica per litre, which cannot be distinguished from zero. The phosphate normally present does not interfere with the reaction.

2. All fresh waters examined were found to contain more silicate than does the water of the English Channel.

3. The water of Plymouth Sound is richer in silicate than that of the sea.

4. At Station E1 in the English Channel silicate decreases during spring, from a winter maximum of 200–240 mg. per cubic metre, so that from April to June, 1925, the amount left, recorded as 40 mg. per cubic metre, was indistinguishable from zero. At this time the water was stripped of phosphate also. Silicate increased again till early July, decreased in August and again in November; the times of decrease are suggested as being those of diatom increase.

5. In deep Atlantic water silicate is much more abundant than in the English Channel; values from 360 mg. per cubic metre at 1000 metres to 1200 mg. at 3000 metres were obtained. In winter at any rate the surface value in the Atlantic is similar to that off Plymouth, about 110 mg. per  $m^3$  in 1925.

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**The Vertical Distribution of Marine Macroplankton. II.  
The Pelagic Young of Teleostean Fishes in the Day-  
time in the Plymouth Area, with a Note on the Eggs  
of certain Species.**

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With 5 Figures in the Text and an Appendix.

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## INTRODUCTION.

DURING the years 1924 and 1925 the writer carried out some preliminary researches on the vertical distribution of the pelagic post-larval stages of Teleostean fishes. It has long been known to those who have studied young fish that there is not absolute uniformity in the vertical distribution of the post-larvæ of different species, and that many forms are comparatively rare in the surface layers in the daytime, occurring most abundantly at a depth of a few fathoms. It is only necessary to examine records given by earlier writers to realise this. It is obvious that their vertical distribution is an important factor in the horizontal scattering of young fish, if currents at different depths vary in strength and direction, thus separating the fish in one layer from those in another. It is now well known that an inshore wind will set up a surface current shorewards, causing a heaping up of the water on the windward shore, and a consequent flow of water in the deeper layers in the reverse direction away from the coast; the opposite effect will be produced by an offshore wind. Such currents might play an important part in carrying the young of some species in to the shore or out into deeper water.

It has not been possible for previous workers to state accurately the depth from which collections have been taken; there has in consequence been no detailed study made of the vertical distribution of pelagic young fish. In this case, however, a graphic depth-recording instrument has been used, and we are thus enabled to state with a considerable amount of accuracy the depths at which the net has been fishing. Apart from studying the vertical distribution of the early stages of fish, observations on that of the other planktonic animals present at the time have been made, that is of those forms which compose the food of the small fish or act as their enemies, and may be of direct importance in their distribution. The results will be given in a future paper.

The writer is indebted to Dr. E. J. Allen, F.R.S., and other members of the staff for much helpful criticism and advice, especially to Mr. E. Ford for his assistance in the identification of many specimens; to Captain V. Lord and the crew of s.s. *Salpa* for the co-operation they have given during the somewhat irksome work of collecting at sea.

I should like also to take this opportunity of expressing my gratitude to Dr. R. S. Clark for the invaluable training he gave me from his wide knowledge of the literature and identification of young fishes, when I first took up the study of this subject.

## METHODS OF COLLECTING.

The majority of the samples were taken with a stramin ring-trawl (diameter at mouth, 2 metres; length, 6 metres). From May to July

in 1924 six daylight stations were made, at each of which the net was used at four or five different depths; in 1925, from April to August, sixteen similar stations were made, in these cases the net was almost always used at six different depths at each station. All these stations were in depths of 50 metres or more. The positions of the various stations are given in the Appendix on page 145. In addition, in 1924, a tow-net of silk (40 strands to the inch), with a mouth 1 metre in diameter and a length of 2 metres 60 centimetres, was used close inshore at four stations sampling four or five depths at each; and also at one station working at six depths in 1925. On the last two occasions on which this net was used it was employed as a closing net towed horizontally: the releasing apparatus used is described in a previous paper (20), and closing took place without fail at every depth. The net was fitted with a folding mouth, as figured by Schmidt (23).

In 1925 a small "medium" silk (50 strands to the inch) tow-net was also used in conjunction with the ring-trawl; this was attached to the warp just above its junction with the bridles of the net. The diameter of the net mouth was 29 cm., and the length of the net 95 cm. The ring at the mouth was made of wood to allow the net always to float clear of the bridles of the large ring-trawl. By this means a sample of the plankton was taken from the same body of water as that from which the young fish were captured; owing to the size of the mesh this collection should give a comparative picture of the vertical distribution of many of the copepods, which form the chief items of food for the young fish.

On every occasion, both with the ring-trawl and the metre net, the depth-recording instrument was used.

The nets were towed horizontally at a speed of about  $1\frac{1}{2}$  to 2 knots: attempts were made to keep this speed as constant as possible. The duration of all hauls from the time at which the required length of wire was out until hauling in began was *ten minutes*. A total of 126 hauls was made with the ring-trawl and 24 with the metre net. Fifty-one hauls were also taken with the ring-trawl between sunset and sunrise on July 15th to 16th, 1924, and June 16th to 19th, 1925, in order to examine the diurnal movements of the young fish: the results of this collection will be given in a future paper. (The observations on macroplankton on July 15th to 16th, 1924, are already published (19).)

All material was preserved in formalin immediately on capture.

#### THE FISHING DEPTHS.

With the help of the depth-recording instrument, kindly lent by Admiralty authorities, the actual path of the net through the water is known in almost every case. Owing to the wavy course that the net very often follows throughout the period of haul it is at times impossible



to state actually that the water level at one depth was sampled. A figure has been found called the "average depth" by taking the depth at ten or more equidistant points along the curve and finding the mean; far more than ten should be taken for greater accuracy, this, however, is not

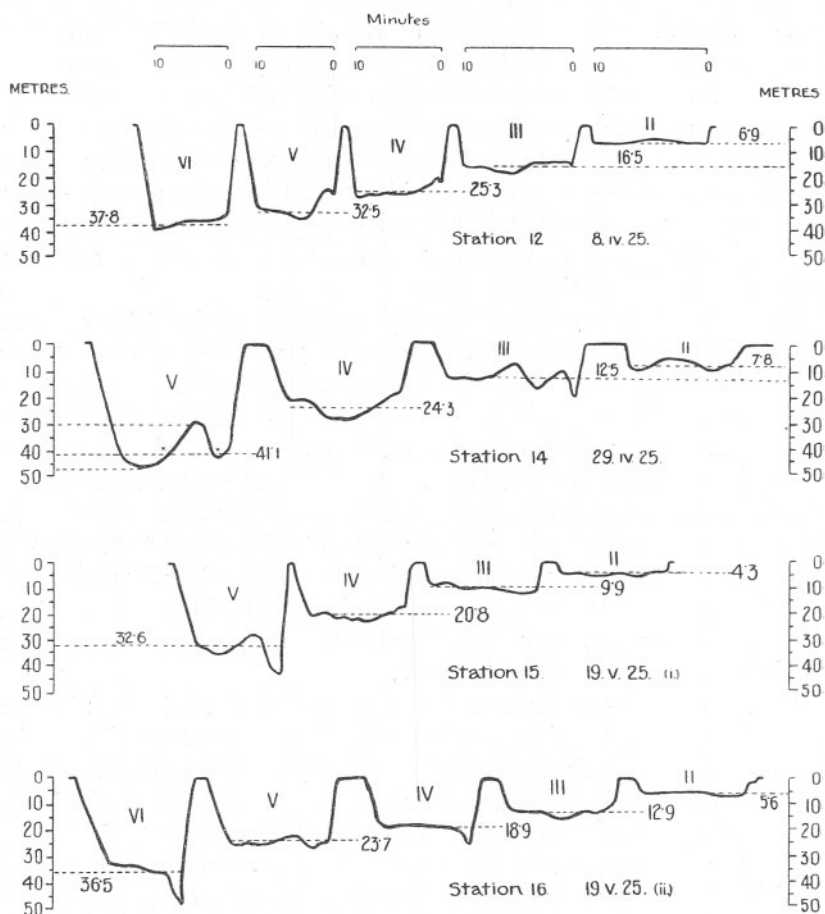


FIG. 1.—Four series of curves obtained on the dates given showing the path of the net through the water for each haul. (The surface haul is not included.) The net enters the water on the right-hand side of each curve. The dotted lines indicate the calculated "average depth." (The differences in the lengths of the curves are due to irregularities in the speed of the recorder clock and not to errors in timing.)

required, as it must be borne in mind that the net itself has a diameter at the mouth of 2 metres. In all tables and text figures these "average depths" have been used; at the same time in the Appendix (p. 146), under the list of stations, I give the outside limits of the depths at which the net has fished in each case. Fig. 1 shows four tracings of the curves

produced by the depth-recorder on the dates indicated: they are a fair sample of the results obtained by the depth-recorder throughout, showing how on one occasion the net fishes fairly constantly at one depth and on another it may rise and sink considerably throughout the ten minutes' haul. Also it can be seen that whereas the "average depth" in many cases is a sufficient approximation to the depth at which the net was fishing, at other times it is in a way a misstatement. For instance, in haul V on April 29th, 1925, the "average depth" is 41.1 m.; in reality the net fished at this level twice for a fraction of a minute only, i.e. at the points indicated where the line 41.1 m. cuts the curve, wandering for the rest of the time up and down between 30 and 47 metres. The tracings for four other stations have been already published. (Stations 4 and 8 (21); 9 and 10 (19).)

During all surface hauls the net was kept so that the top edge of the ring was just cutting the surface of the water.

#### EXAMINATION OF MATERIAL.

After measuring the total volume of each catch by allowing to settle for twenty-four hours in a graduated jar, all the young fish were picked out singly and all species measured to the nearest half millimetre, except *Callionymus* sp., and *Gobius* sp., which were so numerous that it was thought sufficient to measure a few samples only. The remainder of the plankton was then dealt with, the larger organisms being picked out singly, and the rest sampled in the manner described in a previous paper (19). In addition the material collected by the small tow-net attached to the ring-trawl remains to be worked up. It is hoped that with this material, which includes the post-larval fish and the majority of species of copepods that form their food, as well as the larger plankton organisms, some of which are known to prey on the young fish themselves, a general picture may be obtained of the density of these members of the plankton population in relation with one another. These results will be published in a future paper.

#### GENERAL RESULTS.

In considering the results shown in the second half of this report one realises that it has many shortcomings, not the least important of which is the paucity of observations. This is necessarily controlled by the limited amount of material that it is possible for a single worker to examine in a given time. It is, however, regrettable that more observations were not obtained in the month of May, at which time most of the more important food-fish post-larvæ are present in the plankton in greatest abundance; bad weather conditions were responsible.

In order to obtain a true picture of the vertical distribution of young fish regular daily collecting over a considerable area is a necessity. With such observations one should be able better to discern the changes that probably occur at different times of the season and in the various states of the weather and sea. On this account no attempt has been made to trace the effect of weather conditions in this paper: such factors will be considered at a later date, when many more observations are available.

Under the present circumstances the writer does not feel that it is safe to make generalisations. It is, though, fairly evident that during the months, May to August, under the sea and weather conditions existing at the time these collections were made, the post-larval stages of many species of fish were rarely taken in daylight in the water layers between the surface and a depth of 10 metres.\* In the first half of April, however, there were indications that some species, found in the deeper layers in the later months, may frequent higher levels and even the surface at this time. Possibilities of errors arising from irregularities in horizontal distribution must be taken into consideration, in view of this no attempt has been made to locate a depth at which a maximum abundance may be expected for any one species, if, indeed, such exists. I have merely given the depth above which the numbers of fish taken, if any, were low and below which the young fish were abundant. When more observations have been made it may be possible to give evidence on this point, but after results shown by Gardiner and Graham (9), who have recently examined the irregularity in distribution as shown by the Petersen Young Fish Trawl, a net made of the same material as the ring-trawl and probably with a somewhat similar fishing capacity, this is not yet practicable. These workers conclude from the results of ten successive oblique hauls during daylight "that the standard deviation (expressed as a percentage of the mean) varies from  $\pm 27$  to  $\pm 54$  per cent. That of the Cod larvæ of 8 mm. length is  $\pm 38\%$ ;" and that this variation is "due either to the irregularity of the horizontal distribution of the plankton or to the error of the net."

\* Since going to press an interesting paper has reached us by Dr. A. C. Johansen "On the Diurnal Vertical Movements of Young of Some Fishes in Danish Waters": Meddelelser fra Kommissionen for Havundersogelser, Serie Fiskeri. Bind VII, Nr. 2, 1925. In it Dr. Johansen compares results of day and night collections with the ring-trawl at the surface and an intermediate layer. He remarks that the results suggest "that the majority of the larvæ kept down below the 16 metres level during the day." He also discusses the question of young fish avoiding the net in the daytime and comes to the following conclusion: "With regard to fishing experiments with the ring-trawl . . . it may be doubtful whether any conclusions can be drawn from these as to diurnal vertical migrations on the part of large, rapidly moving larvæ; it seems justified, however, in the case of the tiny larvæ." Seeing that throughout the paper the term "larvæ" has obviously been used to include "post-larvæ," this last statement seems confirmed by my results, which show that post-larvæ actually living at the surface, such as those of *Gadus pollachius* and *Onos* sp., are captured by the ring-trawl, indicating that species which only occurred in collections from deeper layers were really absent or very scarce at the surface.

There appear to be specific differences in the vertical distribution of the post-larvæ of the various kinds of fish dealt with. The following types of distribution were indicated by the post-larvæ of the species mentioned, in offshore waters of 50 or more metres depth, at the seasons at which they were common in the plankton, in daylight :—

1. Occurring mostly at surface and in layers immediately beneath the surface. *Gadus pollachius*.

2. Occurring at all depths with at times a preference for the surface layers. *Onos* sp.

3. Distributed apparently indiscriminately from surface to bottom, sometimes showing a preference for deeper layers, at other times most abundant at small depths.

*Clupea* sp. (*Clupea sprattus* and *Sardina pilchardus*); *Ammodytes lanceolatus*; *Gadus merlangus* (in early April).

4. Present at any depth with usually a maximum abundance between the surface and 25 metres.

*Scomber scomber*; *Trachinus vipera*; *Blennius gattorugine*, *Blennius pholis* and *Blennius ocellaris*; Labridæ; *Caranx trachurus*.

5. Abundant from a depth of about 10 metres downwards.

*Gobius* sp.

6. Abundant from a depth of about 15 metres downwards.

*Scophthalmus norvegicus*; *Trigla* sp.; *Callionymus* sp.

7. Abundant from a depth of about 20 metres downwards.

*Pleuronectes limanda*; *Pleuronectes microcephalus*; *Solea variegata*; *Molva molva*.

8. Abundant from a depth of about 25 metres downwards.

*Gadus minutus*.

9. Living below a depth of 30 metres and very near the bottom.

*Liparis montagui*; *Lepadogaster bimaculatus*.

10. Showing a gradual descent with advance of season.

*Gadus merlangus*.

The depths given in the above scheme must not be taken as fixed: they, no doubt, change to a certain extent from day to day. The important feature is that different forms begin to become abundant at different depths. I feel that this conclusion should be regarded as rather tentative to be confirmed or disproved by further evidence. These types of distribution have, however, shown repetition on occasions on which the young fish were sufficiently abundant to indicate definite preferences for different depths.

The differences in the vertical distribution of *Gadus pollachius*, *G. merlangus*, *G. minutus*, and *Onos* sp. are striking. In this case it is interesting to bear in mind the somewhat different abodes haunted by the adolescent stages. The *Onos* sp. probably collected in this case are

definitely inshore fish, and the young of the Pollack frequent the shore line; the post-larvæ of both these species occur commonly at the surface; at the time of the year that they are present in the plankton the prevalent winds are inshore, driving the surface layers towards the coast. Whether similar conditions would hold good elsewhere I do not know.

As with the rest of the plankton (19, p. 770) the post-larvæ of many species of fish become abundant at much smaller depths below the surface close inshore over shallow water than they do a few miles from the coast over depths of 50 m. or more.

That in the study of the horizontal distribution of the pelagic stages of young fish a very thorough sampling of the water from bottom to surface is necessary is a point much emphasised by the results of this research. If, for instance, we were to study the horizontal distribution of *Gadus minutus* post-larvæ over a region with an average depth of 50 metres, surface and midwater hauls might indicate an almost complete absence of this species, seeing that they are rarely found above the 20-metre level. An oblique haul is very necessary, and in depths of ca. 50 m. ten or more levels should be fished: the net should go well to the bottom, and in a haul of thirty-minutes' duration the wire should be wound in a tenth of its original length every three minutes.

The very great quantities of the post-larvæ of *Callionymus* sp. is, as usual, a prominent feature of these collections. Of the total of 21,058 young fish dealt with in this paper 8743 were *Callionymus* sp. Next in importance are the young *Gobius* sp. with a total of 3562, practically all of which were caught in 1924. The figures show an amazing absence of young Gobies during the months dealt with in 1925. In 1924, 3232 young Gobies were captured, and the total number of hauls taken was 44, while in 1925 only 330 were caught in more than twice as many hauls, 98 in all.

The number of the more important fish caught were:—

- Clupea* sp., 1407.
- Gadus merlangus*, 1004.
- Scophthalmus norvegicus*, 954.
- Solea variegata*, 891.
- Ammodytes lanceolatus*, 741.
- Gadus minutus*, 628.
- Trigla* sp., 545.
- Pleuronectes limanda*, 508.
- Pleuronectes microcephalus*, 425.
- Labrid sp., 417.

The Labridæ also showed a marked scarcity, like the Gobies, in 1925; while 359 were taken in 1924, in 1925 there were only 58.

The two stations taken on May 19th, 1925, are of interest: at Station 15

there were four species whose post-larvæ were present at the surface, which were absent at the surface at Station 16, *Gadus merlangus*, *Scophthalmus norvegicus*, *Solea variegata*, and *Callionymus* sp. (see Appendix, p. 155); at Station 15 there was a very large swarm of *Corystes megalopas* at the surface, the numbers being 4050, 3970, 2110, 153, and 1214, from surface to bottom at the five depths; at Station 16, however, they were very scarce, the numbers being respectively 34, 8, 5, 25, 59, and 430.

Little discussion on the possible causes of the various types of vertical distribution is given; the evidence is too small as yet for such considerations to be fruitful: it is considered sufficient at present to try to find out exactly what does actually occur in the sea, and to collect as much information on the conditions as possible. Although on one or two occasions temperatures and chemical conditions are available from different depths, these have not been included in this paper; however, it is to be hoped that in time sufficient observations may be forthcoming to make possible an attempt to throw light on causes that may influence the vertical distribution of the post-larvæ, and bring about the changes that occur in it from time to time.

#### OBSERVATIONS ON SEASONAL DISTRIBUTION.

In Table 1 I have drawn up figures to attempt to show the seasonal distribution for the more important species during the years 1924 and 1925. In order to obtain the average catch per ten minutes' haul at each station I have only included those hauls which occurred below the depth above which each species was scarce in the daytime, that is, as near as possible in the layers in which they were most abundant.\* I have only included the catches made with the ring-trawl, and these should be fairly comparable.

It is at once evident that there is a distinct difference in the seasonal distribution of some of the spring spawning species between the two years. In the table are printed in heavy type all average hauls of ten or more individuals per ten minutes. It will be seen that, while the post-larvæ of *Gadus merlangus*, as shown by the collections, were abundant well into June in both years (in 1924 on June 25th and in 1925 on the 17th), *Gadus minutus*, *Scophthalmus norvegicus*, *Pleuronectes limanda*, *Pleuronectes microcephalus*, and *Solea variegata* all appeared to be suddenly cut short in their seasonal distribution in 1925, at some time about the end of May or beginning of June, whereas in 1924 all these species were abundant up to the end of June and *S. norvegicus* even into the middle of July.

It is extremely unfortunate that there are no accurate observations on the earlier dates from April to May in 1924. I have included, however, at the end of the Appendix (Table 10, p. 159) a list of young fish

\* In most cases this was taken as 5 m. above the depths given on p. 107 to allow a safe margin.

TABLE I.

SHOWING THE AVERAGE NUMBER OF SOME OF THE MORE IMPORTANT YOUNG FISH FOR TEN-MINUTE HAULS, COMPUTED IN EACH CASE FROM COLLECTIONS TAKEN BELOW THE DEPTH ABOVE WHICH EACH SPECIES IS SCARCE IN DAYLIGHT.\*

	Depths in metres from below which these figures are estimated.	April.				May.			June.					July.					Aug.			
		2	8	22	29	19 (i.)	19 (ii.)	29	4 (i.)	4 (ii.)	17	18	19	25	1 (i.)	1 (ii.)	15	16	29	6		
<i>Gadus merlangus</i>	15	{ 1924 1925	8.2	4.5	2.2	36	21.5	74.6	37	17	19.5	21.7	—	7.5	52	3.6 4.3	5	—	—	0.7	0.6	—
<i>Gadus minutus</i>	20	{ 1924 1925	11.5	10.3	23	84	35	50.5	32	12	4	—	—	—	16	3.5	—	—	—	—	—	
<i>Scophthalmus norvegicus</i>	10	{ 1924 1925	—	—	0.25	31.3	84	40	15	5.7	19.6	65.6 2	1	4	9	4.6 0.7	4	16	8 0.7	—	—	
<i>Pleuronectes limanda</i>	15	{ 1924 1925	4.3	6.2	3.2	43	36.5	62.3	20	4.7	4	2.5 0.25	1	1.5	10.5	1.6 0.6	0.6	—	—	—	—	
<i>Pleuronectes microcephalus</i>	15	{ 1924 1925	0.3	0.25	0.5	10	17	16.3	21	3	8	63 0.5	—	2.5	14	3	1	4	3 0.7	0.3	—	
<i>Solea variegata</i>	15	{ 1924 1925	—	—	—	24.5	105.5	46.3	18	2.7	7.5	45.5 3.2	1	3	70.5	1.6 1	0.6	3.5	7 0.25	—	—	
<i>Ammodytes lanceolatus</i>	0	{ 1924 1925	3.1	1.5	—	5.6	6.2	18.6	4	5.3	6	9.2 1.1	—	0.1	5.2	3.4 3	5.8	13	18.8 5.3	11	1.6	
<i>Callionymus</i> sp.	10	{ 1924 1925	3	4.7	9.7	83	308.5	248.2	170	159.5	125.3	148 30.2	22	10.2	490	73.6 57.2	62.3	39.3	42.6 42.7	8	1.7	
<i>Gobius</i> sp.	10	{ 1924 1925	—	—	—	—	0.25	3.5	9	2.6	157 0.25	0.5	1.7	123.6	50 0.7	19	78.6	14.8 9	2	5.7		

\* A dash (—) signifies that although a station was made no post-larvæ of that species were captured at any depth.

taken during this period by the ring-trawl without the depth-recorder: these figures show that the species concerned were fairly abundant as early as they were in 1925, especially is this so if we consider that most probably the "bottom" hauls are not far below the midwater line, and hence that the region of greatest abundance for most of the species has not been thoroughly sampled.

It is natural in considering these results to turn to the temperature observations made in these months. I give below the temperatures existing at the hydrographical Station E1, ten miles beyond the Eddystone Lighthouse, at depths of 10 m. and near the bottom (72 m.). These figures were taken from the *Rapport Atlantique*, 1924 (7), for the year 1924, and I am indebted to Mr. H. W. Harvey for the 1925 observations; the degrees are centigrade.

1924.	E1. 10 m.	Nr. Bottom.	1925.	E1. 10 m.	Nr. Bottom.
Jan. 2nd	9.50°	9.51°	Jan. 19th	10.79°	10.79°
Feb. 15th	8.67°	8.76°	Feb. 17th	10.01°	10.01°
(Mar. 10th	7.90°	7.88°)*	Mar. 14th	9.19°	9.16°
April 8th	8.15°	8.30°	April 22nd	9.47°	9.44°
May 20th	10.84°	9.55°	May 13th	10.3°	9.95°
June 17th	13.89°	10.32°	June 3rd	10.92°	10°

In January, February, March, and April the temperatures in 1924 were considerably lower than in 1925. A curve of the temperature at E1 has been given by Harvey (10), that shows that this year was also considerably lower than the two preceding years, 1922 and 1923.

There appear to be two possibilities:—

1. That in 1924 there was a prolonged spawning season, owing to the long period of low temperature as compared with 1925, when the cold period was extremely short (March), and hence the extended appearance of post-larvæ in the plankton until the end of June in 1924.

2. A later spawning in 1924, due to the water reaching some optimum temperature above the lowest some time later than in 1925.

There is insufficient evidence to argue either way except that as noted above the young fish did not appear, from inaccurately collected samples, to be absent in the hauls in April and May, 1924, at which time they were fairly abundant in 1925; this would point to an extended spawning season in 1924.

I have thought it worth while, however, to draw attention to this point, and record it as a possible guide to elucidating the results obtained in future years.

One other interesting feature is emphasised by these figures: this is the almost complete absence of the young of the various species of *Gobius*

\* Taken at L6, five miles beyond the Eddystone Lighthouse.



(see p. 108) from the 1925 collections. It seems impossible that they could have been missed by the net on so many occasions if they had been present. These with *Callionymus* are always extremely abundant in the ring-trawl collections. Their absence this year is unaccountable, unless spawning for most species took place in August, and is of importance as the young Gobies form an important part of the food of many fish (5). The post-larval Wrasses were also markedly scarce in 1925.

The year 1924 was marked by an unusual abundance of the post-larvæ of *Molva molva* and of *Lophius piscatorius*.

In the following pages the distribution of each species is dealt with in detail. In order to economise in space the actual numbers of the different species taken at each station have been placed together in the Appendix, Tables 3-10; at the end of the paper (pp. 152-158).

### CLUPEIDÆ.

#### CLUPEA SP.

Specimens of young clupeids, 6-20 mm. in length, which consist of a mixture of both *Clupea sprattus* L. and *Sardina pilchardus* (Walb) occurred fairly frequently in my collections. Figures show that they seemed to be somewhat indiscriminately distributed from surface to bottom with perhaps a tendency to avoid the actual surface layer in the hotter months, as shown by the 1925 results. In 1924, however, when they were more numerous, they were also present on the surface in May, June, and July, and showed a tendency to be most abundant between 5 and 25 m. (Fig. 4, p. 128).

A comparison with figures given by Wallace (24) for post-larvæ of *Clupea harengus*, the Herring, shows that for this species also from the months September to April they were distributed irregularly among the surface, midwater, and bottom hauls: the time of day, however, is not given.

A station taken with the metre closing net is worthy of mention here, as at it were captured many very early stages of *Clupea sprattus*, 6-10 mm. in length. Although no depth-recorder was used it can be seen from the figures that there was a definite congregation of these young stages a little below the actual surface.

#### 12.iii.24. C.M.N. Bigbury Bay.

Surface (estimated depth).	Number of young sprat	4
Upper layers, ca. 7 m.	„ „ „	63
Midwater, ca. 13 m.	„ „ „	23
Bottom layers, ca. 19 m.	„ „ „	13
Bottom, ca. 25 m.	„ „ „	13

There is a possibility of this distribution being due to mechanical action of the water movement as the distribution of *Onos* sp. eggs given on page 139 is almost similar.

#### GADIDÆ.

The species of this genus whose pelagic young occur in the Plymouth region are *G. merlangus*, *G. minutus*, *G. pollachius*, *G. luscus*, *Molva molva*, *Merluccius merluccius*, *Raniceps raninus*, *Onos mustelus* and probably *O. cimbrius*, and *O. tricirratus*.

Of these *Merluccius merluccius*, *Raniceps raninus*, and *Gadus luscus* only occurred very rarely in my collections, and insufficient evidence is forthcoming as to their vertical distribution.

Results, however, have shown that there were striking differences in depths at which the post-larvæ of the remaining species occurred in greatest abundance.

*G. pollachius*, the Pollack, preferred the surface and layers immediately below the surface.

*G. minutus*, the Poor Cod, was always found in the deep layers below 20 and 25 metres, increasing in numbers thence towards the bottom.

*Onos* sp., the Rockling, occurred at all depths with perhaps a partiality for the surface layers.

*G. merlangus*, the Whiting, showed a gradual change in its vertical distribution as the season advanced. While in early April it was present, like *Onos*, at all depths, as the year advanced it deserted the surface layers, gradually going deeper until in June the majority were below 24 metres. However, when the Whiting sought the deeper layers the depth at which they became abundant was nearly always higher in the water than that of *G. minutus* (Fig. 2 and Table 2).

#### GADUS MERLANGUS L.

Post-larval Whiting occurred at twelve stations (sixty-seven hauls) in sufficient numbers to bring evidence on their vertical distribution. Collections made with the ring-trawl between April 2nd and June 17th, 1925, showed a marked seasonal change in the depth at which this species was most abundant: at the same time there was a gradual desertion of the surface water layers, as the season advanced.

This is best illustrated by Fig. 2 (p. 118), which shows the curves of percentage distribution at the different depths. If we now look for the points

TABLE 2.\*

	1924 May 29th	June 5th†	June 17th‡	June 21st†	June 25th	1925 April 2nd	April 8th	April 22nd‡	April 29th	May 19th (i)	May 19th (ii)	June 4th (i)	June 4th (ii)	June 17th
(a) GADUS MERLANGUS.														
Between 0 and 5 m.	-	-	-	{	-	13	4	{	-	{	-	-	{	{
" 5 " 10 "		1		10		8	10		2	3	1		1	
" 10 " 15 "	5	23	-	8	3	2	3	1	15		47	1	4	
" 15 " 20 "						3	3				124	9		3
" 20 " 25 "	37	16						2	40	17	85		25	7
" 25 " 30 "			8			{	8					21		44
" 30 " 35 "		8				15	8							
" 35 " 40 "							2			26			14	
" 40 " 45 "							5				15	21		
" 45 " 50 "					69				32					33
" 50 " 55 "					35									
" 55 " 60 "			4					3						
" 60 " 65 "								3						
" 65 " 70 "														
(b) GADUS MINUTUS.														
Between 0 and 5 m.	-	-	-	{	-	-	-	{	-	{	-	-	{	{
" 5 " 10 "				-					1					
" 10 " 15 "	2				1						2			
" 15 " 20 "							1				12			
" 20 " 25 "	32								81	4	43			
" 25 " 30 "			7			{	4							
" 30 " 35 "						19	3					7		
" 35 " 40 "							13			66			8	
" 40 " 45 "							15				58	29		
" 45 " 50 "									87					
" 50 " 55 "					16									
" 55 " 60 "			23		16			36						
" 60 " 65 "								33						
" 65 " 70 "														
(c) GADUS POLLACHIUS.														
Between 0 and 5 m.	-	-	-	{	-	7	-	{	-	8	{	-	-	{
" 5 " 10 "				-		4	10		13					
" 10 " 15 "									5				1	
" 15 " 20 "							4							
" 20 " 25 "									5					
" 25 " 30 "						{	1							
" 30 " 35 "						-								
" 35 " 40 "														
" 40 " 45 "														
" 45 " 50 "														
" 50 " 55 "								1						
" 55 " 60 "														
" 60 " 65 "														
" 65 " 70 "														

\* A dash (-) signifies that none of that species were taken at the depth given.

† These two stations were taken close inshore. ‡ Bottom at depth of 72 metres.

TABLE 2.\*—continued.

	1924 May 29th	June 5th †	June 17th †	June 21st †	June 25th	1925 April 2nd	April 8th	April 22nd †	April 29th	May 19th (i)	May 19th (ii)	June 4th (i)	June 4th (ii)	June 17th
(d) ONOS SP.														
Between 0 and 5 m.	11	-	14	{ 3	-	11	5	{ 14 22	{ 12	5	2	{ -	{ -	
" 5 " 10 "		11		-		4	11	{ 8 11	{ -	-	-	{ -	{ -	
" 10 " 15 "	1	-	7	-	1	1		2 18	-	-	-	-	-	
" 15 " 20 "						1	8							
" 20 " 25 "	3	6				1		7 17	1	5	3	-	-	
" 25 " 30 "			25			{ 1 4	6			2		2		-
" 30 " 35 "														
" 35 " 40 "							2			2			1	
" 40 " 45 "							5				3			
" 45 " 50 "									4					
" 50 " 55 "						1								
" 55 " 60 "			12			2								
" 60 " 65 "								2						
" 65 " 70 "														

on these curves at which the percentage first reaches ten below the surface we find that they occur at the following depths :—

April 2nd	Surface.	Dull and overcast.
" 8th	"	Bright sunshine.
" 29th	10·5 m.	" "
May 19th (i)	10·5 m.	Sunshine.
" 19th (ii)	10·5 m.	Dull and overcast.
June 4th (i)	18·5 m.	Bright sunshine.
" 4th (ii)	14·5 m.	" "
" 17th	24 m.	" "

Thus we see that the period between the beginning of April and mid-June was marked by a gradual descent of the region at which the young Whiting started to increase markedly in abundance.

There may be many causes which bring this about, the most important of which might perhaps be found among the five given below :—

1. Increase in light intensity.
2. Seeking of deeper layers as growth proceeds.
3. Association with *Cyanea*.
4. Descent of organisms, e.g. copepods which form chief food.
5. Rise in temperature of surface layers.

\* A dash (-) signifies that none of that species were taken at the depth given.

† These two stations were taken close inshore. ‡ Bottom at depth of 72 metres.

1. Increase in light intensity is possibly the fundamental factor, and this presumably also controls the distribution of the food and of *Cyanea*.

2. I have closely examined the lengths of all the young Whiting and I can find no evidence that there is necessarily any descent with age. The numbers of Whiting of different lengths found at the depths shown, on April 2nd, 29th, and May 19th, were as follows. It can be seen that

	Depth in metres.	Length in mm.													
		4	5	6	7	8	9	10	11	12	13	14	15	16	17
2.iv.25	S	-	1	2	2	3	4	1	-	-	-	-	-	-	-
	5	-	2	2	4	-	-	-	-	-	-	-	-	-	-
	12.5	-	-	1	1	-	-	-	-	-	-	-	-	-	-
	19	-	-	1	1	1	-	-	-	-	-	-	-	-	-
	27	3	-	1	-	1	2	1	-	-	-	-	-	-	-
	29	2	3	6	1	2	1	-	-	-	-	-	-	-	-
29.iv.25	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	7.8	-	-	1	1	-	-	-	-	-	-	-	-	-	-
	12.5	-	7	2	5	1	-	-	-	-	-	-	-	-	-
	24.3	-	3	13	10	6	3	4	1	-	-	-	-	-	-
	41.1	-	4	4	14	6	3	-	1	-	-	-	-	-	-
19.v.25 (ii)	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	5.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	12.9	-	3	5	5	7	9	2	6	2	5	1	1	-	1
	18.9	-	3	12	14	19	19	24	14	6	2	5	2	3	1
	23.7	-	2	9	23	20	6	9	8	3	3	-	1	1	-
	36.5	-	-	1	4	4	2	2	2	-	-	-	-	-	-

in this case specimens of all sizes were found from 5 mm. to 14 mm. at each depth, if anything there is evidence that the younger forms lie deeper than those slightly larger, the mode at 18.9 metres being 10 mm. and that at 23.7 m. 7 mm. on May 19th, 1925. Results show that whereas there is a slight average increase in size from April to June very small post-larvæ are still present in June, and do not show any difference in distribution from larger specimens.

3. *Cyanea capillata* only appeared in three hauls out of the sixty-seven, the three specimens being all between  $\frac{1}{2}$  in. and 2 in. in diameter. It is doubtful whether these were of a large enough size to afford shelter to the number of Whiting taken. They occurred at 18.9 metres on May 19th, when a specimen of less than 2 in. diameter was present with 124 young Whiting, and on June 17th, one of  $\frac{1}{2}$  in. diameter at 23.4 m. and 2 in. diameter at 29.8 m., both too small to afford protection for 7 and 44 fish respectively.

Damas (6) was convinced that on the Norwegian coast *Cyanea* plays an extremely important part in the distribution of young Whiting, and

that the vertical distribution of these small fish is more or less controlled by that of the jellyfish. When the *Cyanea* migrates to the surface at night the Whiting follow them, and they descend together again the next day. However, Damas says that it is after the fish has almost completely metamorphosed, with a length of 23 mm., that this association begins. None of my post-larvæ had attained this length, in fact the majority were under 12 mm. in length, so that I think it is fairly safe to conclude that the distribution of these stages was not controlled by association with *Cyanea*. Additional evidence is given by the fact that *Cyanea* does not become very abundant in this area until late July and August: it is at the end of June that the Whiting becomes absent from my hauls, probably indicating the new period in their life-history, as at this time if a *Cyanea* is captured there are many Whiting of 30–50 mm. long present with it.

4. Catches of the food of the young fish were made at each depth by the use of a small medium silk tow-net fixed just above the junction of the warp and bridles of the ring-trawl. Thus these samples were taken from the same body of water as the young fish themselves.

These collections have not yet been worked out, but it is hoped at a later date to compare the vertical distribution of the copepods and that of the young fish.

5. From May to September a warm surface layer usually exists in the waters of the English Channel.

The months, however, that concern us at the moment are April, May, and June. I am indebted to Mr. H. W. Harvey for the following temperatures at L4 during these months for 1925:—

April 22nd	Surface	9.7° C.
	40 m.	9.31° C.
May 13th	Surface	10.4° C.
	40 m.	9.81° C.
June 3rd	Surface	12.4° C.
	40 m.	10° C.

Whereas in April the difference in the temperature of the surface from that at the bottom was 0.4° C., in May it was 0.6° C., and in June 2.4° C. The differences in the first two months are too slight to be likely to influence the distribution of the young fish. In June, however, a difference of 2.4° might be considered of importance.

Damas (6, p. 55) says that in the North Sea young Whiting were only present at temperatures above 10° C., and that this isotherm serves as a lower limit for their vertical distribution. In this case it would seem unlikely that a temperature of 12.4° C. would be avoided. A stronger argument against raised temperature being a factor is that in mid-

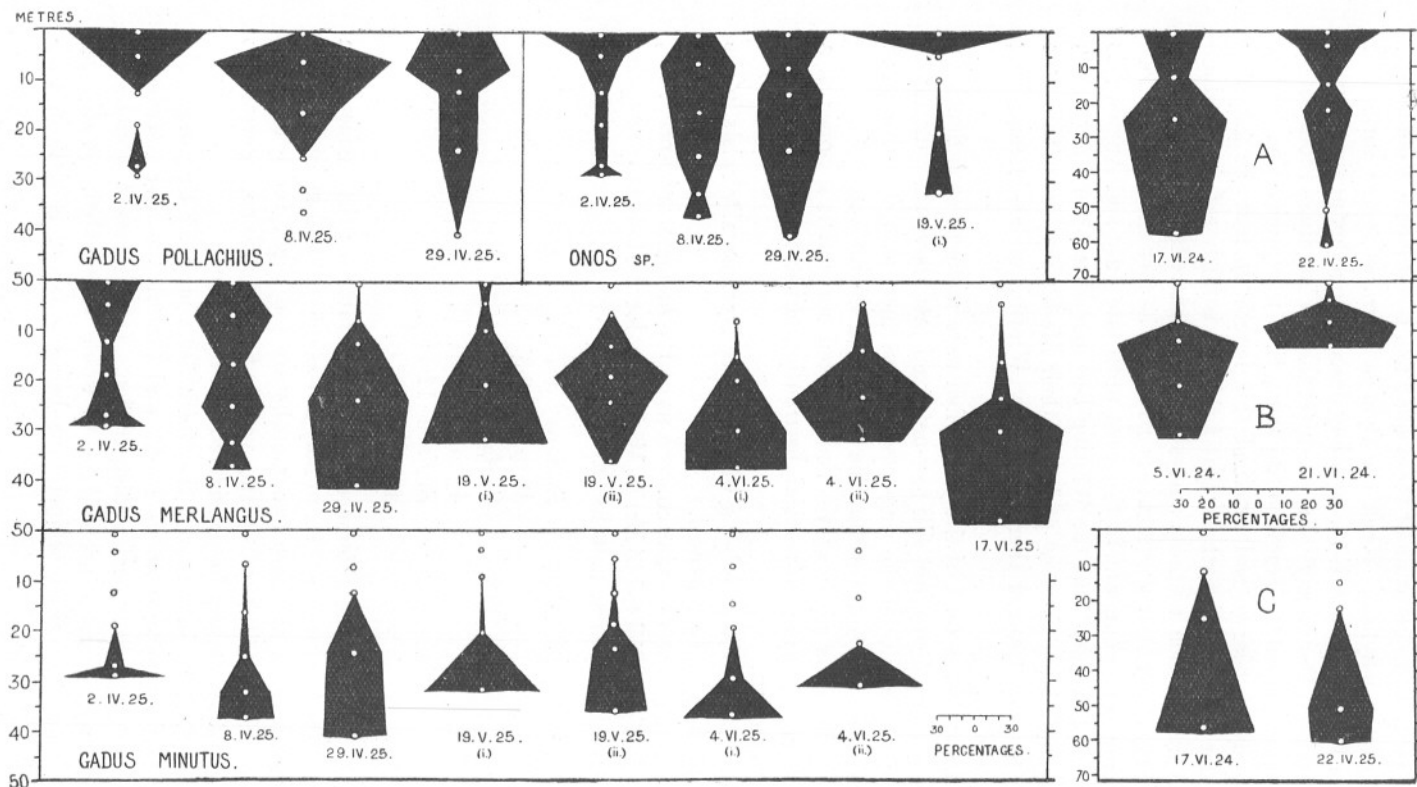


FIG. 2.—Shows percentage vertical distribution of *Gadus pollachius*, *Onos* sp., *Gadus merlangus* and *Gadus minutus* at stations of 50 m. or more depth. A, *Onos* sp., and C, *Gadus minutus* at El. B, *Gadus merlangus* at two close inshore stations.

NOTE. The percentage scale, as marked, for *G. minutus* is half that used for the remaining species. The white spots and black circles indicate the "average depth" at which the hauls were taken.

June Whiting were present in the surface layers in the hours between dusk and dawn.

Whether the higher temperature may set up a state of negative phototropism in the young Whiting is worthy of consideration. On this point there is no experimental evidence.

Two stations taken in shallower water within two miles of the coast show that the Whiting increase in abundance at a smaller depth than farther offshore in the corresponding month: they were both taken in June, and the depths at which increase occurred were about 7 to 10 metres as against 18.5, 14.5, and 24 m. farther out (Fig. 2, B). This is in agreement with the general vertical distribution of most of the larger plankton organisms (*vide* 19, p. 770).

#### GADUS MINUTUS (O. F. Müll).

Post-larval stages of the Poor Cod were present at ten stations (fifty-seven hauls) in sufficient numbers to show their vertical distribution.

It is at once obvious that *G. minutus* differs from the other species of Gadidæ recorded in that the post-larval stages occupy a position normally much deeper in the water in the daytime.

Fig. 2 shows the percentage distribution at different depths. If as in the case of the Whiting we note the depths at which the value 10% first occurs below the surface we find in 1925—

April 2nd	26 metres.	Dull and overcast.
„ 8th	25.5 „	Bright sunshine.
„ 29th	16.5 „	„ „
May 19th (i)	21 „	„ „
„ 19th (ii)	19 „	Dull and overcast.
June 4th (i)	26.5 „	Bright sunshine.

We see from these figures that from April to June the small Poor Cod were always deep in the water in striking contrast to the seasonal changes in depth exhibited by the small Whiting. And further if the above figures be compared with those for the Whiting we see that even when this form has deserted the surface layers, *G. minutus* is considerably deeper in the water.

The majority of post-larvæ caught were between 5 and 10 mm. in length, and there is no evidence of any differentiation in the distribution of the various sizes within these lengths; for those above 10 mm., however, there is an indication that they live deeper down. I give



below the sizes at the two stations at which the post-larvæ were most numerous :

	Depth in metres.	Length in mm.													
		4	5	6	7	8	9	10	11	12	13	14	15	16	
29.iv.25	S	-	-	-	-	-	-	-	-	-	-	-	-	-	
	7.8	-	-	1	-	-	-	-	-	-	-	-	-	-	
	12.5	-	-	-	-	-	-	-	-	-	-	-	-	-	
	24.3	2	13	28	22	13	2	-	1	-	-	-	-	-	
	41.1	-	11	31	32	9	2	1	-	-	1	-	-	-	
19.v.25 (ii)	S	-	-	-	-	-	-	-	-	-	-	-	-	-	
	5.6	-	-	-	-	-	-	-	-	-	-	-	-	-	
	12.9	-	1	1	-	-	-	-	-	-	-	-	-	-	
	18.9	-	5	2	4	-	-	1	-	-	-	-	-	-	
	23.7	-	4	6	10	8	6	7	1	1	-	-	-	-	
	36.5	-	3	8	8	12	11	7	3	1	3	1	-	1	

Of this species Schmidt (22, p. 71) says : " With regard to the depths under the surface in which the pelagic fry of *Gadus minutus* live, our tables show distinctly that but few or none are found close under the surface, but that the numbers increase with the depth."

As regards the vertical distribution of this form in close inshore waters, as shown by the metre-net, it is worthy of note that it hardly ever occurred, possibly showing that it keeps to the deeper water.

Two stations taken at the hydrographical Station E1, twenty miles from land, showed that here the young Poor Cod hugged the bottom layers.

#### GADUS POLLACHIUS L.

At only three stations (seventeen hauls) were the post-larvæ of this species abundant, and then the numbers were comparatively small.

From these observations, however, it is fairly evident that young Pollack, from 4.5 to 10 mm. in length, showed a preference for the surface layers, and regions immediately below the surface (Fig. 2).

Further evidence is available from three stations taken early in 1924 before the depth-recorder was in use, so that we do not know the depths of the deeper hauls.

These were :—

Feb. 7th, Surface	2.	Mar. 30th, Surface	14.	May 7th, Surface	6.
Midwater	—	Midwater	1.	Midwater	—
Bottom	—	Bottom	1.	Bottom	—

This is in agreement with records given by Schmidt, who remarks (22, p. 48) : ". . . this species keeps perhaps in a special degree to the neighbourhood of the surface. . . . Most of our pelagic Pollack were thus taken quite close to the surface, with only 10 metres line out."

## GADUS LUSCUS L.

The post-larvæ of *Gadus luscus* were very rare in both the 1924 and 1925 collections. Only nineteen specimens were taken in the ring-trawl; of these two occurred between 10 and 15 metres, seven between 20 and 30 m., and ten below 30 m.; none were taken at the surface. Close inshore in the metre-net, on June 13th, 1924, two were captured from 3.4 and 8.7 metres respectively, and on June 5th, 1924, in the metre-net two at 31.4 metres.

## ONOS SP.

Young Rockling, perhaps mostly *O. mustelus* although *O. cimbrius* and *O. tricirratus* may have occurred, were present at nine stations (forty-seven hauls) in sufficient numbers to examine their vertical distribution.

From these observations it is obvious that young Rocklings of the lengths captured in this case, 4–10 mm., like the small Pollack, show a partiality for the surface layers; they are, however, to be found in all layers from surface to bottom, although usually the largest numbers are taken near the surface (Fig. 2).

Ehrenbaum (8) says that they are found sporting on the surface or hiding under floating seaweed.

Mielck (17) refers to the young stages of *Onos cimbrius* as surface living forms.

## MOLVA MOLVA L.

Post-larvæ of the Common Ling only occurred in small numbers. In 1924, however, they were unusually abundant for this region, 51 individuals being taken; in 1925 they were only caught on three occasions: May 19th, 3; June 4th, 1; and July 16th, 1. Of the 51 specimens captured in 1924, 45 occurred below 20 metres, and all 5 taken in 1925 came from below 30 m.

The sizes of the post-larvæ at the station at which they were most numerous were:—

Depth in metres.	17.vi.24											
	Length in mm.											
	5	6	7	8	9	10	11	12	13	14	15	16
S	—	—	—	—	—	—	—	—	—	—	—	—
12.4	—	—	—	—	—	1	—	—	—	—	—	—
25.2	1	—	2	1	2	1	2	2	1	—	—	1
57.8	—	—	2	5	1	2	1	—	—	1	—	—

Of this species Clark (5) records in 1919 ten post-larvæ in July; he also states that "For 1914 Dr. Allen records a similar number, 8–20 mm. in length, from May to July"; investigations during the years 1906–13 produced only twenty post-larvæ 5–13 mm. in length (4).

Schmidt (22, p. 99) says: ". . . relatively very few specimens were found near the surface (hauls with 10-25 metres' wire). The majority were taken in depths of 30-100 metres under the surface, and this holds good not only for the slightly older, but also for the smallest specimens."

#### MERLUCCIUS MERLUCCIUS L.

Two specimens only occurred in my collections: these were taken on June 25th, 1924, with the ring-trawl. A specimen, 9 mm. in length, came from a depth of 45 metres, and the other, 5 mm., from 52 metres.

Two post-larval Hake captured in the ring-trawl before the depth-recorder was in use are worthy of record here, on account of the time of year at which they occurred; on January 1st, 1924, at L6 (five miles beyond the Eddystone Lighthouse) in the bottom haul, two specimens occurred 5.5 mm. and 8.5 mm. long respectively.

#### RANICEPS RANINUS L.

Three post-larvæ of this species were taken only: on July 1st, 1925, one of 4.5 mm. at L4 from a depth of 36 metres; one of 4.5 mm. on July 16th, 1925, from 26 metres; and one, of 13.5 mm., on August 6th, from 19 metres.

#### BOTHIDÆ.

##### ARNOGLOSSUS SP.

Post-larvæ of this species, probably *Arnoglossus laterna* (Will), were only abundant at one station, on July 29th, 1925; on this occasion the maximum catch was taken from a depth of 25 metres.

The sizes of these specimens were as follows:—

	Depth in metres.	Length in mm.														
		7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
29.vi.25	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4.8	-	1	-	-	-	-	-	-	-	-	1	-	-	-	
	9.1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
	20.6	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
	25.8	3	4	11	4	3	4	4	5	1	1	-	1	2	1	
	29	-	2	3	-	2	2	1	-	1	3	-	2	-	2	

At other stations at which *Arnoglossus* sp. occurred the numbers taken were very small; none were present in surface hauls, and although they occurred on occasion at as small depths as 5 metres, most were taken below 10 metres.

#### SCOPHTHALMUS NORVEGICUS (Gunther).

Post-larvæ of this species were numerous at seven stations (thirty-three hauls). They generally occurred in greatest numbers below a depth of

about 15 metres, with the exception of April 29th, 1925, when they were decidedly higher in the water.

Fig. 3 shows the percentage distribution of these young fish at three stations. It is interesting to compare these with the distribution of *Pleuronectes limanda* at the same stations (shown on the same figure). It is noticeable that *S. norvegicus* always occurred slightly higher in the water than the young Dab, the value of 10% first occurring below the surface in the case of the Topknot at 5.5, 12.5, and 11.5 m. respectively, and in the case of the Dab at 12.5, 16.5, and 16 m.

The post-larval *S. norvegicus* were almost all of lengths between 4 and 10 mm., and there is no evidence that the larger forms occurred more in the deeper layers than the smaller, as the following figures at the three stations at which post-larvæ were most abundant show :—

	Depth in metres.	Length in mm.									
		4	5	6	7	8	9	10	11	12	13
17.vi.24	S	—	—	—	—	—	—	—	—	—	—
	12.4	2	4	3	6	3	2	—	—	—	—
	25.2	13	29	26	34	23	13	4	1	—	—
	57.8	1	—	7	10	6	6	3	—	—	1
19.v.25 (i)	S	—	3	2	—	—	—	—	—	—	—
	4.3	—	—	—	—	—	—	—	—	—	—
	9.9	—	—	—	—	—	—	—	—	—	—
	20.8	—	4	18	16	21	12	3	—	—	—
	32.6	—	4	34	31	16	8	1	—	—	—
19.v.25 (ii)	S	—	—	—	—	—	—	—	—	—	—
	5.6	—	—	—	—	—	—	—	—	—	—
	12.9	—	14	4	3	2	—	—	—	—	—
	18.9	4	15	17	14	11	2	—	—	—	—
	23.7	2	15	11	12	7	2	2	—	—	—
	36.5	—	3	6	8	6	—	—	—	—	—

This species was not at all abundant at the stations close inshore at which the silk metre-net was used.

#### ZEUGOPTERUS PUNCTATUS (Bloch.).

Post-larvæ of *Zeugopterus punctatus* were fairly abundant at only one station, on May 19th, 1925. The lengths of the specimens from the different depths were :—

	Depth in metres.	Length in mm.					
		5	6	7	8	9	10
19.v.25 (ii)	S	—	—	—	—	—	—
	5.6	—	—	—	—	—	—
	12.9	—	—	1	—	—	1
	18.9	—	1	4	3	2	—
	23.7	4	5	2	3	2	—
	36.5	1	1	5	6	3	—

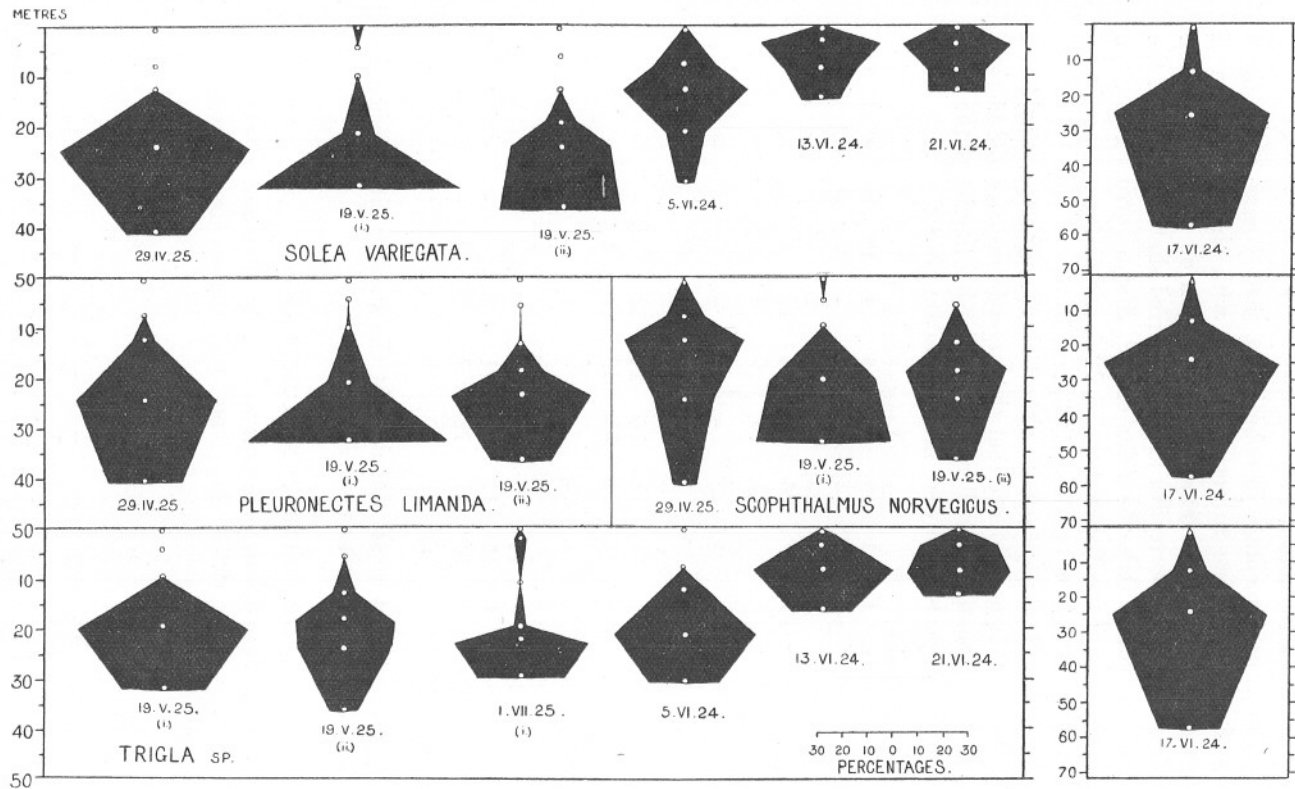


FIG. 3.—Shows percentage vertical distribution of: *Solea variegata* at three 50-m. stations, three inshore stations and E1 respectively; *Pleuronectes limanda* at three 50-m. stations; *Scophthalmus norvegicus* at three 50-m. stations and E1; *Trigla* sp. at three 50-m. stations, three inshore stations, and E1. The white spots and black circles indicate the "average depth" at which the hauls were taken.

On other occasions on which this species occurred the numbers were very small: all, however, were caught below a depth of 10 metres.

*SCOPHTHALMUS UNIMACULATUS* (Bnp).

Only three post-larvæ of this species occurred in the collections; on June 17th, 1924, at 12.4 m. one of 4.5 mm. length, and at 25.2 m. one of 7 mm.; on July 1st, 1925, at position A, one of 4.5 mm. was caught at 23.1 m.

PLEURONECTIDÆ.

*PLEURONECTES LIMANDA* L.

The post-larval Dab only occurred abundantly at five stations (twenty-three hauls). Results show that in the daytime their region of maximum abundance occurred always below 20 metres, and that they were present in considerable numbers between that depth and the bottom (Fig. 3). At other stations at which only few individuals were caught they were always taken below a depth of 15 to 20 metres.

Below are shown the numbers in which the different sized fish occurred at the depths sampled at the three stations at which they were most numerous:—

	Depth in metres.	Length in mm.											
		5	6	7	8	9	10	11	12	13	14	15	
29.iv.25	S	—	—	—	—	—	—	—	—	—	—	—	—
	7.8	—	—	—	—	1	1	—	—	—	—	—	—
	12.5	1	1	2	4	2	—	—	—	—	—	—	—
	24.3	—	2	5	9	19	7	5	7	1	—	1	—
	41.1	—	—	5	3	7	2	5	3	3	2	—	—
19.v.25 (i)	S	—	—	—	—	—	—	—	—	—	—	—	—
	4.3	—	—	—	—	—	—	—	—	—	—	—	—
	9.9	—	1	—	—	—	—	—	—	—	—	—	—
	20.8	—	1	1	5	6	1	—	—	—	—	—	—
	32.6	—	1	8	12	14	12	11	—	1	—	—	—
19.v.25 (ii)	S	—	—	—	—	—	—	—	—	—	—	—	—
	5.6	—	—	—	—	—	—	—	—	—	—	—	—
	12.9	—	1	—	1	—	—	—	—	—	—	—	—
	18.9	1	1	6	18	7	1	—	—	—	—	—	—
	23.7	1	—	16	37	23	19	10	1	—	—	—	—
36.5	—	—	4	9	12	13	5	3	—	—	—	—	

From these figures we see that young Dab between the lengths of 7 and 12 mm. occurred in all the hauls below 20 metres. Perhaps there is a tendency for the fish with greater lengths to occur in proportionately larger numbers in deepest hauls, but this can in no case be said to be at

all marked. It seems most likely that the post-larval Dabs may be met with at any depths below 20 metres until they have attained the length at which they normally descend to the bottom, and that they do not necessarily sink deeper as growth proceeds, which would give rise to a congregation in the bottom layers of fish just ready to adopt their new mode of life.

Ehrenbaum says (8, p. 156) that Dabs of 13-14 mm. upwards are seldom taken in the plankton, as at this length they seek the bottom.

#### PLEURONECTES MICROCEPHALUS (Don).

Post-larvæ of this species occurred at seven stations (thirty-two hauls) in fair numbers.

It would appear that their distribution is very similar to that of the small Dab, the region of maximum abundance being below a depth of 20 metres. There was one exception to this when, on April 29th, 1925, they were numerous at a depth of 12.5 metres.

I give below the lengths of the young *P. microcephalus* occurring at different depths at the two stations where they were most abundant:—

	Depth in metres.	Length in mm.										
		4	5	6	7	8	9	10	11	12	13	
17.vi.24	S	-	1	-	1	1	-	-	-	-	-	
	12.4	-	3	5	4	4	2	1				
	25.2	1	7	23	28	24	13	10	8	2	-	
	57.8	-	-	1	4	2	-	1	-	1	1	
19.v.25 (ii)	S	-	-	-	-	-	-	-	-	-	-	
	5.6	-	-	-	-	-	-	-	-	-	-	
	12.9	-	1	2	-	1	2	1	-	-	-	
	18.9	-	-	2	-	3	1	-	-	-	-	
	23.7	-	-	2	6	11	7	6	1	-	-	
	36.5	-	-	-	-	5	2	1	2	-	-	

#### PLEURONECTES FLESUS L.

Only thirteen specimens of post-larval Flounders occurred in the collections: of these nine were taken from depths greater than 20 metres.

#### SOLEIDÆ.

##### SOLEA VARIEGATA (Don).

Post-larval Thickback occurred at five stations (twenty-four hauls) in the ring-trawl in sufficient numbers to show its vertical distribution. These young fish were never in quantity above a depth of 20 metres over water 50 or more metres deep.

Fig. 3 shows their distribution at four offshore stations. Below are given the sizes of fish caught at various depths at three stations:—

	Depth in metres.	Length in mm.									
		3	4	5	6	7	8	9	10	11	12
19.v.25 (i)	S	—	—	—	7	1	1	—	1	—	—
	4.3	—	—	—	—	—	—	—	—	—	—
	9.9	—	—	—	—	—	—	—	—	—	—
	20.8	—	3	7	12	5	3	1	—	—	—
	32.6	—	9	48	45	34	28	10	4	1	1
19.v.25 (ii)	S	—	—	—	—	—	—	—	—	—	—
	5.6	—	—	—	—	—	—	—	—	—	—
	12.9	—	—	1	—	—	—	—	—	—	—
	18.9	—	—	5	9	3	—	—	—	—	—
	23.7	—	4	18	19	4	6	2	2	—	—
	36.5	—	2	9	10	18	8	9	6	4	1
25.vi.24	S	—	—	—	—	—	—	—	—	—	—
	13.6	—	—	4	2	1	—	—	—	—	—
	45.5	—	1	6	18	21	11	1	1	—	—
	52	2	10	29	23	12	3	3	—	—	—

From these figures it would seem that up to 9 mm. the post-larval Thick-back may be met with at any depth below 20 m., but after this length they tend to keep to the deeper layers. Although metamorphosis is not complete at 12 mm., it is probable that by the time this length is attained the majority are seeking the bottom for their new mode of living.

In addition to these records *S. variegata* post-larvæ occurred at three stations taken closer inshore, on June 5th, 1924, over a depth of ca. 35 m., and June 13th and 21st, 1924, over a depth of ca. 25 m. On these occasions we see that the young fish were abundant at a much higher level in the water than farther offshore, the largest numbers being taken at 12.5 m., 3.4 m. and 3.8 m. respectively (Fig. 3):—

	Depth in metres.				Length in mm.					
	3	4	5		3	4	5	6	7	
5.vi.24	S	—	—	13.vi.24	S	3	—	—	—	—
	8	1	—		3.4	—	17	6	—	—
	12.4	15	—		8.7	—	6	6	1	1
	21.2	3	2		—	14.5	—	1	2	2
	31.4	1	—							

	Depth in metres.			Length in mm.			
	3	4	5	6	7	8	
21.vi.24	S	—	2	2	1	—	—
	3.8	3	3	—	5	3	3
	9	—	6	1	—	2	—
	13.3	—	5	—	1	2	1



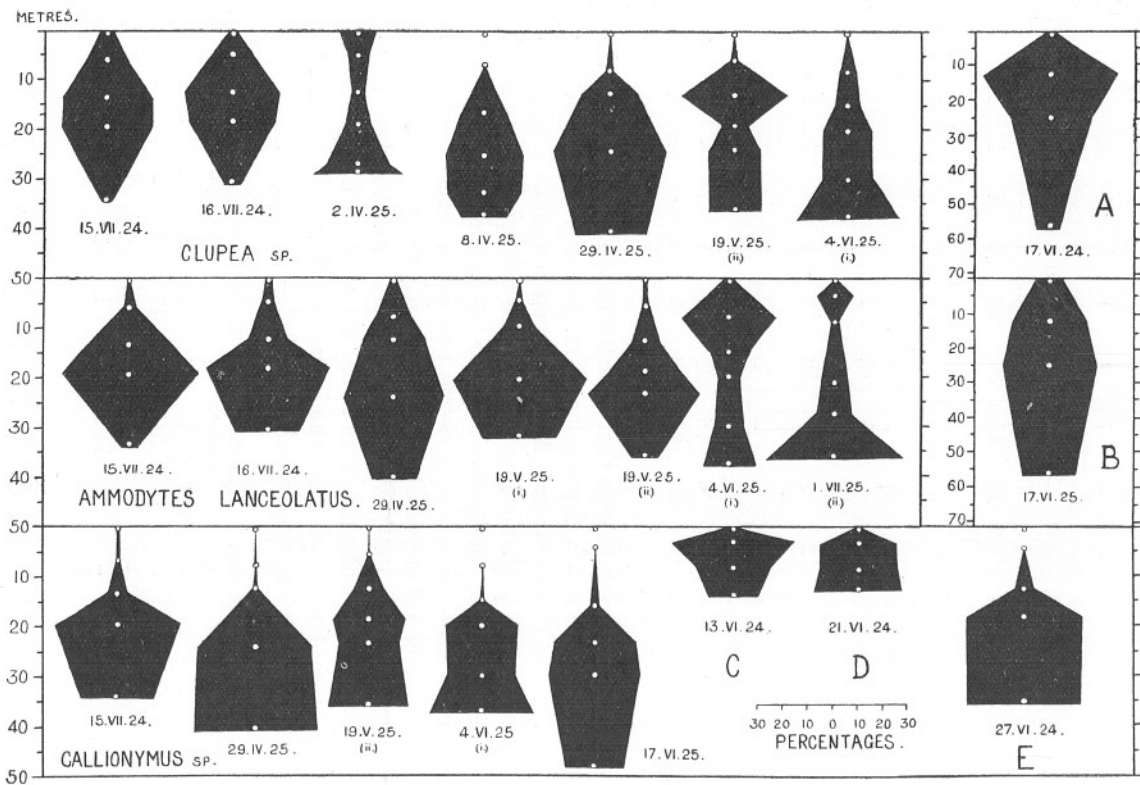


FIG. 4.—Shows percentage vertical distribution of *Clupea* sp. at seven 50-m. stations and one at E1; *Ammodytes lanceolatus* at similar stations, and *Callionymus* sp. at five 50-m. stations, two inshore stations, and one over 45 m. with the metre closing net. The white spots and black circles indicate the "average depth" at which the hauls were taken.

## SOLEA VULGARIS (Quenn).

Only thirty specimens of the post-larvæ of the Common Sole occurred in the collections, of these none were taken between the surface and 10 metres, one was caught at 12 metres, six between 20 and 25 metres, and the remaining twenty-three below 25 metres, most of these occurring at depths greater than 30 metres.

## SOLEA LUTEA (Risso).

Only one post-larval, *S. lutea*, was caught: this was taken from a depth of 23 metres on July 1st, 1925, in the ring-trawl.

## CARANGIDÆ.

## CARANX TRACHURUS (L.).

Post-larvæ of this species occurred on only two occasions, on July 15th and 16th, 1924, at L4 in the ring-trawl. All specimens were taken above a depth of 20 metres. On July 16th, five, 4-5 mm. in length, occurred at a depth of 12.5 metres: at the four other depths sampled on this day none were taken.

The following were the sizes of the individuals at the five depths sampled on July 15th:—

Depth in metres.	Length in mm.					Total number of fish.
	4	5	6	7	8	
S	1	1	—	—	—	2
6.6	3	2	—	—	—	5
13.6	1	9	1	—	1	12
19.5	1	5	2	—	—	8
34.5	—	—	—	—	—	—

## AMMODYTIDÆ.

## AMMODYTES LANCEOLATUS (Lesauv).

Of the two species of Sand-eel taken in this region *Ammodytes lanceolatus* was most evident in my collections, *A. tobianus* only occurring singly on one or two occasions.

In their vertical distribution *A. lanceolatus* post-larvæ, mostly 5-20 mm. in length, show a distinct resemblance to that of *Clupea* sp., being somewhat irregularly distributed from the surface downwards with a tendency to be absent from the superficial layers (Fig. 4).

## CALLIONYMIDÆ.

## CALLIONYMUS sp.

Probably the majority of post-larvæ under this heading were *Callionymus lyra*: *C. maculatus* being a late spawner (5) the young stages would be in the plankton mostly in July and August, later than most of the stations were made.

This species was by far the most abundant of all the young fish in the collections. In 1924 of 11,553 young fish examined 4595 were *Callionymus*, and in 1925 out of 9505 examined 4148 were *Callionymus*. So that of the 21,000 young fish over 8700 were *Callionymus*. This is a very large proportion, and one naturally concludes that this species is a serious competitor for the food of other young fish.

These post-larvæ, nearly all below 8 mm. in length, occurred abundantly at almost every station, both close inshore and far out. Generally they increased in number suddenly below about 12 m.; from this level downwards they were very abundant, usually increasing in numbers towards the deeper layers, the region of maximum abundance lying below 20 metres (Fig. 4). Above 12 metres to the surface very few were taken (see Appendix). At the stations taken close inshore, as with other species of fish, post-larval *Callionymus* were present in large numbers much higher up in the water than farther offshore.

With the metre-net the following results were obtained:—

	Depth of water,	Depth below which <i>Callionymus</i> species were abundant.
13.vi.24 . . . . .	25 m.	2.3 m.
21.vi.24 . . . . .	27 m.	2.3 m.
5.vi.24 . . . . .	35 m.	ca. 10 m.
27.vi.24 . . . . .	45 m.	10 m.

## LABRIDÆ.

Post-larvæ of the Wrasses were never very numerous in the catches. All species showed a tendency to be most abundant above 20–25 metres.

## LABRUS BERGYLTA Asc.

This species was never numerous. I give below the sizes of the specimens from different depths on the two dates when they were most abundant:—

25.vi.24.	L4.	R.T.				Total number of fish.
		Depth in metres.	Length in mm.			
		5	6	7	8	
	S	—	—	—	—	—
	13.6	3	5	3	1	12
	45.5	3	4	5	—	12
	52	—	5	2	1	8

1.vii.24.	L4.	R.T.					Total number of fish.
		Depth in metres.	Length in mm.				
		5	6	7	8	9	
	S	—	—	—	1	—	1
	5.4	3	1	—	3	—	7
	16.4	4	—	1	2	—	7
	29.2	—	2	2	—	1	5
	39.3	—	—	1	1	—	2

In these two cases the post-larvæ occurred slightly higher in the water than many other species of fish. In the remaining collections in 1924 and 1925 with the ring-trawl only twenty-three individuals occurred, of these sixteen came from levels above 25 m. and eight below this depth.

#### LABRUS MIXTUS (L.).

Post-larvæ of this species were even less abundant than those of *L. bergylta*. The largest numbers were taken with the ring-trawl on July 1st, 1924.

The details were as follows:—

Depth in metres.	Length in mm.				Total number of fish.
	7	8	9	10	
S	—	—	—	—	—
5.4	—	3	1	—	4
16.4	3	4	—	1	8
29.2	2	1	—	—	3
39.3	—	1	—	—	1

Only nineteen specimens appeared in the remaining collections, of which thirteen came from above a depth of 25 metres.

#### CRENILABRUS MELOPS (L.).

The two most abundant catches of this species with the ring-trawl were on July 1st and 16th, 1924, when the details were:—

1.vii. 24.	L4.	R.T.				Total number of fish.
		Depth in metres.	Length in mm.			
		4	5	6	7	
	S	—	—	—	1	1
	5.4	2	7	4	3	16
	16.4	1	4	2	—	7
	29.2	—	—	1	—	1
	39.3	—	—	—	1	1

16.vii.24. L4. R.T.

Depth in metres.	Length in mm.			Total number of fish.
	4	5	6	
S	1	—	—	1
5.3	1	5	1	7
12.5	1	5	4	10
18.3	1	6	3	10
31.1	1	—	1	2

In the remaining catches with the ring-trawl only twenty-two specimens occurred, twelve of which came from depths above 25 metres.

This species occurred fairly abundantly at two inshore stations with the metre-net : in both cases there was a marked maximum of abundance just below the surface at about 3 to 4 metres.

13.vi.24. M.N.

Depth in metres.	Length in mm.			Total number of fish.
	3	4	5	
S	1	—	—	1
3.4	20	16	1	37
8.7	—	4	—	4
14.5	—	5	—	5

21.vi.24. M.N.

Depth in metres.	Length in mm.		Total number of fish.
	3	4	
S	2	—	2
3.8	23	2	25
9	6	3	9
13.3	1	1	2

## CTENOLABRUS RUPESTRIS (L.).

Only forty-four specimens (4–9 mm. in length) occurred in the catches with the ring-trawl in 1924 and 1925 ; of these 15 came from above 10 metres, 18 between 10 and 20 metres, 2 between 20 and 25 m., and 9 between 25 m. and the bottom.

## CENTROLABRUS EXOLETUS (L.).

Only fifty specimens occurred in the catches with the ring-trawl in 1924 and 1925 ; of these 5 were caught above 10 metres, 32 between 10 and 20 m., 1 between 20 and 25 m., and 12 between 25 m. and the bottom.

## TRACHINIDÆ.

## TRACHINUS VIPERA C. and V.

Post-larvæ of *Trachinus vipera* were never numerous in the collections. In all fifty-one specimens were taken in the ring-trawl and closing

metre-net in water of 50 m. depth ; of these 19 occurred between the surface and 10 metres, 12 between 10 and 20 metres, 9 between 20 and 25 metres, and 11 between 25 metres and the bottom. Thus there would appear to be a tendency for these post-larvæ, most of which were between 5 and 8 mm. in length, to occur in the upper water layers above 25 metres in the daytime. At the majority of stations, however, at which they occurred the weather was extremely dull ; this is a factor that must not be lost sight of, but many more observations will be required before it will be possible to determine such causes.

## SCOMBRIDÆ.

## SCOMBER SCOMBER (L.)

Post-larval Mackerel were never very numerous ; the main spawning region is probably considerably farther to the westward. They appeared to show a preference for the levels above a depth of 25 metres.

I give below the sizes of the specimens at the three stations at which they were most numerous :—

	Depth in metres.	Length in mm.										Total number of fish.	
		4	5	6	7	8	9	10	11	12	13		15
17.vi.24	S	-	-	-	-	-	-	1	-	-	-	-	1
El. R.T.	12.4	5	1	1	7	3	1	1	-	-	-	-	19
	25.2	-	2	1	5	4	2	-	2	-	-	-	16
	57.8	-	-	2	1	3	-	-	-	-	-	-	6
15.vii.24	S	-	1	1	-	1	-	-	-	-	-	-	3
L4. R.T.	6.6	-	1	-	-	3	7	2	3	-	-	-	16
	13.6	-	-	-	-	-	-	1	1	-	-	-	2
	19.5	-	-	-	1	-	1	-	-	-	-	1	3
	34.5	-	-	-	-	-	-	-	-	-	-	-	-
17.vi.25	S	-	-	-	-	-	-	-	-	-	1	-	1
L4. R.T.	4.5	-	-	4	-	5	1	4	1	1	-	-	16
	16.2	-	-	-	4	-	-	1	-	-	-	-	5
	23.4	-	-	-	1	1	1	-	-	-	-	-	3
	29.8	-	-	-	-	3	1	2	1	-	-	-	7
	48.8	-	-	-	-	-	-	-	1	-	-	-	1

## GOBIIDÆ.

## GOBIUS sp.

In 1924 there were large numbers of post-larval Gobies (species unidentified) at almost all the stations. At all the stations of a depth of 50 metres or more these post-larvæ became suddenly very abundant just below the 10-metre level, between 10 metres and the surface they were

either absent or present in comparatively very small numbers. As with other species they occurred in abundance close under the surface well inshore (Fig. 5).

In 1925 they were extremely rare: on the few occasions on which the largest numbers were taken they occurred mostly much deeper down than in 1924, below 25 metres.

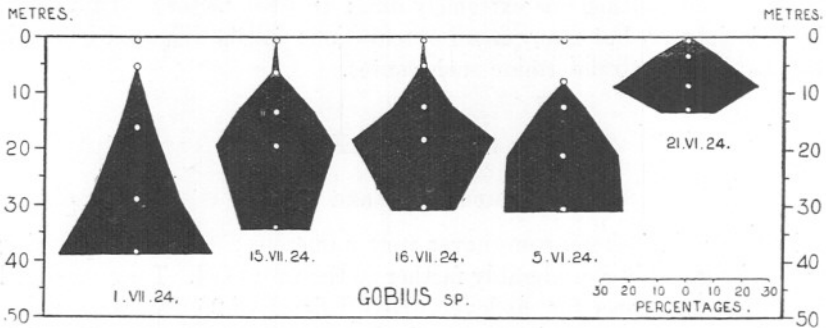


FIG. 5.—Shows the percentage vertical distribution of *Gobius* sp. at three offshore stations where the depth was 50 or more metres, and at two inshore stations in a depth of 35 and 27 metres respectively. The white spots and black circles indicate the "average depth" at which hauls were taken.

#### LEBETUS SCORPIOIDES (Coll.)

Only thirty-one post-larvæ of this species occurred in the ring-trawl collections: none were taken from between 10 metres and the surface, 10 occurred between 10 and 20 metres, 7 between 20 and 30 metres, and 14 between 30 metres and the bottom.

#### BLENNIIDÆ.

Post-larvæ of three species occurred in the collections in the ring-trawl: *Blennius ocellaris* L., *B. pholis* L., and *B. gattorugine* L. Of these *B. gattorugine* was the most common: none of the three, however, were abundant in any haul, six being the highest catch recorded for a single species.

#### BLENNIUS OCELLARIS (L.)

Nine specimens only occurred: of these 2 occurred between the surface and 10 metres, 2 between 10 and 20 metres, 4 between 20 and 25 metres, and 1 below 25 metres.

#### BLENNIUS GATTORUGINE (L.)

In all ninety-one individuals were captured in the ring-trawl in 1924 and 1925: of these 37 were taken between the surface and 10 metres, 27 between 10 and 20 metres, 12 between 20 and 25 metres, and 15 between 25 metres and the bottom.





## COTTIDÆ.

## COTTUS BUBALIS (Euphr.)

Only eight post-larvæ of this species occurred in the ring-trawl collections, of these seven were taken below a depth of 20 metres.

## CYCLOPTERIDÆ.

## LIPARIS MONTAGUI (Donov.)

Thirteen post-larvæ of this species were taken in the ring-trawl; of these twelve occurred below a depth of 30 metres. Three specimens only were caught in the metre-net. This points to *L. montagui* post-larvæ being very deep living forms.

## GOBIESOCIDÆ.

## LEPADOGASTER BIMACULATUS (Penn.)

In all fifty-nine individuals occurred in the collections in the ring-trawl; of these 8 were caught between a depth of 10 and 20 metres, 6 between 20 and 30 metres, and 45 between 30 metres and the bottom. This species is then most probably a deep living form in the daytime. Ehrenbaum (8, p. 120) says that larvæ 5 and 5.5 mm. long were taken in the deeper water layers.

## LEPADOGASTER CANDOLLI (L.)

Only one specimen of this species was caught: this was taken from a depth of 33.6 metres in the ring-trawl on August 6th, 1925.

## LOPHIIDÆ.

## LOPHIUS PISCATORIUS (L.)

The post-larvæ of this species occurred in unusual abundance in 1924, when sixteen specimens, 5-8½ mm. in length, were taken; in 1925 none occurred in the collections. They were captured from depths between 12 and 25 metres in the deeper offshore water, and between depths of 4 and 15 metres at the stations close inshore with the metre-net.

The early pelagic stages of the Angler are not often taken in this region: Allen (1) records one of 6.2 mm. taken seven miles west of Rame Head on July 16th, 1914; my specimens in 1924 occurred from June 4th until July 16th; on June 18th a small portion of angler spawn was caught at L4 (Lebour, 16).

THE VERTICAL DISTRIBUTION OF THE EGGS OF  
CERTAIN SPECIES.

In the spring of 1924 I attempted to obtain evidence on the vertical distribution of fish eggs, particularly that of the later developmental stages.

Much evidence is required on this problem, especially as the observations of previous workers appear somewhat conflicting.

Hensen and Apstein (11) state that the older stages are generally suspended at greater depths than the younger. Hjort and Dahl (13), however, found no evidence for this, working in Norwegian waters. Kramp (15), in 1913, could not confirm Apstein's statements. "On the contrary," he says, "in each species the percentage of eggs with pigmented embryo is larger in the upper water layers than in the bottom-surface hauls."

Bowman (2), however, states that "as the embryo advances in development the specific gravity of the egg increases, and it tends to sink to the lower water layers." And in a previous paper (3) he gives figures that substantiate this statement.

Jacobsen and Johansen (14) have shown that the egg is capable of altering its specific gravity after extrusion into the sea-water throughout its development, the changes depending "partly on the temperature and salinity of the water in which the eggs remain." Remotti (18) showed an increase in specific gravity for the eggs of many species with age, preceded in some cases by a slight decrease in specific gravity. He found that the eggs of deep water fish behaved very differently from those of shallower water forms, showing at first a decrease in specific gravity and then a great and sudden increase in weight during development.

My observations are somewhat meagre, but as they deal with fairly large numbers of eggs I think they are worthy of record.

The three stations made with the ring-trawl unfortunately occurred before the depth-recorder was in use. We have, therefore, no certain idea at what depths the samples were collected. It is probable from results shown by the recorder that they were not nearly as deep as the expressions "Midwater" and "Bottom" indicate: perhaps in the region of 15 and 25 metres respectively. However, it is fairly safe to conclude that "bottom" hauls were taken at deeper levels than "mid-water," while the latter will most certainly have been deeper than the surface hauls.

Three other stations were taken with a closing metre-net towed horizontally, and here again no depth records are available. However, care was taken to keep the angle of the warp extremely steep, and furthermore

a large weight suspended a fathom below the net was felt to touch bottom at the beginning of each bottom haul.

Practically all the material was examined alive, so that error due to identification is very small, in fact with the species I record here it is nil; eggs of *Clupea sprattus*, *Onos* sp., and *Clupea (Sardina) pilchardus* being at once separable from those of other species.

The eggs were laid on a slide with grooves made by cementing fine glass rods parallel with one another as designed by Todd and used by Wollaston (25).

I have divided the eggs into five or six stages of development, splitting Bowman's stages  $\beta$  and  $\gamma$  (3) each into two. The stages were, 0 equal to Bowman's  $\alpha$ , i.e. the egg in its earliest period of development before there is any indication of form in the embryo;  $\frac{1}{4}$  in which the formation of the embryo is appearing, but not completely visible towards the caudal region;  $\frac{1}{4}^*$  in which the embryo is more advanced, but the tail does not go beyond half-way round the egg, and has not yet lifted from the yolk;  $\frac{1}{2}$ , with the embryo over half-way round the yolk, but under three-quarters;  $\frac{3}{4}$  the embryo three-quarters way round the yolk, but not completely; and 1 in which the embryo is completely coiled round the yolk equivalent to Bowman's  $\delta$ -stage.

I am much indebted to my wife for the great assistance she rendered me in recording the results while I examined the eggs under the microscope.

The results for the eggs of *Clupea sprattus* were as follows:—

February 2nd, 1924. L4. R.T. Sea: moderate. 25 min. hauls.

	0	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1
Surface . . . . .	2826	640	186	38	3
Midwater . . . . .	2910	411	469	159	2
Bottom . . . . .	2353	182	104	60	6

March 3rd, 1924. L4. R.T. Sea: moderate, after two days' storm.

	0	$\frac{1}{4}$	$\frac{1}{4}^*$	$\frac{1}{2}$	$\frac{3}{4}$	1
Surface . . . . .	1234	58	24	45	45	31
Midwater . . . . .	1860	49	23	36	38	38
Bottom . . . . .	1105	49	17	44	36	25

March 6th, 1924. L4. Closing net. Sea: calm. 15 min. oblique hauls.

	0	$\frac{1}{4}$	$\frac{1}{4}^*$	$\frac{1}{2}$	$\frac{3}{4}$	1
Surface (oblique haul from ca. 15 m. to surface)	189	88	11	54	67	13
Midwater (ditto from ca. 30 m. to 20 m.)	171	130	11	88	79	18
Bottom (ditto from ca. 50 m. to 40 m.)	50	32	5	13	27	6

March 6th, 1924. L4. Closing net. Sea : calm. 15 min. horizontal hauls.

	0	¼	¼*	½	¾	1
Surface . . . . .	298	270	1	41	31	23
Midwater (ca. 26 m.) . . . . .	414	128	33	40	41	21
Bottom (ca. 41 m.) . . . . .	445	276	3	75	68	32

March 7th, 1924. L4. R.T. Sea : moderate.

	0	¼	¼*	½	¾	1
Surface . . . . .	70	40	17	62	49	26
Midwater . . . . .	82	38	11	29	25	30
Bottom . . . . .	48	40	18	56	44	41

These results show little evidence of the accumulation of the more developed eggs in the deeper layers. If under calm conditions such sinking might occur it is probably counteracted by the effects of the boisterous weather prevalent at this time of the year which keeps all water layers tolerably well mixed.

Observations were made on eggs of *Onos* sp. at five different depths with the metre closing net.

March 12th, 1924. Bigbury Bay. Closing metre-net. Hauls, 10 min. horizontal.

	0	¼	¼*	½	¾	1
Surface . . . . .	102	15	15	10	3	6
Upper Layers (ca. 7 m.) . . . . .	632	128	111	82	24	28
Midwater (ca. 13 m.) . . . . .	516	91	93	46	29	10
Bottom Layers (ca. 19 m.) . . . . .	379	44	15	18	5	9
Bottom (ca. 25 m.) . . . . .	207	16	14	14	8	8

Eggs at all stages were present at all depths, but there was a tendency for the majority of all stages to lie a little below the surface. This may possibly be due to movements of the water, as young Sprat showed the same type of distribution (see p. 112). In addition to the above observations I obtained samples from four depths with the ring-trawl on July 9th, 1924, at the Hydrographical Station E2, half-way across the English Channel between Plymouth on the English coast and Ushant on the French coast. On this occasion the depth-recorder was used. The collections contained large numbers of eggs of the Pilchard, *Sardina pilchardus*: this is the first occasion on which Pilchard eggs have been taken in really large quantities in the Plymouth records.\* The catches were additionally remarkable in that they were practically devoid of all the plankton organisms that are usually taken at this time

\* Further large catches varying from one to three thousand were made on April 22nd, 1925, at E1.

of the year, they may be said to have consisted almost exclusively of pilchard eggs. One is tempted to wonder whether the water had been stripped of the larger plankton organisms by the large shoal of Pilchards that had evidently been spawning in that body of water. This scarcity of plankton is even more extraordinary seeing that the samples were taken at dusk, at a time at which on the following day and a fortnight later in localities nearer the coast (Longships Lighthouse and L4), the upper water layers were teeming with organisms that had migrated up from deeper levels.

The material was preserved in formalin: on examination I separated the eggs into two groups only. I picked out all those in which the embryo was fully formed and evidently very nearly ready to hatch out: these could be at once distinguished from all other stages, even with the naked eye, by the appearance of the small fish curled up in the large clear egg. All other stages I lumped together in a separate group. The following table gives the numbers of the two stages at the depths indicated by the depth-recorder. (The tracings obtained have been reproduced elsewhere (21).)

July 9th, 1924. E2. R.T. Sea: moderate. Dusk.

Depth.	1st stage.	2nd stage (embryo fully formed).
1.2 metres	2623	155
15     ,,	2209	1849
24.6   ,,	2633	1325
60     ,,	1453	691

Clearly here we have the earlier stages distributed at all depths with a falling off towards 60 metres. The latest stages of development, however, seem definitely to be massed about the 15-24 metre region: they are very few in number at the surface, but at what depth they began to become abundant we do not know.

That this sinking is a purely mechanical phenomenon accounted for by increase in specific gravity as development advances does not seem probable from the figures; if that were the case, one would expect the numbers from the surface to 60 metres to show a steady increase, the reverse is, however, the case, the increase in numbers taking place as we pass up from 60 metres to 15 metres. The possibility that these figures may be an expression of variations of the time of development for individual eggs combined with the time taken to sink should, however, not be lost sight of.

I am fortunate in having hydrographical observations taken at the same station just an hour before the ring-trawl was used. These figures have been published elsewhere (7), but I will repeat them here.

July 9th, 1924. E2.

Depth in metres.	Temperature °C.	Salinity ‰
0	15.7°	35.19
5	15.53°	35.18
15	14.43°	35.18
25	13.90°	35.18
35	11.99°	35.19
50	11.69°	35.17
70	11.69°	35.16
85	11.61°	35.17

The figures given show that as regards the salinity the water from top to bottom was homogeneous. There is, however, a definite temperature gradient, a warm layer of water being present above 25 metres: this will give rise to a considerable decrease in the viscosity of the water (12), and hence a sinking of those objects that maintain the same specific gravity. If, however, decrease in viscosity were the cause of the sinking of the most developed eggs we should expect to find also sinking of the early stages unless they alter their specific gravity to meet the circumstances.

In the warmer layers development will be accelerated and the majority of the later stages might have already hatched out; there is, though, no evidence of the presence of newly hatched larvæ in the collection; although very fragile, it is probable that if they had been present in large numbers in the water layers a few at any rate would have appeared in the catch; actually there was only one.

There is the further possibility that the well-advanced embryo is already susceptible to light of strong intensity, and may be able to alter its specific gravity, and so sink into the dimly lit layers, where it would once more resume its original weight. This should be possible to test experimentally.

We have further evidence of the sinking of later stages of the Pilchard egg from a previous station at which the ring-trawl was used, but the fishing depths unknown.

30.iv.24. R.T. L4. Sea: rough.

	0	$\frac{1}{4}$ *	$\frac{1}{2}$	$\frac{3}{4}$	1
Surface . . . . .	407	176	9	24	11 9
Midwater . . . . .	163	151	63	32	24 14
Bottom . . . . .	353	224	118	74	50 27

In this case there are definitely less of the more advanced stages at the surface than in the deeper layers: whether there are necessarily more

in the "bottom" than "midwater" hauls is rather open to question; it may be that where the "bottom" haul was taken all stages were more numerous in the water, i.e. floating in a denser mass, as the proportions of all stages in "midwater" and "bottom" hauls are very similar, the number of eggs in the "bottom" haul being just about twice as many as in the "midwater."

From the above evidence it would appear that while the eggs of *Clupea sprattus* were evenly distributed from surface to bottom at all stages, those of *Sardina pilchardus* differed in that the later stages were found deeper in the water. Far more evidence is, however, required before conclusions can be drawn, as the conditions are constantly changing. In these times, however, when the cry is for more and more observations, I am convinced that every observation, in which the conditions and definite numbers can be given, should be recorded to swell the evidence of past workers and assist future observers.

#### SUMMARY.

1. Horizontal hauls were made with a "stramin" ring-trawl and a silk net at different depths in 1924 and 1925 to determine the vertical distribution of the pelagic post-larval stages of Teleostean fish in daylight. The depths at which the nets fished on every occasion were obtained by means of a graphic depth-recorder.

2. It was indicated that there are specific differences in the behaviour of the post-larvæ of various fishes as to their vertical distribution in daylight, some preferring the surface layers, others apparently indifferently distributed from surface to bottom, and others preferring the deeper layers and avoiding the surface; of these last it was found that some species became abundant at deeper levels than others. A tentative list of distribution types is given on page 107.

3. Results emphasise the necessity when examining the horizontal distribution of young fish of sampling *all* layers: oblique hauls are to be desired fishing at as many levels as possible.

4. Mention is made of seasonal distribution: the year 1924 appeared to differ from 1925 in that certain post-larvæ which were prevalent in the plankton well into June or July in the former year were cut short a month earlier in 1925.

The post-larvæ of *Molva molva* and of *Lophius piscatorius* were unusually abundant in 1924; post-larval Gobies (*Gobiidæ*) and Wrasses (*Labridæ*) were extremely scarce in 1925 during the months April to beginning of August.

5. Certain observations on the vertical distribution of the floating eggs of *Clupea sprattus*, *Onos* sp., and *Sardina pilchardus* are

given. While all stages of development of the eggs of the Sprat were equally abundant at all depths, on the two occasions on which Pilchard eggs were taken in quantity the more advanced stages were more numerous a little way below the surface. The eggs of *Onos* sp. at all stages on this occasion were most numerous a few metres beneath the surface.

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## APPENDIX.

The three positions at which stations were made, mentioned in these lists, are situated as follows :—

- L4. Half-way between the coast and the Eddystone Lighthouse.
- A. Two to three miles east of the Eddystone Lighthouse.
- L6. Five miles beyond the Eddystone Lighthouse in a south-westerly direction.
- E1. Ten miles beyond the Eddystone Lighthouse in a south-westerly direction.

Abbreviations :—

- R.T. Ring-trawl (not closing). (Stramin).
- M.N. Metre-net (not closing). (Silk).
- C.M.N. Closing metre-net. ( ,, ).

All depths and lengths of warp are given in metres.

All times are Greenwich mean.

An asterisk \* denotes that the clockwork drum of the recorder was not rotating ; the depth given is therefore the maximum depth attained and not the average depth.

† Denotes on 2.iv.25 that the recorder was damaged, indications of depth were, however, shown, and the figures arrived at are guessed by comparison with other results : if anything they probably err in that they are not quite deep enough.

On 4.vi.25, Station 17, the clockwork drum was loose and the tracings badly confused, the figures are in consequence possibly not highly accurate.

## LIST OF STATIONS.

Station.	Date.	Position.	Depth.	Net.	Time.	Duration of Haul.	Length of Warp.	Fishing Depths		Remarks.
								Average.	Limits.	
1	29.v.24	L4	51	R.T.	10.58 a.m.	10	—	—	Surface	Sea : moderate.
					10.40 „	10	36	11.2	7-12	
					10.20 „	10	73	22.2	16-26	
2	5.vi.24	4°11'30"W. 50°17'20"N.	35	M.N.	1.10 p.m.	10	—	—	Surface	Weather : Dull and overcast. Sea : calm.
					12.53 „	10	13	8*	—	
					12.21 „	12	23	12.4	8-16.5	
					11.57 a.m.	11	38	21.2	15-22.5	
					11.35 „	10	53	31.4	25-35	
3	13.vi.24	4°10'W. 50°18'N.	25	M.N.	10.45 a.m.	10½	—	—	Surface	Weather : Bright intervals. Sea : calm.
					10.31 „	10	10	3.4	2-4	
					10.14 „	10	20	8.7	5-10	
					9.56 „	9	30	14.5	12-18	
4	17.vi.24	E1	72	R.T.	12.34 p.m.	10	—	—	Surface	Weather : dull. Fres heasterly wind. Sea : moderate.
					12.14 „	9	55	12.4	7.5-22	
					11.56 a.m.	9	101	25.2	20-31.5	
					11.30 „	8	184	57.8	53-70	
5	21.vi.24	4°10'W. 50°18'30"N.	27	M.N.	10.7 a.m.	10	—	—	Surface	Weather : bright in- tervals. Sea : calm.
					9.48 „	10	10	3.8	3.5-4	
					9.30 „	10	20	9*	—	
					9.1 „	10	35	13.3	11-16	

6	25.vi.24	L4	55	R.T.	9.10 a.m.	10	—	—	Surface	Weather : dull.
					9.26 "	10	36	13.6	8-20.5	Sea : very calm.
					9.44 "	10	75	45.5	34-50	
					10.5 "	10	110	52	48-54	
7	27.vi.24	4°11'W. 50°17'N.	45	C.M.N.	12.33 p.m.	9	—	—	Surface	Weather : sunny.
					12.51 "	10	10	4.3	2-5	Sea : calm.
					1.9 "	10	20	12.7	11-15	
					1.29 "	10	30	18.1	15-20	
					1.53 "	10	50	36.2	30-42	
8	1.vii.24	L4	51	R.T.	9.20 a.m.	10	—	—	Surface	Weather : cloudless,
					9.47 "	10	18	5.4	2.5-7.5	bright sunshine.
					10.3 "	11	36	16.4	14.5-17	Sea : very calm.
					10.20 "	10	55	29.25	22-35	
					10.40 "	9½	92	39.3	32-45.5	
9	15.vii.24	L4	51	R.T.	4.34 p.m.	10½	—	—	Surface	Weather : bright
					4.18 "	10	18	6.6	—	sunshine. Sea :
					4.1 "	10	36	13.6	—	calm.
					3.44 "	10	55	19.5	—	
					3.25 "	10	92	34.5	—	
10	16.vii.24	L4	51	R.T.	10.00 a.m.	11	—	—	Surface	Weather : sun shin-
					9.43 "	10	18	5.3	—	ing. Sea : moder-
					9.26 "	10	36	12.5	—	ate.
					9.8 "	10	55	18.3	—	
					8.47 "	10	92	31.1	—	
11	2.iv.25	L4	51	R.T.	10.7 a.m.	10	—	—	Surface	Weather : very dull
					10.26 "	10	18	5†	—	and overcast. Sea :
					10.45 "	10	36	12.5†	—	calm. No wind.
					11.4 "	10	55	19†	—	
					11.24 "	10	73	27†	—	
					11.45 "	10	92	29†	—	

LIST OF STATIONS—*continued.*

Station.	Date.	Position.	Depth.	Net.	Time.	Duration of Haul.	Length of Warp.	Fishing Depths.		Remarks.
								Average.	Limits.	
12	8.iv.25	L4	51	R.T.	10.33 a.m.	10	—	—	ca. 2 m.	Weather : bright sunshine. Sea : very calm.
					10.52 „	10	18	6.9	5-7.5	
					11.10 „	10	36	16.5	15-18.5	
					11.29 „	10	55	25.3	20-27.5	
					11.48 „	10	73	32.5	25-36	
					12.7 p.m.	10	92	37.8	35-40	
13	22.iv.25	E1	72	R.T.	12.30 p.m.	10	—	—	Surface	Weather : sunshine. Sea : moderate.
					12.48 „	10	18	4.6	3.5-6.5	
					1.9 „	10	46	15	12.5-18.5	
					1.30 „	10	73	22.1	20-24.5	
					1.54 „	10	110	51.4	47-58	
					2.17 „	10	146	61.2	52-63	
14	29.iv.25	L6	65	R.T.	1.2 p.m.	10	—	—	Surface	Weather : cloudless, bright sunshine. Sea : very calm.
					1.20 „	10	18	7.8	5-10	
					1.42 „	11	46	12.5	7-20	
					2.4 „	10	73	24.3	18.5-28	
					2.27 „	10½	110	41.1	30-47	
15	19.v.25 (i)	A	54	R.T.	12.10 p.m.	10	—	—	Surface	Weather : sunshine until 1.18 p.m. Sea : moderate.
					12.29 „	10	18	4.3	3-5	
					12.48 „	10	36	9.9	7.5-12	
					1.9 „	10	55	20.8	17.5-22.5	
					1.31 „	10	92	32.6	27.5-42	

16	19.v.25 (ii)	L4	51	R.T.	9.36 a.m.	10	—	—	Surface	Weather: dull and overcast. Sea: moderate.
					9.54 "	10	18	5.6	5-6	
					10.12 "	10	36	12.9	11-15	
					10.33 "	10	55	18.9	17-25	
					10.55 "	10	82	23.7	21.5-25	
					11.18 "	10	110	36.5	32.5-48	
17	4.vi.25 (i)	A	54	R.T.	10.14 a.m.	10	—	—	Surface	Weather: cloudless, bright sunshine. Sea: calm.
					10.32 "	10	18	8†	—	
					10.50 "	10	36	15†	—	
					11.10 "	10	55	20†	—	
					11.31 "	10	92	30†	—	
					11.55 "	11	128	38†	—	
18	4.vi.25 (ii)	L4	51	R.T.	12.50 p.m.	10	—	—	Surface	Weather: cloudless, bright sunshine. Sea: calm.
					1.9 "	10	18	4.6	2.5-5.5	
					1.48 "	10	36	13.6	10-15.5	
					1.29 "	10	55	23.4	15-27	
					2.8 "	11	82	31.8	25-40	
19	17.vi.25	L4	51	R.T.	4.19 p.m.	10	—	—	Surface	Weather: cloudless, brilliant sunshine. Sea: calm.
					4.00 "	10	18	4.5	4-5.5	
					3.40 "	10	36	16.2	15-17.5	
					3.21 "	10	64	23.4	18-27.5	
					2.58 "	10	82	29.8	26-33	
					2.35 "	11	110	48.8	37-52	
20	18.vi.25	L4	51	R.T.	9.3 a.m.	11½	—	—	Surface	Weather: sunshine. Sea: calm.
					8.45 "	10	18	3.2	2-5	
					8.27 "	10	36	7.5	6-9	
					8.6 "	10	64	9.9	7-13	
					7.46 "	10	82	20.8	17-25	
					7.25 "	9½	110	31.4	22.5-35	

LIST OF STATIONS—*continued.*

Station.	Date.	Position.	Depth.	Net.	Time.	Duration of Haul.	Length of Warp.	Fishing Depths.		Remarks.
								Average.	Limits.	
21	19.vi.25	L4	51	R.T.	9.12 a.m.	10	—	—	Surface	Weather : cloudless, bright sunshine. Sea : calm.
					8.54 "	10	18	4	1-5-6	
					8.35 "	10	36	11.1	5-13	
					8.16 "	10	64	12.7	6.5-20	
					7.56 "	10	82	23.3	15.5-26	
					7.35 "	10	110	28.5	25.5-32	
22	1.vii.25 (i)	A	54	R.T.	9.51 a.m.	10	—	—	Surface	Weather : cloudless, bright sunshine. Sea : calm.
					10.12 "	10	18	2	exact	
					10.31 "	10	36	11	exact	
					10.50 "	10	64	19.8	18-21.5	
					11.14 "	10	82	23.1	20-26	
					11.35 "	10	110	30.2	26.5-32	
23	1.vii.25 (ii)	L4	51'	R.T.	12.25 p.m.	10	—	—	Surface	Weather : cloudless, bright sunshine. Sea : calm.
					12.41 "	10	18	3.5	exact	
					12.57 "	10	36	8.8	7-11	
					1.15 "	10	64	21.3	16-25	
					1.33 "	10	82	27.1	21.5-29	
					1.53 "	10	110	36.7	31.5-40	
24	16.vii.25	A	54	R.T.	9.40 a.m.	10	—	—	Surface	Weather : very dull and foggy. Sea : very calm.
					9.58 "	10	20	4	1-8	
					10.16 "	10	40	16.5	14.5-20	
					10.36 "	10	60	22.2	17.5-25.5	
					11.00 "	10	80	32.3	30-36.5	
					11.24 "	10	110	38.8	35-41.5	

25	16.vii.25	A	54	C.M.N.	12.43 p.m.	10	—	—	Surface	Weather : very dull and foggy. Sea : very calm.
					12.58 "	10	10	2.7	1-5	
					1.13 "	10	20	6.5	5-8.5	
					1.30 "	10	40	25.8	17-35	
					1.47 "	10	60	26.8	23.5-32.5	
					2.5 "	10	80	41.8	32-51	
26	29.vii.25	A	54	R.T.	10.4 a.m.	10	—	—	Surface	Weather : mist and rain, very thick, dull. Sea : moder- ate.
					10.24 "	10	18	4.8	2-6	
					10.43 "	10	36	9.1	7.5-14	
					11.3 "	10	64	20.6	18-24	
					11.21 "	10	82	25.8	22.5-30	
					11.45 "	10	110	maximum	only 31*	
27	6.viii.25	A	54	R.T.	9.52 a.m.	10	—	—	Surface	Weather : raining, very dull. Sea : moderate.
					10.12 "	10	18	5	exact	
					10.32 "	10	36	11.1	10-14	
					10.52 "	10	64	19.2	17-24	
					11.4 "	10	82	23.1	21-25	
					11.26 "	10	115	33.6	30-37	



TABLE 3.

		<i>Depth in metres.</i>																																
		Clupea sp.	Gadus merlangus.	G. minutus.	G. pollachius.	G. luscus.	Molva molva.	Onos sp.	Arnoglossus sp.	Scophthalmus norvegicus.	S. unimaculatus.	Zeugopterus punctatus.	Pleuronectes limanda.	P. microcephalus.	Solea variegata.	Ammodytes lanceolatus.	Callionymus sp.	Labrus bergylla.	L. mixtus.	Ctenolabrus rupestris.	Crenilabrus melops.	Centrolabrus exoletus.	Scomber scomber.	Gobius sp.	Lebetus scorpioides.	Blennius ocellaris.	B. gattorugine.	Trigla sp.	Lepadogaster bimaculatus.	Cottus bubalis	Lophius piscatorius.	Liparis montagni.	Total Young Fish.	
May 29th, 1924.	<i>S</i>	7	-	-	-	-	-	11	-	2	-	-	1	-	3	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33
L4. R.T.	<i>11-2</i>	20	5	2	-	1	1	1	-	-	-	2	4	-	2	4	21	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	64
	<i>22-2</i>	45	37	32	-	2	9	3	-	30	-	9	20	21	18	5	320	-	-	-	-	-	-	6	-	-	-	8	-	1	-	-	566	
June 5th, 1924.	<i>S</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4° 11' 30" M.N.	<i>8</i>	4	1	-	-	-	-	11	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22
50° 17' 20"	<i>12-4</i>	20	23	-	-	-	1	-	-	4	-	-	6	15	-	25	2	-	-	3	1	9	25	-	-	-	-	4	-	-	1	-	-	139
	<i>21-2</i>	10	16	-	-	-	-	6	-	-	-	-	1	5	-	70	-	-	-	1	4	-	-	62	-	1	-	12	-	-	-	-	188	
	<i>31-4</i>	5	8	-	-	2	1	-	-	4	-	-	2	2	-	52	-	-	2	4	-	-	67	-	-	-	5	-	1	-	-	-	155	
June 13th, 1924.	<i>S</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3	11	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	15
4° 10' M.N.	<i>3-4</i>	1	3	-	-	1	-	-	-	5	-	-	4	23	1	433	4	1	-	37	1	-	217	-	-	-	1	6	1	-	-	-	739	
50° 18'	<i>8-7</i>	1	6	1	1	1	-	-	-	7	-	-	-	14	1	256	-	-	-	-	4	-	1	70	-	-	-	16	-	-	1	-	380	
	<i>14-5</i>	1	4	1	-	-	2	-	-	3	-	-	-	8	-	178	-	-	-	5	-	-	73	1	-	-	6	1	1	-	-	-	284	
June 17th, 1924.	<i>S</i>	11	-	-	-	-	-	14	-	-	-	-	3	2	4	-	-	-	-	-	-	-	1	7	-	-	-	-	-	-	-	-	-	42
Et. R.T.	<i>12-4</i>	184	-	-	-	-	1	7	3	20	1	-	1	19	8	11	12	-	1	1	1	2	19	114	1	-	-	13	-	-	-	-	-	419
	<i>25-2</i>	107	8	7	-	1	13	25	1	143	1	1	5	116	59	14	121	1	-	-	-	1	16	262	3	-	-	53	1	-	2	-	961	
	<i>57-8</i>	35	4	23	-	1	12	12	-	34	-	-	10	32	8	311	-	1	-	1	-	1	6	95	4	-	-	21	8	-	-	-	618	
June 21st, 1924.	<i>S</i>	-	-	-	-	-	-	3	-	1	-	-	-	-	5	-	5	-	-	-	-	2	-	-	7	-	-	-	-	-	-	-	-	23
4° 10' M.N.	<i>3-8</i>	1	1	-	-	-	-	-	-	2	-	-	1	17	3	144	1	1	-	25	4	1	107	1	-	-	-	9	-	-	1	-	-	319
50° 18' 30"	<i>9</i>	-	10	-	-	-	-	-	-	2	-	-	-	9	5	149	-	3	1	9	-	1	229	-	-	-	1	12	1	-	-	-	432	
	<i>13-3</i>	4	8	-	-	-	-	-	-	5	-	-	5	9	3	166	-	2	-	2	-	-	83	-	-	-	8	-	-	1	1	-	297	

TABLE 4.

		<i>Depth in metres.</i>																																		
		<i>Clupea</i> sp.	<i>Gadus merlangus.</i>	<i>G. minutus.</i>	<i>G. luscus.</i>	<i>Molva molva.</i>	<i>Merluccius merluccius.</i>	<i>Onos</i> sp.	<i>Arnoglossus</i> sp.	<i>Scophthalmus norvegicus.</i>	<i>Pleuronectes limanda.</i>	<i>P. microcephalus</i>	<i>Solea variegata.</i>	<i>Ammodytes lanceolatus.</i>	<i>Callionymus</i> sp.	<i>Labrus bergylla.</i>	<i>L. mixtus.</i>	<i>Ctenolabrus rupestris.</i>	<i>Crenilabrus melops.</i>	<i>Centrolabrus exoletus.</i>	<i>Scomber scomber.</i>	<i>Gobius</i> sp.	<i>Lebetus scorpioides.</i>	<i>Blennius ocellaris.</i>	<i>B. pholis.</i>	<i>B. gattorugine.</i>	<i>Trigla</i> sp.	<i>Cottus bubalis.</i>	<i>Lepidogaster bimaculatus</i>	<i>Lophius piscatorius.</i>	<i>Caranx trachurus.</i>	<i>Liparis montagui.</i>	<i>Trachinus vipera.</i>	<i>Total Young Fish.</i>		
June 25th, 1924.	<i>S.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
L4.	R.T.	13-6	3	3	1	-	-	1	-	2	-	1	7	9	52	12	-	-	1	-	8	78	-	-	-	4	-	-	-	-	-	-	-	-	-	192
		45-5	22	69	16	1	6	1	1	12	16	16	59	8	884	12	2	1	6	1	7	165	-	-	-	1	55	2	7	-	-	-	2	-	1873	
		52	13	35	16	1	4	1	2	-	13	5	12	82	3	534	8	1	1	-	4	128	1	-	1	-	21	-	8	-	-	3	-	897		
June 27th, 1924.	<i>S.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4° 11' C.M.N.	4-3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50° 17'	12-7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	49	
	18-1	1	1	-	-	1	-	-	-	1	-	1	3	8	172	2	-	-	-	-	1	474	1	-	-	-	4	-	-	-	-	-	-	-	670	
	36-2	-	1	-	-	-	-	-	-	1	-	1	3	1	166	-	1	-	3	-	-	101	-	-	-	-	1	-	1	-	-	1	-	281		
July 1st, 1924.	<i>S.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
L4.	R.T.	5-4	4	-	-	-	-	1	2	-	-	1	1	1	7	4	-	16	3	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	42	
	16-4	13	6	-	-	-	-	1	5	2	1	-	2	11	64	7	8	2	7	4	3	20	-	-	1	1	17	-	-	4	-	-	-	179		
	29-2	4	5	2	-	-	-	-	-	7	2	5	1	2	50	5	3	-	1	-	-	47	-	-	-	-	9	-	1	-	-	-	-	144		
	39-3	5	-	5	-	-	-	-	2	5	1	4	2	3	107	2	1	1	1	1	-	83	-	-	2	-	7	-	4	-	-	-	-	236		
July 15th, 1924.	<i>S.</i>	11	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	2	-	-	20	
L4.	R.T.	6-6	33	-	-	-	-	1	-	1	-	-	3	3	-	1	7	1	-	16	9	-	1	-	3	-	3	-	-	-	-	5	-	84		
	13-6	70	-	-	-	-	-	-	2	10	-	2	22	14	-	2	3	-	10	2	68	-	1	-	4	2	-	1	-	12	-	-	-	225		
	19-5	70	-	-	-	-	-	1	1	37	-	7	36	62	-	4	2	1	1	3	106	1	-	1	5	6	-	4	1	8	-	-	-	361		
	34-5	8	-	-	-	-	-	-	-	1	-	1	3	4	42	-	-	-	1	-	62	1	-	-	1	-	-	2	-	-	-	-	-	126		
July 16th, 1924.	<i>S.</i>	4	-	-	-	-	-	-	-	-	-	-	3	-	-	-	1	1	-	1	2	-	-	-	6	-	-	-	-	-	-	-	-	18		
L4.	R.T.	5-3	20	-	-	-	-	-	-	-	-	-	5	2	-	-	2	7	1	9	10	-	-	-	4	-	-	-	-	-	-	-	-	60		
	12-5	45	-	-	-	-	-	-	5	2	-	-	3	15	19	-	4	2	16	5	2	103	-	1	1	-	2	-	-	2	5	-	3	229		
	18-3	41	-	-	-	-	-	1	3	14	-	3	12	47	59	-	3	10	5	3	236	2	-	-	4	4	-	1	1	-	-	-	449			
	31-1	8	-	-	-	-	-	-	1	8	-	3	2	24	50	-	-	3	2	4	-	105	-	-	-	2	2	-	5	-	-	-	-	219		

VERTICAL DISTRIBUTION OF YOUNG FISHES.

TABLE 5.

	<i>Depth in metres.</i>	<i>Clupea</i> sp.	<i>Gadus merlangus.</i>	<i>G. minutus.</i>	<i>G. pollachius.</i>	<i>G. luscus.</i>	<i>Onos</i> sp.	<i>Scophthalmus norvegicus.</i>	<i>Zeugopterus punctatus.</i>	<i>Pleuronectes limanda.</i>	<i>P. flesus.</i>	<i>P. microcephalus.</i>	<i>Solea vulgaris</i>	<i>S. variegata.</i>	<i>Ammodytes tobianus.</i>	<i>A. lanceolatus.</i>	<i>Callionymus</i> sp.	<i>Labrus bergylta.</i>	<i>Chirolophis</i> sp.	<i>Trigla</i> sp.	<i>Cottus bubalis.</i>	<i>Liparis montagui.</i>	<i>Total Young Fish.</i>
April 2nd, 1925. L4. R.T.	S.	30	13	-	7	-	11	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	63
	5	18	8	-	4	-	4	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	39
	12.5	12	2	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	18
	19	21	3	-	-	-	1	-	1	5	-	-	-	-	-	4	1	-	-	-	-	-	36
	27	49	8	4	1	-	1	-	4	4	-	1	3	-	-	5	3	-	-	-	-	-	79
29	75	15	19	-	-	4	-	-	4	-	-	2	-	-	6	7	-	-	-	-	-	132	
April 8th, 1925. L4. R.T.	S.	-	4	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
	6.9	1	10	-	10	-	11	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	34
	16.5	19	3	1	4	-	8	-	-	8	-	-	-	-	-	2	1	-	-	-	-	-	46
	25.3	33	8	3	-	-	6	-	-	6	1	-	-	-	-	-	3	-	-	-	-	-	60
	32.5	32	2	13	-	-	2	-	-	6	3	1	3	-	-	6	7	-	1	-	-	-	76
	37.8	20	5	15	-	1	5	-	-	5	1	-	2	-	-	1	8	-	-	-	-	-	63
April 22nd, 1925. E1. R.T.	S.	-	-	-	-	-	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14
	4.6	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
	15	3	1	-	-	-	2	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	9
	22.1	1	2	-	-	-	7	-	-	4	-	-	3	-	-	-	1	-	-	2	-	-	20
	51.4	1	3	36	1	-	1	-	3	-	-	2	4	-	-	-	24	-	-	-	-	-	75
61.2	3	3	33	-	-	2	-	-	5	-	-	5	-	-	-	13	-	-	-	-	-	64	
April 29th, 1925. L6. R.T.	S.	-	-	-	8	-	22	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	31
	7.8	1	2	1	13	-	11	19	-	2	1	6	-	-	-	4	4	-	-	-	-	-	64
	12.5	9	15	-	5	1	18	55	3	10	1	16	1	-	-	7	7	-	-	3	-	-	151
	24.3	17	40	81	5	4	17	28	4	56	-	16	2	37	-	11	117	-	-	3	-	-	438
	41.1	11	32	87	-	4	4	11	1	30	-	4	1	12	1	5	125	1	-	1	1	1	332

TABLE 6.

	Depth in metres	Clupea sp.	Gadus merlangus.	G. minutus.	G. pollachius.	Molva molva.	Onos sp.	Scophthalmus norvegicus.	Zenogopterus punctatus.	Pleuronectes limanda.	P. flesus.	P. microcephalus.	Solea vulgaris.	S. variegata.	Ammodytes lanceolatus.	Callionymus sp.	Labrus bergylla.	L. mixtus.	Scomber scomber.	Gobius sp.	Lebetus scorpioides.	Blennius pholis.	Trigla sp.	Lepadogaster bimaculatus.	Cottus bubalis.	Liparis montagui.	Total Young Fish.	
May 19th, 1925 (i) A. R.T.	S.	-	3	-	-	-	12	5	-	-	-	-	-	10	-	15	-	-	-	-	-	-	-	-	-	-	-	45
	4-3	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2
	9-9	1	4	-	-	-	-	-	-	1	-	1	-	-	4	7	-	-	-	-	-	-	-	-	-	-	-	18
	20-8	1	17	4	-	-	1	74	1	14	-	15	-	31	17	109	-	1	-	-	-	-	47	-	-	-	332	
	32-6	3	26	66	-	3	2	94	4	59	-	19	-	180	9	508	1	-	-	-	-	-	22	-	-	-	996	
May 19th, 1925 (ii) L4. R.T.	S.	-	-	-	-	-	5	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	7
	5-6	1	-	-	-	-	-	-	-	-	-	-	-	-	4	11	-	-	-	-	-	1	-	-	-	-	-	17
	12-9	16	47	2	-	-	-	23	2	2	-	7	-	1	13	130	3	-	-	1	-	-	6	-	-	-	253	
	18-9	4	124	12	-	-	5	63	10	34	1	6	-	17	32	292	-	-	-	-	-	29	-	-	-	-	629	
	23-7	8	85	43	-	-	2	51	16	107	3	33	1	55	50	249	1	-	-	-	-	28	-	-	2	1	735	
36-5	8	15	58	1	-	3	23	16	46	1	10	3	67	12	322	1	-	-	-	-	8	1	-	4	599			
June 4th, 1925 (i) A. R.T.	S.	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	4
	8	2	-	-	-	-	-	-	-	-	-	-	-	-	12	-	3	-	-	-	-	-	-	-	-	-	-	17
	15	3	1	-	-	-	-	-	-	-	-	-	-	5	8	1	-	-	-	1	-	-	1	-	-	-	-	20
	20	6	9	-	-	-	3	2	-	2	-	2	-	3	187	-	-	-	-	-	-	1	-	-	-	-	217	
	30	6	21	7	-	-	2	6	1	9	-	7	-	3	4	173	1	-	-	12	-	5	-	-	-	-	257	
38	12	21	29	-	1	-	15	1	8	-	3	-	6	7	270	-	2	-	23	-	1	3	-	-	-	402		
June 4th, 1925 (ii) L4. R.T.	S.*	(4)	(6)	(4)	-	-	(7)	-	(2)	-	-	-	(4)	(2)	(161)	-	-	-	(6)	-	-	(1)	-	-	-	-	-	(197)
	4-6	1	1	-	-	-	-	-	-	-	1	-	-	12	23	1	-	-	-	-	-	-	-	-	-	-	-	39
	13-6	-	4	-	1	-	6	-	1	-	-	-	8	4	54	-	-	-	-	1	-	1	-	-	-	-	80	
	23-4	1	25	-	-	-	45	-	6	-	12	-	8	5	164	2	-	-	2	-	-	6	-	-	-	-	276	
31-8	8	14	8	-	-	1	8	-	2	-	4	-	7	3	158	1	-	-	5	1	-	2	-	1	-	223		

\* This catch contained a certain amount of obvious deep-living forms both of plankton organisms and postlarval fish. I think there can be no doubt that a small portion of the previous deep-haul collection must have been overlooked either in a fold of the net or bottom of the bucket. This haul has accordingly been discounted.

TABLE 7.

		<i>Depth in metres.</i>																			<i>Total Young Fish.</i>								
		Clupea sp.	Gadus merlangus.	G. luscus.	Onos sp.	Armoglossus sp.	Scophthalmus norvegicus.	Zeugopterus unimaculatus.	Pleuronectes limanda.	P. microcephalus.	Solea variegata.	Solea lutea.	Ammodytes tobianus.	A. lanceolatus.	Callionymus sp.	Labrus bergylla.	Ctenolabrus rupestris.	Crenilabrus melops.	Centrolabrus exoletus	Scomber scomber.	Gobius sp.	Lebetus scorpioides.	Blennius pholis.	B. gattorugine.	Trigla sp.	Lepadogaster bimaeculatus	Trachinus vipera.		
June 17th, 1925 L.A. R.T.	S.	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	3
	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	16	-	-	1	-	-	-	-	-	18
	16.2	4	3	-	-	-	-	-	-	-	-	-	1	6	-	-	-	-	5	1	-	-	-	-	-	-	-	-	21
	23.4	4	7	-	-	-	4	-	-	-	7	-	-	1	40	-	-	-	3	-	-	-	-	-	-	-	-	-	66
	29.8	10	44	-	-	-	3	-	-	2	5	-	-	5	45	-	1	-	7	-	-	-	-	-	3	-	-	125	
48.8	3	33	1	-	-	1	-	1	-	1	-	-	1	30	1	-	-	-	1	-	-	-	-	-	2	-	-	75	
June 18th, 1925 L.A. R.T.	S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	3
	7.5	4	1	-	-	-	-	-	-	-	1	-	-	-	2	-	1	-	-	4	-	-	-	-	-	-	-	-	13
	9.9	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	4	1	-	-	-	-	-	-	-	9
	20.8	2	-	-	-	-	-	-	-	-	-	-	-	-	26	-	-	-	-	1	1	-	-	3	1	-	-	-	34
31.4	8	-	-	-	-	2	-	2	-	2	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-	-	32	
June 19th, 1925 L.A. R.T.	S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2
	4	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	3
	11.1	5	3	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	12
	12.7	4	10	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	3	1	-	-	1	-	-	-	-	29
	23.3	1	2	-	-	-	8	-	2	2	5	-	-	1	21	-	-	-	-	2	3	-	-	2	2	-	-	-	51
28.5	4	13	-	1	-	7	-	1	3	1	-	-	-	9	-	-	-	-	10	2	-	-	-	2	-	-	-	53	
July 1st, 1925 (i) A. R.T.	S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	4	-	-	-	1	1	-	-	-	12
	11	5	2	-	-	2	-	-	-	-	-	-	-	1	13	-	2	1	-	1	-	-	1	5	-	-	1	34	
	19.8	2	1	-	-	-	-	-	1	-	-	-	-	4	31	-	2	-	-	1	-	-	1	4	1	-	1	49	
	23.1	5	10	-	-	-	1	1	-	-	1	1	-	5	56	1	-	-	-	1	1	1	1	4	11	-	1	101	
30.2	12	2	1	-	-	2	-	-	-	2	-	-	7	129	1	-	-	-	-	2	1	-	2	7	-	3	171		

TABLE 8.

	<i>Depth in metres.</i>	<i>Clupea</i> sp.	<i>Gadus merlangus.</i>	<i>Molva molva.</i>	<i>Arnoglossus</i> sp.	<i>Scophthalmus norvegicus.</i>	<i>Pleuronectes limanda.</i>	<i>P. microcephalus.</i>	<i>Solea variegata.</i>	<i>Ammodytes lanceolatus.</i>	<i>Callionymus</i> sp.	<i>Labrus bergyllia.</i>	<i>Ctenolabrus rupestris.</i>	<i>Crenilabrus melops.</i>	<i>Centrolabrus exoletus.</i>	<i>Scomber scomber.</i>	<i>Gobius</i> sp.	<i>Lebetus scorpioides.</i>	<i>Blennius pholis.</i>	<i>B. ocellaris.</i>	<i>B. gattorugine.</i>	<i>Trigla</i> sp.	<i>Lepidogaster bimaculatus.</i>	<i>Trachinus vipera.</i>	<i>Raniceps raninus.</i>	<i>Total Young Fish.</i>
July 1st, 1925 (ii) L4. R.T.	S.	-	-	-	-	-	-	-	-	9	9	-	-	-	-	1	-	-	1	-	2	-	-	-	-	13
	3.5	4	-	-	-	-	-	-	-	5	4	-	-	-	-	2	-	-	1	-	3	-	-	-	-	19
	8.8	5	-	-	4	-	-	-	-	1	10	-	-	-	-	4	-	-	-	-	3	1	-	3	-	31
	21.3	1	12	-	1	-	-	-	-	4	23	-	-	-	-	-	1	-	-	-	3	4	-	3	-	53
	27.1	2	2	-	3	1	-	-	-	5	21	-	-	2	-	-	-	-	-	-	4	2	-	3	-	45
	36.7	10	1	-	2	11	2	3	2	20	143	-	-	-	-	-	56	-	2	-	1	11	1	1	1	267
July 16th, 1925. A. R.T.	S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
	4	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	3	-	-	1	-	5
	16.5	-	3	-	-	-	-	-	-	7	34	1	1	-	-	-	11	1	-	-	2	-	2	4	-	66
	22.2	1	-	-	5	1	-	-	-	11	59	-	-	-	-	3	8	-	-	-	2	1	3	3	-	94
	32.3	-	-	-	3	1	-	2	1	8	43	-	-	-	-	9	1	-	-	-	-	2	2	-	-	70
	38.8	-	-	1	-	1	-	1	-	6	35	-	-	-	-	2	8	-	1	-	-	3	2	1	-	62
July 16th, 1925. A. C.M.N.	S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
	6.5	3	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	-	-	9	-	15
	25.8	14	-	-	2	-	-	-	-	24	43	-	-	-	-	9	-	-	-	-	-	1	-	2	-	95
	26.8	5	-	-	1	1	-	-	-	13	88	-	-	-	-	25	-	-	-	1	-	1	-	1	-	136
	41.8	9	1	-	-	2	-	2	-	10	149	-	-	-	-	116	-	-	-	-	-	2	1	-	-	292
July 29th, 1925. A. R.T.	S.	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	4
	4.8	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	4
	9.1	-	-	-	2	-	-	-	-	3	9	-	-	-	1	-	-	-	-	-	-	-	-	1	-	16
	20.6	1	-	-	1	-	-	-	-	11	5	-	-	-	-	1	-	-	-	1	-	-	1	-	-	21
	25.8	-	1	-	44	-	-	1	-	21	5	-	-	-	1	-	-	-	-	-	-	-	-	1	-	74
	29	1	1	-	18	-	-	-	-	30	14	-	1	-	3	-	5	3	-	-	3	-	-	-	-	79

August 6th, 1925.  
A. R. T.

S.	Depth in metres.	
5		
11-1		
19-2		
23-1		
33-6		
1	1	Clupea sp.
2	1	Arnoglossus sp.
1	8	Ammodytes lanceolatus.
3	4	Callionymus sp.
1	1	Ctenolabrus rupestris.
1	3	Crenilabrus melops.
1	3	Centrolabrus exoletus.
9	11	Gobius sp.
5	3	Lebetus scorpioides.
1	1	Blennius pholis.
1	3	B. ocellaris.
2	1	B. gattorugine.
1	1	Trigla sp.
1	1	Lepadogaster candolli.
2	1	L. bimaculatus.
2	1	Liparis montagui.
1	3	Trachinus vipera.
1	1	Raniceps raninus.
28	0	Total Young Fish.

TABLE 9.

TABLE 10.

		<i>Depth in metres.</i>																							
		Clupea sp.	Clupea sprattus.	Gadus merlangus.	G. minutus.	G. pollachius.	G. luscus.	Molva molva.	Onos sp.	Scophthalmus norvegicus.	Zeugopterus punctatus.	Z. unimaculatus.	Pleuronectes flesus.	P. limanda.	P. microcephalus.	Solea vulgaris.	S. variegata.	Ammodytes tobianus.	A. lanceolatus.	Ammodytes sp.?	Callionymus sp.	Chirolophis sp.	Trigla sp.	Lepadogaster bimaculatus	Cottus bubalis.
March 3rd, 1924. L4. R.T.	S.	3	38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	2	-	-	-
	M.	8	86	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	B.	17	77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
April 25th, 1924. L4. R.T.	S.	3	-	7	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-
	M.	4	-	20	1	-	-	-	1	-	-	-	-	14	1	13	-	2	-	-	-	21	-	3	-
	B.	11	-	7	7	-	1	-	1	-	-	-	-	14	-	5	-	1	-	-	-	18	-	2	-
April 30th, 1924. L4. R.T.	S.	40	-	9	-	14	-	-	-	1	-	1	-	-	-	-	-	3	1	-	3	-	-	-	2
	M.	5	-	4	-	1	-	-	1	-	-	-	-	14	-	2	-	3	-	6	2	-	1	-	-
	B.	13	-	5	3	1	-	-	1	1	-	-	-	13	-	3	-	1	-	4	3	-	-	-	-
May 7th, 1924. L4. R.T.	S.	1	-	14	-	6	-	-	1	-	-	-	-	3	-	-	-	-	-	-	8	-	1	-	2
	M.	8	-	17	2	-	-	-	-	1	-	-	-	11	-	1	4	-	14	-	46	-	3	1	-
	B.	1	-	35	13	-	2	-	-	6	2	1	-	42	1	12	1	-	-	13	83	-	8	-	-
May 12th, 1924.* L4. R.T.	S.	3	-	-	-	-	-	-	7	3	-	-	-	-	2	2	-	-	-	-	4	-	-	-	-
	M.	1	-	11	5	-	-	-	2	19	-	-	-	54	1	4	-	-	14	-	67	-	6	-	-
	B.	3	-	24	165	-	1	3	-	41	-	-	-	80	3	6	26	-	66	-	195	-	10	-	2
May 19th, 1924. L4. R.T.	S.	-	-	1	-	-	-	-	2	1	-	-	-	-	-	-	2	-	-	-	4	-	-	-	-
	M.	1	-	23	3	-	-	-	-	2	1	-	-	21	-	-	1	-	-	1	17	-	5	-	-
	B.	-	-	7	4	-	-	-	-	2	1	-	-	12	1	-	1	-	-	1	34	-	3	-	-

\* 20 min. hauls.

S. = Surface. M. = Midwater. B. = Bottom.





# Notes on Experiments on the Early Developmental Stages of the Portuguese, American and English Native Oysters, with Special Reference to the Effect of Varying Salinity.

By

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With 1 Figure in the Text.

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## 1. INTRODUCTION.

WHILE staying at the Marine Biological Laboratory, Plymouth, in the summer of 1925, I spent my time chiefly in the study of oysters, of which the following three species were available, the American, *Ostrea virginica*: the Portuguese, *O. (Gryphæa) angulata*: and the English native oyster, *O. edulis*. These three species are cultured in this country, although the first two were originally introduced from other countries.

It is well known that there is an intimate relation between the development and growth of the oyster and the salinity of the surrounding medium, the sea-water.

The chief purpose of this study was to determine to what extent the early developmental stages of the oyster are affected by the various concentrations of salinity of the sea-water, in what range of salinity its development is possible, and whether the range of salinity differs for the different species of the oysters, and if so, to find the optimum salinity for each species.

I am greatly indebted to Dr. E. J. Allen, the director of the Marine Biological Laboratory, Plymouth, who afforded me every facility for my study, and to Dr. J. H. Orton for his valuable suggestions and the trouble he took to enable me to obtain the material. I wish to acknowledge also my thanks to Mr. H. W. Harvey, the hydrographer of the Laboratory, for his kind help in determining the salinity of culture-media.

## 2. CULTURE-MEDIA.

In the present study, observations were made on the metamorphosis of the larvæ in the course of their development. Culture-media of different grades of salinity were prepared, using sea-water collected a few miles from Plymouth in the English Channel. Media of higher salinity were obtained by evaporating this water in the air. Those having lower salinity were prepared by the addition of distilled water. Thus, culture-media of different grades of salinity, from a very low to an exceedingly high one, were obtained.

Two series of culture-media were always prepared. In the one series the media (200 c.c.) were kept in glass finger bowls with glass covers. In the other series, which acted as a control, the same volumes of media were kept in honey jars, the lids of which were tightly screwed down, so as to avoid evaporation, leaving enough space in the jars for the air. The salinities of the media were determined by titration and checked against "normal water" sent from Copenhagen.

## 3. AMERICAN OYSTER (*Ostrea virginica*).

### (a) *Observations on development in waters of different salinities.*

This oyster has been introduced from America, and is now cultured in some parts of England. The material for the present study was sent from the Orford Oysterage of the Mac Fisheries Ltd., Orford, Suffolk, to whom I express my thanks.

The sexes in this species are normally separate and a hermaphrodite condition has only once been recorded in a single specimen by Kellogg (11). The ova when just spawned or squeezed out of the ovary artificially are not spherical, but rather irregular in shape, having a peculiar form resembling a flask or a pear; with a round body and a long tapering process. They have no gelatinous covering as often occurs in other bivalve mollusks. The surface of the ovum soon after it is shed into the water does not appear smooth, having many polygonal facets and ridges which, probably, are caused by the mutual pressure of the ova in the ovary, where they are packed closely together. However, after a little while in the water, the ovum changes its form and becomes spherical. The diameter of the egg when it has become spherical measures from 0.045 mm.

to 0.054 mm. The nucleus is comparatively large and very clear, but soon after fertilisation has taken place, it disappears, so that it is easy to discern which eggs have been fertilised.

The present experiment was carried out late in July, i.e. in the spawning season of the species in this country.

Artificial fertilisation was very successful; almost 100 per cent of the eggs developed, provided the culture medium was favourable.

The following table shows the periods of time after insemination necessary for attaining the respective developmental stages. The temperature during the experiment fluctuated from 18° C. to 21.5 C. As there is variation according to individuals, the average time is given in all cases.

TABLE I.

Appearance of 1st polar body . . .	40-50 min.
"    "    2nd    "    "    . . .	45-60 min.
1st segmentation . . . . .	1 hour 15 min.-1 hour 30 min.
2nd    "    . . . . .	1 hour 20 min.-2 hours.
Blastula, at the beginning of rotating movement, about . . . . .	6 hours 30 min.
Beginning of invagination; the larva swims about . . . . .	8 hours.
Trochophore larva, about . . . . .	24 hours.
Larval shell grows large to cover the body except prototroch, about . . . . .	52 hours.
Larval shell measures $67 \times 78 \mu$ , the larva begins to feed, about . . . . .	60 hours.

In other concentrations of salinity which are unfavourable, development does not proceed so well, and retardation and other abnormal phenomena inevitably occur.

The following twenty-four culture-media which have varying grades of salinity were prepared for the rearing of embryos and the observation of effects of the different concentrations upon their development.

TABLE II.

	Salinity ‰		Salinity ‰		Salinity ‰
No. 1	52.1	No. 9	38.5	No. 17	24.5
No. 2	50.4	No. 10	36.8	No. 18	22.8
No. 3	48.7	No. 11	35.1	No. 19	21.0
No. 4	47.0	No. 12	33.3	No. 20	19.3
No. 5	45.3	No. 13	31.6	No. 21	17.5
No. 6	43.6	No. 14	29.8	No. 22	15.8
No. 7	41.9	No. 15	28.0	No. 23	14.0
No. 8	40.1	No. 16	26.3	No. 24	12.3

Ripe eggs and sperm were taken from female and male parents respectively. They were mixed, inseminated by the dry method, and then about 0.25 c.c. of the mixture was transferred to each culture medium.

To examine the course of the development in the media, the embryos or larvæ were picked up from each receptacle by a small pipette, dropped in rows on to one slide and studied simultaneously under the microscope.

The following description gives a rough outline of the course of development in the various concentrations :—

- No. 1. Soon after having been transferred into the medium, the eggs shrink greatly and become irregular in their outline. At the end of 24 hours, very few eggs exhibit segmentation, which if it occurs is always abnormal. The greater part of the eggs remain unchanged, and show no sign of development. All degenerate in 3 days.
- No. 2. Only very few eggs give off polar bodies at the end of 5 hours or more, or segment a few times at the end of 8 hours. Embryos are all abnormal, and no further progress of the development is seen. All degenerate before the morula stage.
- No. 3. As in No. 2.
- No. 4. The majority of eggs remain undeveloped, while some give off polar bodies in 3 hours or more and form embryos, almost all of which are abnormal. A very few produce at the end of 28 hours ciliated embryos which are unhealthy and very abnormal in structure, yet exhibit a rotating movement at the bottom of the receptacle. They all degenerate in 3 days.
- No. 5. Some of the eggs remain undeveloped. A number develop to form embryos and larvæ. Their progress in development is very uneven; at 20 hours after insemination, some are in the first or second segmentation stage, some in the morulæ, others in the ciliated rotating larval stage; after 28 hours some become swimming larvæ. All of them are abnormal, and none can attain further stages of development.
- No. 6. The greater part of the eggs begin to develop, but their segmentation is abnormal and the progress of development uneven. A few of them become trochophores at the end of 48 hours, but no further stages are observed.
- No. 7. Almost all the eggs begin to develop, but their segmentation is abnormal and the developmental process irregular and uneven. Those which attain the swimming trochophore stage with a small anlage of the laval-shell are fairly numerous, but none become good shell-larvæ.

- No. 8. Segmentation and the subsequent course of development are abnormal and uneven. Many eggs attain the swimming larvæ and trochophore stage, but hardly any become good shell-larvæ.
- No. 9. Only a small number of the embryos can produce good, healthy shell-larvæ.
- No. 10. The progress of development is uneven, and many abnormal forms are to be seen. Some produce healthy shell-larvæ.
- No. 11. All eggs develop well, but some abnormal embryos and larvæ are observed. The progress of development is rather uneven.
- No. 12. Fairly many produce good shell-larvæ.
- No. 13. The progress of development is quite even. Almost no abnormal forms are met with. Very many produce good shell-larvæ.
- No. 14. The progress of development is very even. No abnormal forms of embryos or larvæ are observed. All are very active, and produce the shell-larvæ at the end of 2 days.
- No. 15. As in No. 14.
- No. 16. As in No. 15.
- No. 17. As in No. 16.
- No. 18. Almost the same as in No. 17, but the progress of development is a little retarded.
- No. 19. As in No. 18.
- No. 20. A small number of eggs remain undeveloped. The progress of development is uneven and fairly retarded. The blastomeres are swollen. Many shell-larvæ are produced at the end of 4 days.
- No. 21. Many eggs remain undeveloped. Abnormal embryos are numerous. The development is much retarded. Many swimming larvæ, but only a few shell-larvæ are produced.
- No. 22. Blastomeres are very much swollen, and have a tendency to separate from each other. Non-segmenting eggs are numerous. The progress of development is very uneven and retarded. Many abnormal forms are observed. Fairly many swimming larvæ, fewer trochophores, and almost no shell-larvæ are produced.
- No. 23. A number of the eggs remain undeveloped. Many exhibit abnormal segmentation. Some produce abnormal and unhealthy swimming larvæ, but no shell-larvæ.
- No. 24. Abnormal segmentation occurs in a number of eggs. All degenerate before attaining the ciliated embryo stage.

The preceding description shows roughly how the development of the oyster embryos is affected by the various grades of salinity.

From this result it can be seen that in high salinity, such as No. 1–No. 3, the eggs are much plasmolysed and a large proportion show no sign of development, remaining unsegmented. Although a few form polar bodies and reach the early segmentation stage, this process is very slow, they are all abnormal and the arrangement of the blastomeres is irregular. They all degenerate and disintegrate sooner or later before attaining the ciliated stage.

In No. 4–No. 8, there are some non-segmenting eggs; others are developing ones, and their number as well as the stage which they can attain are both variable and depend on the grade of salinity; the number increases and the stage reached progresses further with the decrease of salinity. However, the development never reaches the stage of shell-larvæ. Moreover, it is noticeable that in high salinity as in No. 1–No. 8, the progress of development is uneven, and segmentation and growth are abnormal.

In No. 9–No. 12, the conditions become more favourable, and this is even more marked in No. 13. Normal healthy shell-larvæ are obtained in these cases, and they increase much in number in No. 13, although more or less abnormal forms are still present.

In No. 14–No. 17, the conditions are most favourable; all eggs develop, the process of development is very even, and very short, the larvæ are very active, and almost all develop up to the shell-larvæ and further stages.

In No. 18–No. 19, the conditions are not so favourable as in the previous Nos.; there are some non-segmenting eggs. The progress of development is a little retarded, and some embryos develop abnormally.

In No. 20 and No. 21, eggs become swollen soon after being placed in the media. There are non-segmenting eggs, the number of which increases very much in No. 21. Many embryos with an irregular and abnormal arrangement of blastomeres are produced. The progress of development is uneven, much so in No. 21. There is an abrupt decrease in the number of the normal shell-larvæ in No. 21 compared with No. 20.

In No. 22 and No. 23, eggs become much swollen and non-segmenting eggs are many. Abnormal forms are also numerous. The developmental process is very uneven; at the end of three days, all the stages of development are represented, i.e. segmentation, morula, blastula, young swimming larva, trochophore, and a few shell-larvæ.

In No. 24, a number of eggs remain undeveloped. Others segment only abnormally and very slowly, but none can attain the ciliated moving or swimming larval stages. All degenerate and disintegrate in two days.

(b) *Some phenomena observed.*

I wish now to discuss some particular phenomena in the developmental process caused by unfavourable salinity of the medium, although several points regarding the phenomena have already been mentioned above.

*Retardation of development owing to unfavourable salinity conditions*; It is a well-known fact that the rate of development of any animal is influenced by temperature. Stafford (16) and others have already observed its influence on the development of the oyster.

However, as far as I am aware, the effect of salinity on the rate of development of the oyster or any other animal has not yet been well studied. As shown above, oyster eggs used in the experiments which were fertilised at the same time and cultured under the same conditions, except in regard to salinity, took different periods of time for their development; a short time in a moderate concentration, and longer when the concentration was too high or too low. Thus, the retardation increases in both directions, in the higher and the lower concentrations of salinity.

This fact is one of the characteristic marks for determining the favourable salinity of a medium for the development of the oyster.

*Abnormal forms due to the too high and the too low concentrations of the salinity*; O. and R. Hertwig (10) observed in the frog egg abnormal early development in plasmolysed condition in salt water; in certain circumstances segmentation took place in the form of "Knospenfurchung." Loeb (12) showed that in high concentration (addition of NaCl to the natural sea-water) of the medium cleavage of *Arbacia* eggs was irregular and abnormal. Herbst (6, 7, and 8) also observed that the blastomeres of *Echinus* in its early development have a great tendency to lie apart or become isolated from each other in Ca-free or other artificial sea-water.

In the case of the oyster, I also observed a phenomenon similar to those noted by previous authors, although the media which I used were different; their component salts and their mutual ratios are unaltered as compared with the natural sea-water, only the concentration as a whole is altered. The process of cleavage of the oyster embryos has some difference embryologically from that of either the sea-urchin or the frog, but they are all similar in that their early development is by total segmentation.

In the oyster, in too high as well as in too low concentration of salinity, many individuals showing abnormal segmentation occur which they exhibit in some peculiar features. For example, some very small blastomeres are often formed abnormally resembling budding of fungus plants, as "Knospenfurchung," described by O. and R. Hertwig (10) in the case of the egg of the frog. The arrangement of blastomeres of such abnormal oyster embryos is therefore somewhat reminiscent of a colony



of yeast. Such a deformed larva cannot remain alive long and dies sooner or later.

Moreover, in too high and too low salinity, the blastomeres which are formed by segmentation have a great tendency to lie apart from each other, while in normal development they lie closely attached and applied to one another. In some cases, some of the blastomeres often separate from their fellows, and in this state they undergo further development, so that they cannot become normal larvæ. Accordingly, this leads to abnormality or monstrosity of the embryos and larvæ.

Such abnormal forms continue their further development to some extent, especially in the too high concentration, and can often attain a swimming stage, developing cilia on the body surface.

As regards the development of isolated blastomeres of the embryo, there exists evidence relating to other animals. Amongst those, the results of studies on echinoderm eggs by Driesch (6), Loeb (12), and Morgan (13) are most useful for reference. They succeeded in producing small, complete larvæ, "partial larvæ" of Morgan. Their methods of obtaining the isolated blastomeres were not always the same. Driesch used the application of Ca-free artificial sea-water, the other workers mechanical ways, but their results agree fairly well with each other in that they succeeded in producing complete dwarf larvæ of sea-urchins (*Arbacia*, *Echinus*, and *Sphærechinus*).

Although the primary aim of this study was not the investigation of "partial larvæ" in the case of the oyster, it was observed that they did occur not infrequently in the natural sea-water whose salinity is very high.

The isolated blastomere or blastomeres can attain a trochophore or more advanced stage of larva whose size is naturally much smaller than normal, yet it is very active and swims very well in the medium. However, I cannot help doubting whether such dwarf larva can develop further to produce healthy normal spat.

The production of abnormal forms of oyster larvæ in too high as well as too low salinity is, in my opinion, entirely due to the exceedingly high or low osmotic pressure of the medium.

The appearance of abnormal forms in the medium is also a good indication as to whether the concentration of the medium is moderate or not.

*Non-segmenting eggs due to unfavourable salinity*; In higher and lower concentrations of salinity more frequently than in a moderate one, there are eggs which do not undergo segmentation and remain long undeveloped, eventually dying. They are impregnated eggs, and it would appear that the fertilisation is well performed as their nuclei disappear. Some of them give off the first polar body or also the second, but then cease to develop further. Such non-segmenting eggs are met with both in the higher

and in the lower salinity, but not in the moderate one. Their number increases divergently from the moderate salinity towards the higher on the one hand and the lower on the other.

It is thus obvious that their occurrence is the direct result of an unfavourable effect of the unsuitable salinity.

*Consideration of the effect of salinity conditions on the development*; As described above, the early development of the oyster is affected by the grades of salinity whose influence is manifested in many ways, namely, the rate of development, irregularity of development in unsuitable conditions, the occurrence of non-segmenting eggs, of abnormal forms, and of plasmolysed and plasmoptysed states of the embryos. These facts are good indications of the effect of salinity conditions on the development of oyster larvæ. For the American oyster they may be summarised in the following table:—

TABLE III.

Salinity ‰			
15	.	.	Lowest limit.
17-21	.	.	Too low.
22-24	.	.	Favourable.
25-29	.	.	Optimum.
30-33	.	.	Favourable.
34-38	.	.	Too high.
39	.	.	Highest limit.

*Feeding experiments on young shell-larvæ*; I wish to add here some notes on the feeding of larvæ which begin to take food at least two days after fertilisation.

Previous investigators as, for instance, Stafford (16), have noticed that the larvæ which have developed to the stage of young shell-larvæ are very difficult to keep alive long and to grow in the culture-media; this was probably due to a lack of suitable food, which consists of very minute organisms.

Dr. E. J. Allen has several kinds of minute algæ in his laboratory kept in the condition of "persistent culture." He placed very kindly samples of his important cultures at my disposal for the feeding of oyster larvæ. At first, I used for the feeding a species of *Nitzschia*, a plankton alga, one of the smallest Diatoms, but this alga is still too large to be taken by the larvæ, and they cannot feed on it. Next, *Pontosphaera Huxleyi*, a flagellate, 2.5-3 $\mu$  in size, was tried. The oyster larvæ feed on it well; the algæ taken are easily discernible in the stomachs of the larvæ whose bodies are quite transparent when young. They grow until their shells become 145 $\times$ 130 $\mu$  in diameter; the intestinal part of their digestive tract, which was at first short and quite simple, elongates much and becomes twisted to form a loop. The umbo of the shells swells up and

protrudes in the form of a vault. The liver is tinged with a green pigment which makes this organ very conspicuous in the body which itself becomes gradually dark and opaque under the microscope.

The larvæ live in jars of sea-water containing this flagellate for as long as two weeks or more, but their growth is not so successful as to attain a larger size than that mentioned above, although there is no marked sign of other unhealthy conditions.

#### 4. PORTUGUESE OYSTER (*O. (Gryphæa) angulata*).

The sexes of the species are normally separate, as has been investigated and reported by M. Bouchon-Brandley (2), J. A. Ryder (15), and J. L. Dantan (3, 4, and 5). However, I. Amemiya (1) observed the occurrence of hermaphroditism of this species, when ripe eggs and sperm were found in the same individual and in the same tubule of the gonad.

Oysters used for the present study were sent from Whitstable Oysterage, where they had been relaid and cultured.

The experiment was performed in the last half of July. Their reproductive elements were fully ripe at that time. The size of the egg is exactly the same as that of the American species.

Artificial fertilisation is very successful. The following table shows the time which under most favourable conditions it takes after insemination to attain the respective developmental stages. The temperature during the experiment fluctuated from 20° C. to 23.°5 C.

TABLE IV.

Appearance of 1st polar body . . . . .	40-50 min.
"    "    2nd    "    "    . . . . .	45-60 min.
1st segmentation . . . . .	1 hour 10 min.-1 hour 20 min.
2nd    "    . . . . .	1 hour 20 min.-1 hour 30 min.
Blastula, at the beginning of rotating movement, about . . . . .	5 hours 30 min.
Beginning of invagination; the larva swims about . . . . .	8 hours.
Trochophore larva . . . . .	14 hours.
Larval-shell grows large to cover the body except prototroch, about . . . . .	24 hours.
Larval-shell measures 70 × 75μ and the larvæ begin to feed, about . . . . .	40 hours.

Thus, the progress of development is very speedy, as the temperature was fairly high. This table is the record of development in the medium with optimum salinity.

To observe the conditions in the various grades of salinity, many media of graded concentration were prepared, and the development of fertilised eggs was studied just in the same way as in the American oyster. The course of development and the phenomena observed in the experiment are also similar, so that it would be unnecessary to describe them in detail for this species particularly.

From results I obtained, it may be concluded that the salinity conditions for the Portuguese oyster are as shown in the following table:—

TABLE V.

Salinity ‰			
21	.	.	Lowest limit.
22-24	.	.	Too low.
25-27	.	.	Favourable.
28-35	.	.	Optimum.
36-38	.	.	Favourable.
39-42	.	.	Too high.
43	.	.	Highest limit.

Shell-larvæ which have attained the size above mentioned by about 2 days, do not grow further, as they are in rather a starving condition owing to the lack of suitable food in the medium, yet they are very active and healthy and live for many days in the Laboratory.

##### 5. ENGLISH NATIVE OYSTER (*O. edulis*).

This species has long been known as hermaphrodite, and its sexual phenomena were studied very fully by Dr. J. H. Orton (14, *a* and *b*).

It has very large eggs, much larger than those of dioecious species, such as the American and the Portuguese oysters. The ovum measures on an average 0.10 mm. in diameter.

The mode of fertilisation and early development are quite different from those of dioecious species, as fertilisation takes place in the parent's shell cavity, and the early part of the life of the offspring is normally spent there. The segmentation of the fertilised eggs and the general course of development are, however, morphologically the same.

Artificial fertilisation is not successful in this species, but it does not seem difficult to obtain embryos of the early developmental stage, as the parent oyster in the spawning season, if it is taken out of the water and left in the air, very often extrudes its very young spawn from the shell.

The material used for the present study was placed at my disposal by Dr. J. H. Orton, who was at that time engaged in another line of study on the oyster.

By the time the material was obtained and the experiment started the embryos were already young morulae, whose age could be computed as about 20 hours after fertilisation. They were put into the graded media, and their developmental conditions were observed in the same way as in the previous experiments. The time was late July, and the temperature during the experiment fluctuated from 16.2° C. to 18° C.

The development of embryos in the media of moderate salinity was normal in that they reached the trochophore stage in 3 days and a half. Invagination began 7 hours after the embryos were put into the medium; ciliated, rotating larvae were obtained after 2 days, and good trochophores after 3 days and a half. They were very active and healthy.

On the fifth day, a few attained the stage having shell-anlage, but many of them died and some unhealthy signs were observed. On the sixth day all were dead, and the experiment could not be continued to observe further developments.

Observations on the course of development in the graded media were made as in other species. Phenomena which were noticed in the American and the Portuguese oysters occurred, namely, the speedy process of development in moderate salinity, retardation in the unfavourable ones, the occurrence of abnormal embryos and larvae, etc. But it is unfortunate that the experiment ceased before satisfactory results were obtained.

However, from the record which was obtained, the following result (Table VI) may be derived, which shows the relation between salinity and development of the English native oyster:—

TABLE VI.

Salinity ‰	.	.	.	Lowest limit.
24	.	.	.	Too low.
25-26	.	.	.	Favourable.
27-30	.	.	.	Optimum.
31-35	.	.	.	Favourable.
36-40	.	.	.	Too high.
41-43	.	.	.	Highest limit.
45	.	.	.	

As stated already, observations were not made at the very beginning of the development of the fertilised eggs.

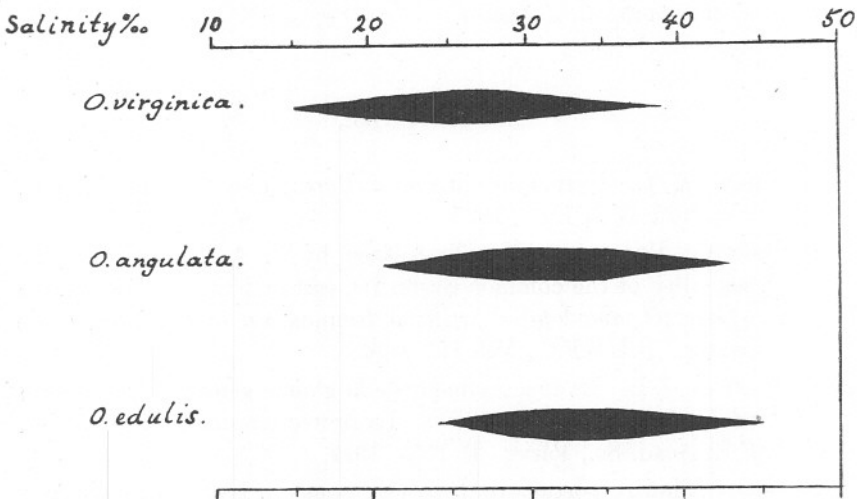
The rearing of young larvae is not easy in this species, and to follow the metamorphic changes of larvae in the culture medium in the laboratory is very difficult. Yet, in the present experiment, embryos lived for 5 days and exhibited reliable reactions to graded concentrations.

I am not inclined to regard the results obtained as sufficient to form conclusions on, but as far as they go they appear to be quite reliable.

## 6. GENERAL CONSIDERATION OF SALINITY EFFECTS ON THE THREE SPECIES.

As has been described, the three species of oyster here dealt with have each their own salinity ranges for early development.

Fig. 1 is a graphic representation which shows at a glance how these ranges compare with one another.



TEXT FIG. 1.—Diagram showing the Salinity ranges for the three species of oyster *O. virginica*, *O. angulata* and *O. edulis*. The thickest portion in each case represents the range of optimum salinity.

It can be seen from the diagram that, with some characteristic variations, the three salinity ranges coincide in their main portions. The American oyster lies in the lowest, the Portuguese is intermediate, while the English native lies in the highest salinity range.

## SUMMARY.

1. The period of time which the oyster larva requires to attain its respective developmental stages was measured and recorded in *O. virginica* and *O. angulata*.
2. The development in various concentrations of salinity was studied in the three species, *O. virginica*, *O. angulata*, and *O. edulis*.
3. In optimum salinity, all the impregnated eggs undergo segmentation and further development; the rate of development is uniform and its progress speedy.

4. In the too high as well as in the too low salinity, "Knospenfurchung" and abnormal larvæ were observed. In the too high salinity, "partial larvæ" were not infrequently met with.

5. Ranges of salinity optimal and possible for the development of the three species were determined.

6. The larvæ of the American oyster which were raised by artificial fertilisation and fed with *Pontosphaera Huxleyi* grew until their shells measured  $130 \times 145\mu$  in diameter.

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## On the Penetration of Light into Sea Water.

By

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With 3 Figures in the Text.

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AN account has recently been given by one of us (1) of a telephone method of measuring photo-electric currents, which enables measurements of submarine illumination to be made in a small vessel by means of photo-electric cells; also of some preliminary measurements made by its aid near Plymouth, in the autumn of 1924. The present paper contains a brief description of the apparatus employed, and a record of the results of further observations made on board the steam trawler *Salpa*, belonging to the Marine Biological Association, near Plymouth in the autumn of 1925. For details as to the construction of the apparatus reference must be made to the previous paper.

### METHOD OF MEASURING THE PHOTO-ELECTRIC CURRENT.

Fig. 1, which is reproduced from the previous paper, shows the general scheme of the electrical connections. All subsidiary circuits, such as the potentiometer standard cell, the amplifier circuits, etc., have been omitted from the diagram for the sake of simplicity. B is the high tension battery, of the usual wireless receiver type, which provides the anode potential for whichever of the photo-electric cells, D or E, is plugged into it. The current, which passes through the cell when exposed to light, also passes through a "Zenite" wire resistance, R, of 51,300 ohms, and a similar safety resistance, S, of about 19,000 ohms. The potential difference between the ends of R is measured by means of a potentiometer, P. Telephones, T, are used to detect any current due to lack of balance, this current being rendered intermittent by means of a special form of interrupter, I. The sensitivity is increased to a suitable extent by means of a two-stage Marconi note magnifier, A, the amplification being controlled by varying the filament currents of the valves. The condenser, C, also increases the sensitivity. Guard ring wires, to prevent errors due to surface leakage, are connected to the negative terminal N.

The interrupter, which is worked by an electric buzzer, forms an independent unit, which must be kept 5 or 6 feet away from the other circuits to prevent induction effects. The rest of the apparatus, with the exception of the photometers and their leads, and, of course, the head telephones, is rigidly mounted in a strong wooden box, which can be firmly lashed to the bench in the deck cabin in which the apparatus is set up. Thus even violent motion of the ship does not interfere with the taking of readings.

As this cabin is generally warm and dry very little trouble has been experienced afloat from "dark currents," i.e. leakage currents which prevent the potentiometer from reading zero when the photometer is screened from light. This effect, as mentioned in the previous paper, was sometimes troublesome when the apparatus was exposed on an open pier, so that dew was liable to deposit on the insulating surfaces.

#### PHOTOMETERS AND PHOTO-ELECTRIC CELLS.

Two photometers are employed. One, which we will call the air photometer, consists of a light-tight wooden box with a sheet metal cover, in the centre of which is a circular aperture 5 cm. in diameter closed by a thin glass window, which is fixed to the under side of the cover with waterproof cement. The under side of this window is coated with the special matt varnish used for obscuring electric lamps. In contact with this surface is an opaque screen of black card with a central aperture 2.4 cm. in diameter, forming the pupil of the photometer. This method of mounting ensures that the pupil receives light from almost a complete hemisphere, the screening due to the thin sheet metal surrounding the window being negligible.

A vacuum photo-electric cell made by the General Electric Company is mounted inside the box so that its pupil is almost in contact with the diffusing surface at the centre of the window.

The photometer is mounted on gimbals, so that its diffusing surface remains very nearly horizontal, independent of the motion of the ship. It is carried on the roof of the deck house in a position as free as possible from all shading by spars and rigging, and is connected to the measuring apparatus by rubber insulated flexible leads.

The water photometer is shown in part section in Fig. 2. The case is a massive one of gun-metal, and the window is of plate glass 1 cm. thick, the joints being made with sheet rubber gaskets. The under side of this window is also coated with matt varnish, and the effective diameter of the pupil is limited to 2.4 cm. by an annulus of black card. The general construction is fairly evident from the figure, which shows the leads,

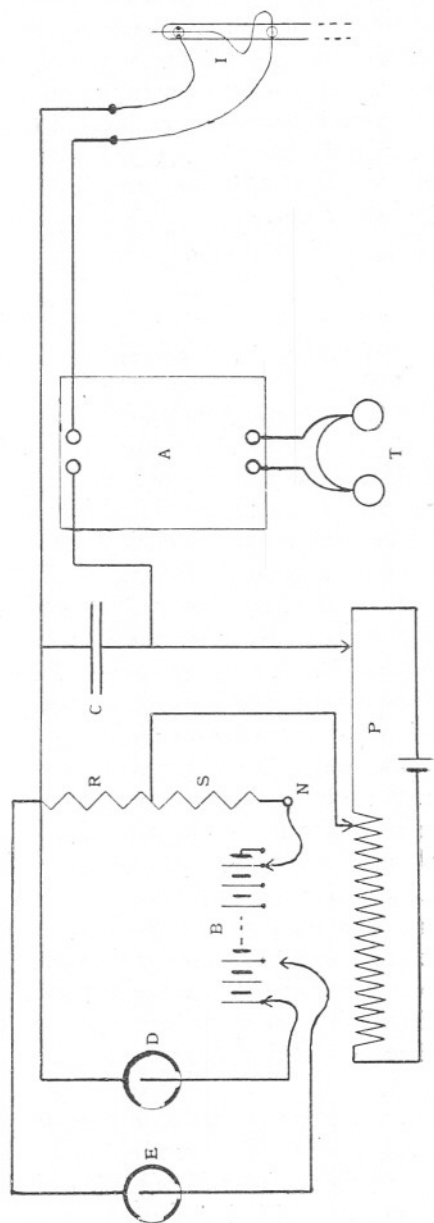


FIG. 1.

of high tension ignition cable, 11 mm. outside diameter, and one of the four supporting wire ropes, which form a bridle suspending the photometer with the window horizontal. An external metal shutter enables all light to be cut off from the photometer, and can be worked by strings, so that "dark currents" can be tested with the photometer submerged. This shutter, when open, drops below the level of the window, so that it cannot possibly cast a shadow on it.

The photo-electric cell, which is mounted just below the diffusing surface, is of the Kunz gas-filled type, in which the sensitivity is greatly increased by ionisation due to collision.

#### OPTICAL CONSIDERATIONS.

We must evidently define what we mean by the illumination at a given point in air or water. The problem is complicated by the fact that we have to deal with light travelling in many different directions, the angular distribution varying greatly at different times, and being quite different in the two media. Thus with a uniform cloudy sky the angular distribution of the light in air may be approximately uniform over one hemisphere. In addition to this direct sky light there will be some light reflected off the water. This does not directly affect the air photometer or the submarine illumination, and is disregarded here. The illumination just below a smooth water surface will be confined within a cone of semi-vertical angle  $48.5^\circ$ , and will not be uniformly distributed throughout this solid angle. On the other hand, if the sun is shining perhaps 75% of the light in air may be direct sunlight, and may be treated as parallel rays making a definite angle with the horizon. Below the water surface these rays will, of course, still form a parallel beam, but inclined more steeply to the horizon, owing to refraction.

Several definitions of illumination are possible. Thus we may define the Vertical Illumination as the illumination in metre candles falling on a horizontal surface. This is what is actually measured by the photometers when certain small corrections have been applied for reflection losses at the front faces of the glass windows, and is denoted throughout by the letter V.

Another definition, which is very useful in photometric measurements on shore, is the illumination in metre candles on a surface set to catch the maximum amount of light. We will call this the Maximum Illumination, and denote it by the letter M. Evidently in the case of pure sunlight the photometer must be set perpendicular to the sun's rays. For actual sunlight, which contains some diffuse sky light, a setting rather nearer the horizontal would receive more light. This setting of the photometer

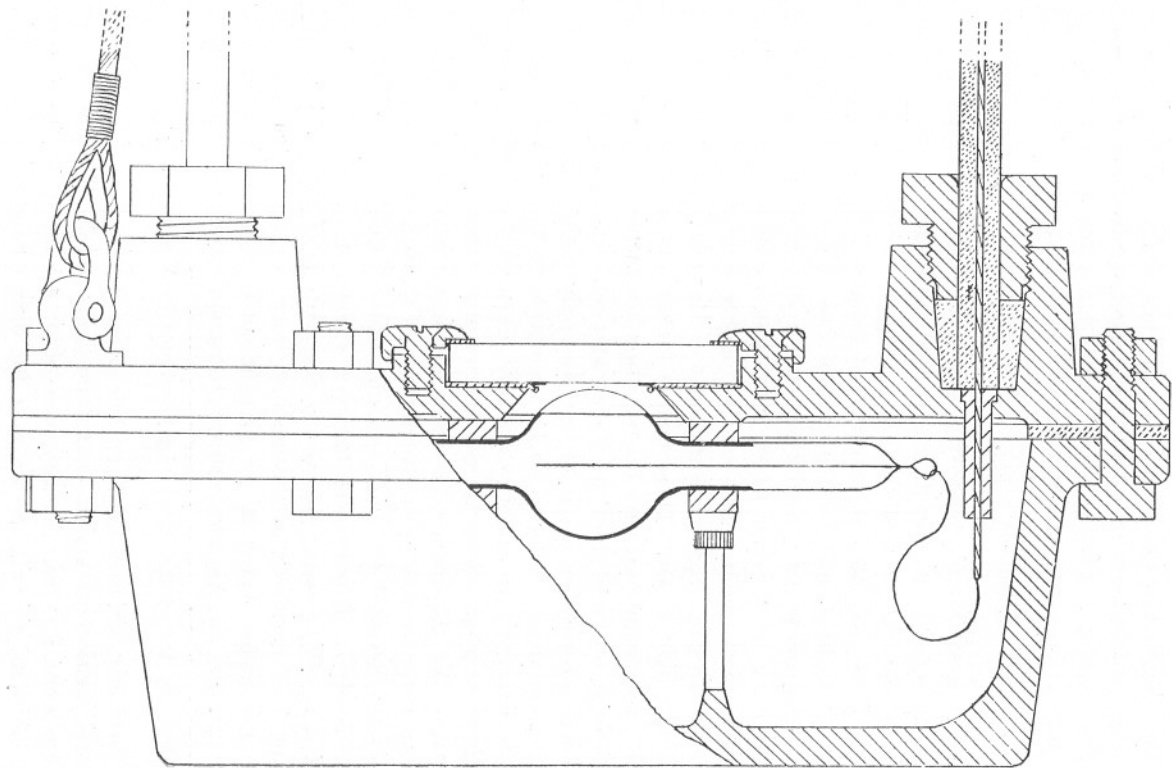


FIG. 2.

with its surface in a definite plane other than the horizontal is easy on shore, but would be most inconvenient afloat.

A third definition is the one which was adopted in the previous paper, being there denoted by the letter I. It may be called the Total Illumination, and measures the total quantity of light regardless of angle, being defined as follows: Let  $i d\Omega$  be the illumination in metre candles due to a small pencil of rays of solid angle  $d\Omega$  on a small area placed perpendicular to the pencil. Then  $I = \int_0^{2\pi} i d\Omega$ . This measures the total illumination that is available for photosynthesis at a given point (neglecting, however, reflected light travelling upwards), although no single surface could be set to receive it all at once, except in the ideal case of pure sunlight. It is probably the best way of recording the photosynthetic activity of the light, and for that reason was adopted in the previous paper. Unfortunately it can only be found from the photometer reading by multiplying by a factor whose magnitude depends on the angular distribution of the light. This can be roughly estimated, knowing the altitude of the sun, from measurements of the relative proportions of sun and sky light in air. These factors for air and water were, in the previous paper, combined with the reflection loss factors, and in this way I was directly obtained from the photometer reading. As, however, the reflection loss correction is a small one, and only slightly affected by the angular distribution, it seems to be preferable to apply it separately, and thus obtain V, the quantity actually measured by the photometer. Accordingly in what follows all results are stated in terms of the Vertical Illumination V. The factor for deducing the corresponding value of I for air or water for any given distribution of light may be obtained by interpolation between the pure sunlight and diffused sky light values given in Table 1. It is evident that, for a point in air lit by pure sunlight,  $I_a = M_a = V_a \operatorname{cosec} \alpha$ , where  $\alpha$  is the altitude of the sun, and the subscript "a" denotes that the medium is air, for, in this case, to find M the photometer should be set perpendicular to the sun's rays, and, since  $i$  vanishes all over the hemisphere except in the small solid angle subtended by the sun's disc,  $\int_0^{2\pi} i d\Omega$  reduces to M simply.

For perfectly diffused light, on the other hand,  $M_a = V_a$ , since the horizontal position catches the maximum light, and, as  $i$  is uniform over the hemisphere,  $I_a = 2\pi i$ . An easy piece of integration shows that, under these conditions,  $V_a = \pi i$ . So we have for diffused light  $I_a = 2M_a = 2V_a$ .

For a point just below a smooth water surface we have, for pure sunlight,  $I_w = M_w = V_w \operatorname{cosec} \theta$ , where  $\theta$ , the angle between the refracted ray and the horizon, is connected with  $\alpha$  by the relation  $\cos \alpha = 1.333 \cos \theta$ . It is evident that  $V_w$  must be somewhat less than  $V_a$ , since a beam

of such a width as just to cover a given horizontal area in air would still cover the same horizontal area in water, and some of the light would be reflected from the surface. Hence, since  $\text{cosec } \theta$  is always less than  $\text{cosec } \alpha$ , there must be a still greater reduction in  $I$  in passing through the surface. By making use of Fresnel's formulæ for the reflection losses we can calculate the ratios  $\frac{V_w}{V_a}$  and  $\frac{I_w}{I_a}$ . These are shown in the table. It will be noticed that for low altitude sunlight the reduction in total illumination caused by the surface is much greater than the reduction in vertical illumination.

For diffused light it is evident that, as before,  $M_w = V_w$ . To find the relations between  $V_w$  and  $I_w$  and the corresponding air values  $V_a$  and  $I_a$  we proceed as follows. The sky is divided into nine zones, the extension of each in altitude being  $10^\circ$ . Then, assuming the sky to be uniformly bright, each zone will contribute a total illumination proportional to its area, and at a mean altitude equal to the mean altitude of the zone. Since in finding either  $V_w$  or  $I_w$  we are not concerned with the azimuth of the rays, we may represent the effect of each zone as that of a beam of the corresponding intensity and altitude. We thus have to find the effect in water produced by nine beams of known relative intensities, and of altitudes (in air)  $5^\circ, 15^\circ, \dots, 85^\circ$ . Using the factors already found for the different altitudes, we find the corresponding values of  $M_w$  for the nine beams. Then evidently  $I_w = \Sigma M_w$  and  $V_w = \Sigma M_w \sin \theta$ , the summation in each case consisting of nine terms. Hence we find the values of  $\frac{I_w}{V_w}, \frac{V_w}{V_a}$ , and  $\frac{I_w}{I_a}$  for diffused light, as given in the last line of the table, the value of  $\frac{I_a}{V_a}$  being 2, as already pointed out. The corresponding mean values of  $\alpha$  and  $\theta$  are obtained from those of  $\frac{I_a}{V_a}$  and  $\frac{I_w}{V_w}$  respectively.

Actual daylight may be represented as a mixture of pure sunlight and perfectly diffused sky light. This is obviously only a rough approximation as the sky is seldom uniformly bright all over, but it is the best that is practicable. An estimate of the relative proportions of sunlight and sky light can be made by taking readings of the air photometer when freely exposed, and when shaded from direct sunlight by the interposition of a small object at a distance of several feet. If  $\beta$  is the ratio of the unshaded to the shaded reading it can be shown that  $x = x_1 + \frac{x_2 - x_1}{\beta}$  approximately, where  $x$  is the required value of any factor, and  $x_1$  and  $x_2$  are the values for pure sunlight (of the correct altitude) and diffused light, respectively. Under  $f$  in Table 1 are shown



values for the reflection loss factor as explained in the following section :—

TABLE 1.

	$\alpha$	$\theta$	$\text{cosec } \alpha = \frac{I_a}{V_a}$	$\text{cosec } \theta = \frac{I_w}{V_w}$	$\frac{V_w}{V_a}$	$\frac{I_w}{I_a}$	$f$
Pure Sunlight	5°	41.7°	11.47	1.505	0.42	0.055	2.50
„ „	10	42.4	5.76	1.485	0.65	0.17	1.56
„ „	15	43.6	3.86	1.45	0.79	0.295	1.295
„ „	20	45.2	2.92	1.41	0.87	0.42	1.16
„ „	25	47.2	2.37	1.365	0.915	0.525	1.095
„ „	30	49.5	2.00	1.315	0.94	0.62	1.06
„ „	35	52.1	1.745	1.265	0.955	0.695	1.03
„ „	40	54.9	1.555	1.22	0.965	0.76	1.02
„ „	45	58.0	1.415	1.18	0.975	0.815	1.015
„ „	50	61.2	1.305	1.14	0.975	0.855	1.01
„ „	55	64.5	1.22	1.11	0.98	0.89	1.005
„ „	60	68.0	1.155	1.08	0.98	0.915	1.005
„ „	65	71.5	1.105	1.055	0.98	0.94	1.00
„ „	70	75.1	1.065	1.035	0.98	0.955	1.00
„ „	75	78.8	1.035	1.02	0.98	0.965	1.00
„ „	80	82.5	1.015	1.01	0.98	0.97	1.00
„ „	85	86.3	1.005	1.00	0.98	0.975	1.00
„ „	90	90.0	1.00	1.00	0.98	0.98	1.00
Diffused Light	30.0	57.0	2.00	1.19	0.935	0.56	1.06

## REFLECTION LOSSES AT PHOTOMETER WINDOWS.

Since it is obviously necessary to protect the diffusing surfaces, these form the inner faces of the glass windows. We must, accordingly, correct for the variation with obliquity of the reflection loss at the front surface of the window, and for the effect of the external medium. We can, as before, calculate the loss for any obliquity of the incident light from Fresnel's formulæ. We find that, if we assume the refractive index of the window glass to be 1.51, the loss at normal incidence in air is about 4.1%. For oblique angles the loss increases, very slowly at first, and more and more rapidly with increasing obliquity. The air photometer was standardised in air at normal incidence, as described below, and hence the factor,  $f$ , by which the reading must be multiplied to correct for reflection losses, reduces to unity in this case. The values for other values of the obliquity are shown in the last column of the table.

The water photometer is calibrated at least once for each series by comparison with the air photometer. It is generally convenient to do

this with the window covered with a shallow layer of water contained by the brass rim. This renders it unnecessary to haul the photometer on board and dry it before making a calibration at the end of a series of submarine measurements. It also almost entirely eliminates the screening out of light of altitude less than  $10^\circ$ , which would otherwise be caused by the rim. Thus during the calibration there are two reflecting surfaces in front of the diffusing surface, namely, the air-water surface and the water-glass surface. When measuring the illumination in the water we have only the latter to consider. The losses, for normal incidence, at the air-water and water-glass surfaces are found by calculation to be 2.0% and 0.4% respectively, the total loss being 1.7% less than it would be for a dry photometer. This reduction of loss due to the water was actually observed in some experiments in 1924.

The small loss at the water-glass surface is sensibly constant over the whole range of obliquity covered by the light in the water. As it, therefore, affects all calibrations and readings equally its effect is nil.

The loss at the air-water surface, however, only affects the calibration. We may correct for its effect by multiplying the calibration reading of the photometer by  $\frac{V_a}{V_w}$ . In this way we obtain the corrected value of the reading corresponding to the air illumination recorded by the air photometer.

#### STANDARDISATION OF THE AIR PHOTOMETER.

It has been shown by the Research Staff of the General Electric Co. (2) that the sensitivity of a vacuum photo-electric cell, such as is used in this photometer, is constant, and the current through the cell is very nearly proportional to the illumination. The photometer was accordingly standardised in the laboratory, and used in the marine observations to measure the light in air, and to calibrate the water photometer, whose sensitivity varied daily.

Both of the cells make use of potassium as an active element, and so their colour sensitivity should be somewhat similar.

Shinomiya (3) and Miss Seiler (4) have shown that the maximum sensitivity of these cells is in the neighbourhood of 4500 A.U., i.e. in the blue part of the spectrum. The cells accordingly measure chiefly blue light, and in standardising it is best to use a source as similar as possible to daylight. For this reason an open carbon arc was used to standardise the air photometer, although it is in other respects somewhat unsatisfactory, owing to its irregularity.

During the 1924 experiments a ground-glass window was used, and the sensitivity had been found to be 195 metre candles per potentiometer scale division [ $10^{-4}$  volt, equivalent to  $1.95 \times 10^{-9}$  ampere]. As, however,

doubt was felt as to the diffusing efficiency of the ground-glass surface at large obliquities, the window was subsequently replaced by the matt varnished one, mentioned above, and the photometer was restandardised.

A 36-watt 12-volt gas-filled lamp was compared by means of a flicker photometer first with a 16-C.P. standard carbon filament lamp working at 4.05 watts per candle, and then with an open carbon arc, carrying a current which was kept as nearly as possible at 10.0 amperes by hand regulation, the voltage across the arc being about 59.5. The mean of four readings gave the candle power of the arc as 953, the maximum and minimum values being 1070 and 856.

Five readings of the photometer were then taken with the arc at a distance of 50 cm., and three with the arc at 30 cm. from the window. The readings showed considerable variations, due to fluctuations in the arc, but the means of the two sets, 12.7 and 34.5 scale divisions, respectively, agree within 2% with the inverse square law. A sensitive galvanometer was used as a detector, thus considerably increasing the accuracy of the setting. As the "Zenite" resistance used at sea was not available, a similar one was used instead, its resistance being 48,070 ohms. The anode potential was 118.5 volts. With the resistance used at sea the sensitivity would be increased 1.067 times, while increasing the anode potential to 120 volts would raise it about 0.45%. Making allowance for these corrections we find that, with an anode potential of 120 volts one potentiometer division corresponds to 282 metre candles.

An alternative standardisation with a Mazda gas-filled "Daylight" lamp, i.e. a lamp with a blue-tinted bulb giving a light resembling daylight in appearance, gave 466 metre candles per scale division. This large difference may possibly be due to lack of ultra violet in the light of the metal filament lamp. It seems probable that arc light resembles daylight much more closely than does that of the "daylight" lamp as regards its effect on the photo-electric cell. Accordingly the arc lamp standardisation has been used throughout, although there is little doubt that, as daylight is bluer than arc light, its effect on the photometer is relatively greater, so that the results found for daylight illumination on this photo-electric scale are all higher than they would be on the visual scale.

The effect of obliquity on the reading of the deck photometer was also tested, the "daylight" lamp being used as a constant source. The photometer readings, when corrected for reflection losses, should be proportional to the cosine of the angle of incidence. The readings decreased rather more rapidly than they should have done with increase of obliquity, until at an angle of incidence of  $70^\circ$  the actual reading was only 96% of the theoretical. For still larger angles the readings apparently increased again (relatively) until the very small reading at

85° was apparently slightly higher than the theoretical. These variations are probably chiefly due to lack of perfect diffusion in the window. As, however, they are of small importance compared with the variations in the light in the sea they may be neglected without serious error.

#### VARIATIONS IN THE SENSITIVITY OF THE WATER PHOTOMETER.

As a vacuum cell such as is used in the air photometer would scarcely be sensitive enough for submarine measurements, the cell employed in the water photometer is of the Kunz gas-filled type. Shelford and Gail (5), who employed cells of this type in their work on submarine illumination, found that, for their cells, the current was not proportional to the illumination for values of the latter above 1000 metre candles. They relied on a single standardisation of their cells, and, apparently, were not troubled by changes of sensitivity, even though they used anode potentials from 80 to 160 volts with the cells exposed to bright light, and so obtained currents up to at least 24 microamperes. As, however, they did not re-standardise their cell it may possibly have varied considerably during the course of their work. With our cell any current exceeding 3 microamperes causes a rapid temporary increase in the sensitivity, and, even if precautions are taken to prevent the passage of such large currents, the sensitivity varies irregularly from day to day. To limit the current the anode potential employed is only about 18—20 volts for bright light, and only increased to about 120 volts when the light is known to be weak enough for this to be done safely.

#### RELATION OF THE ILLUMINATION TO THE CURRENT THROUGH THE WATER PHOTOMETER.

On the other hand, if these precautions are taken, the current through our cell, at a given anode potential, is very nearly proportional to the illumination over the entire range, if the time interval between the readings is not too long. This proportionality was first proved for various anode potentials, and illuminations up to 25,000 m.c. by laboratory experiments with a lamp at different distances.

It is now tested afloat by means of a set of neutral tinted dark glass screens. The transmitting powers of these screens and their combinations at various angles of obliquity were measured in the laboratory, using the "daylight" lamp and the air photometer, as described in the previous paper (1). It was subsequently found, however, that the screens are appreciably more transparent to daylight than to the light of the lamp. Moreover, the transparency depends greatly on the obliquity, and so laboratory tests are not of very much use for finding the transmission

factor for daylight, whose average angle of obliquity is generally only roughly known.

The best method of using the screens is to find the percentage transmitted by a given screen or combination, first with one photometer and then with the other, under, as nearly as possible, similar conditions. The results of such a set of tests is shown in Table 2.

TABLE 2.

Screens.	I.	II.	I+II.	III.	I+III.	II+III.
Percentage Transmitted. Air						
Photometer . . . . .	41	22	11	3.7	1.7	1.1
Percentage Transmitted. Water						
Photometer* . . . . .	39	22	8.8	3.6	1.5	0.9

The tests with the two photometers were made on successive days. Those with the air photometer being made in bright sunlight at an average altitude of  $47^\circ$  and with  $V_a=63,000$  m.c., the others also in bright sunlight of an average altitude  $45^\circ$  and with  $V_a=75,000$  m.c. It would have been better to test each screen or combination first with one photometer and then with the other, but the idea of calibrating the screens once and for all had not been abandoned when these tests were made. It is evident that with an anode potential of 18 volts the current through the Kunz cell is, at least, approximately proportional to the light.

Similar tests were made with weak light and an anode potential of 119.3 volts on the Kunz cell, by keeping the window of the latter permanently covered by screen No. III and finding the effects of adding screens I and II. As the screens are not absolutely non-selective their transmission factors are not strictly multiplicative, and the factor for a combination must be found by trial. Unfortunately the air photometer is not sensitive enough to measure the transmission factor of a dense combination accurately, so that only approximate results could be obtained. These were satisfactory as far as they went, and showed that there was no evidence for suspecting that any change had occurred in the characteristics of the cell since it had been tested with weak illuminations and high anode potentials in the laboratory.

#### METHOD OF TAKING READINGS.

The water photometer is suspended by a warp from a spar lashed to the mizzen boom so that it hangs about three feet clear of the counter, which is rather low with a steep "tumble home" to the bulwarks. Comparative readings of the photometer when suspended thus just clear of the

\* Anode potential for Kunz cell 18.0 volts.

surface, and on deck, respectively, showed that, with the ship's head in a suitable direction, the shading effect is small.

It is generally convenient to allow the ship to drift, when taking readings in fairly deep water. She generally lies more or less in the trough of the swell, so that the chief motion is rolling, which does not greatly affect the depth of submergence of the photometer below the mean water level. If the wind is strong, and the drift rapid, the upper end of the warp may make an appreciable angle,  $\phi$ , with the vertical. Owing to the weight of the photometer the lower end of the warp must be very nearly vertical. The curve assumed by the warp must be approximately parabolic, but may be treated as an arc of a circle without serious error. Then, to find the depth of submergence we must evidently multiply the apparent depth, which is measured on the warp, by  $\frac{\sin \phi}{\phi}$ , where  $\phi$  is in circular

measure. If  $\phi$  is measured in degrees and does not exceed  $30^\circ$ , we may write this factor as  $1 - 5 \times 10^{-5} \phi^2$ . The correction is thus proportional to  $\phi^2$  and amounts to 0.5% if  $\phi = 10^\circ$  and 2% if  $\phi = 20^\circ$ , which was the limit reached with a manilla warp. A wire rope was used in the later experiments, so it is probable that this correction will be negligible in future.

The procedure generally adopted in 1925 was to work from the bottom up, the first reading being taken at the maximum depth, which was limited either by the depth of water or the length of the photometer leads. When working in deep water the light was so faint that about 120 volts could safely be applied to the Kunz cell. A set of readings at a given depth consists of an odd number of alternate readings of the two photometers, made at the briefest possible intervals, often about 20 seconds. Whichever photometer is read first is also read last, so that there is one more reading of it than of the other. Thus, there might be four of one and three of the other, or, if the light were somewhat variable, perhaps as many as nine of one and eight of the other. The mean of each set is taken as the reading of that photometer at the mean clock time of the sets. The reading of the air photometer multiplied by the reflection loss factor  $f$ , and by 282, gives the vertical illumination in air,  $V_a$ .

Readings are taken at various depths until the light becomes so bright that further increase would necessitate a reduction in the anode potential applied to the Kunz cell. At this depth a triple set is taken, i.e. readings of the water photometer at about 120 volts, and also at about 20 volts, and of the air photometer, whose anode potential is always maintained at very nearly 120 volts. From these the relative sensitivities of the water photometer at the two pressures is found, thus enabling the deep readings to be reduced to what they would have been with the lower anode potential, which is used for the rest of the series.

The series concludes with the calibration set, which is taken with

the water photometer just clear of the surface. This reading of the water photometer is multiplied by the reflection loss factor, as already explained, and the product is divided into the simultaneous value of  $V_a$ , as obtained from the air photometer reading. We thus find the number of metre candles per scale division of the water photometer for that particular series, and so find the actual illuminations at the different depths.

In some cases the water photometer was calibrated at the commencement, and also at the end of the series, and any small change of sensitivity which was observed was allowed for, the sensitivity being assumed to change uniformly with time. It is proposed always to adopt this procedure in future.

Another improvement would be the taking of readings both when descending and ascending, so that the deep readings come in the middle. This would generally reduce the effect of progressive changes in conditions such as the altitude of the sun or the position of the ship. These changes may, with the system adopted, cause a slight difference between the earlier, deep, and the later, shallow readings. That this effect is generally unimportant is shown by the fact that readings made quite out of the regular order usually accord quite well with the others. Some such irregular readings were specially made to test this point.

Readings of the "dark currents" of both photometers are made at intervals. No such current has ever been detected as actually passing through the photometers themselves. When a "dark current" is detected it always means that the insulating surfaces in the measuring apparatus are damp. This very seldom happens with the apparatus in the deck house, but occasionally a "dark current" of a couple of scale divisions was noted and allowance made for it.

In order that the results in a series should be as far as possible comparable, the conditions should be as uniform as possible. Thus if clouds are passing across the sky it is best to take readings at all depths with the sun shining. Extra readings with the sun obscured are of some interest. The relative proportions of sunlight and skylight may be deduced from the ratio,  $\beta$ , of the readings of the air photometer when exposed to, and shaded from, direct sun. This ratio is found at least once during each series, unless the sun is obscured, when of course,  $\beta=1$ . Rapid variations in light during a test are generally caused by variations in the direct sunlight. The corresponding change of  $\beta$  is readily estimated on the assumption that the diffused light remains constant.

## RESULTS.

The results of the 1925 measurements are given in Table 3, where T is the clock time (G.M.T.),  $d$  the depth in metres,  $V_a$  and  $V$  the illuminations in metre candles found from the readings of the air and water

photometers respectively, and  $p = \frac{100 V}{V_a}$ . The letter  $a$  in the depth column indicates that the water photometer was above the surface, the reading being a calibration.

In comparing these results with those given in the previous paper it must be remembered that the former were given in terms of the calculated total intensity  $I$ .

The results are plotted in Fig. 3 on a logarithmic scale. It is obviously necessary, in plotting the submarine illumination to correct for irregular variations in the surface illumination. This might be done by merely plotting the percentage,  $p$ , but the resulting six curves would be hopelessly superposed and confused, and it is more interesting to show the approximate values of the illumination. Accordingly, the mean surface illumination is found for each series, and the submarine illuminations for the series all reduced to the corresponding values. In one case [series 5 at 18.3 m.], where duplicate sets of readings were made at one depth owing to rapid variations in the surface light, the result obtained with abnormally low surface light has not been plotted; it would be about 6% lower than the corresponding figure obtained with surface light nearer to the average for the series. Where there is a possibility of confusion circles of different sizes are used for different series. A vertical

TABLE 3.

Date, Remarks, etc.	T (G.M.T.)	$\alpha$	Light	$\beta$	d metres	$V_a$ m.c. $\times 10^3$	V m.c. $\times 10^3$	$p$ %
SERIES 1. 1.9.'25.								
In Cawsand Bay. Ap- prox. depth 12 m. High	10.2 a.m.	40	dull	1	10.1	33.2	2.13	6.4
water 4.9 a.m. Wind W.,	10.14 "	41	"	1	8.1	46.9	4.46	9.5
moderate. Slight swell,	10.33 "	43	"	1	6.1	43.9	6.98	15.9
with ripples, some of	10.40 "	43	"	1	4.1	50.2	13.8	27.5
which broke, forming	10.46 "	44	"	1	2.1	54.2	25.7	47.5
"white horses." Ship	10.57 "	45	"	1	1.1	43.6	27.5	63.0
rolling slightly.	11.6 "	46	"	1	$a$	31.7	31.7	100
SERIES 2. 2.9.'25.								
About 3 miles S. of	9.37 a.m.	37	Bright sun	3.5	34.4	75.8	0.28	0.37
Mewstone. Approx. depth	9.47 "	38	" "	3.5	31.8	76.7	0.46	0.60
40 m. (chart). Wind W.,	9.55 "	39	" "	3.5	28.7	72.3	0.69	0.96
moderate. Rise and fall	10.5 "	40	" "	3.5	26.0	71.3	1.08	1.52
of swell about 0.6 m.	10.10 "	40	Cloud	1.5	22.7	37.7	0.84	2.23
Surface disturbed. Ship	10.14 "	41	Bright sun	3.5	22.7	73.6	2.00	2.72
rolling slightly.	10.20 "	41	" "	3.5	19.8	73.6	3.31	4.50
	10.25 "	42	" "	3.5	20.0	77.5	3.45	4.45
	10.32 "	42	" "	3.5	16.9	84.4	5.53	6.55
	10.37 "	43	Light cloud	2.5	13.8	47.0	5.16	11.0
	10.42 "	43	Sun	3	10.8	63.6	11.7	18.4
	10.51 "	44	" "	3	7.8	65.0	19.6	30.2
	10.56 "	44	" "	3	4.7	63.8	28.6	44.9
	11.8 "	45	" "	3	$a$	60.7	60.7	100



Date, Remarks, etc.	T (G.M.T.)	$\sigma$ $\alpha$	Light	$\beta$	d metres	V <sub>a</sub> m.c. $\times 10^3$	V m.c. $\times 10^3$	p %
SERIES 3. 2.9.'25.								
In Cawsand Bay. Ap- prox. depth 10-18 m. (chart). High water 5.6 a.m. Fresh N.W. wind, causing rapid off-shore drift. Ship moved in- shore between 2nd and 3rd readings.	3.10 p.m. 3.18 " 3.32 " 3.35 " 3.38 " 3.42 " 3.48 " 3.55 "	35 34 32 32 31 30 29 28	Dull " " " " " " "	1 1 1 1 1 1 1 1	10.2 8.15 6.35 4.4 2.2 1.25 4.2† a	20.8 20.5 15.8 13.7 12.6 13.4 15.6 18.5	3.02 3.94 3.09 4.26 6.65 8.67 5.81 18.5	14.5 19.2 19.6 31.1 52.8 64.7 37.3 100
SERIES 4. 3.9.'25.								
Anchored in Cawsand Bay. Depth, 10.4 m. at 9.50 a.m. (sounding). High water, 5.54 a.m. Fresh N.W. wind causing waves to break. No swell.	9.32 a.m. 9.43 " 9.50 " 9.54 " 10.0 " 10.5 " 10.11 " 10.23 " 10.31 "	36 37 37 38 39 40 40 41 42	Bright sun " " " " " " " " " " " " " " " "	3 3 3 3 3 3 3 3 3	a 5.9† 10.35* 9.85 8.3 6.5 4.35 2.35 a	65.8 64.8 65.6 66.1 66.1 69.3 70.3 74.0 68.7	65.8 19.8 7.42 11.5 14.1 19.0 25.8 37.8 68.7	100 30.5 11.3 17.4 21.3 27.4 36.7 51.1 100
SERIES 5. 3.9.'25.								
About 3 miles S. of Mewstone. Approx. depth 40 m. (chart). High water 6.6 p.m. Fresh W. wind and considerable swell, lumpy surface. Ship roll- ing heavily.	12.34 p.m. 1.0 " 1.11 " 1.19 " 1.23 " 1.34 " 1.41 " 1.52 "	47 46 45 45 44 43 43 42	Dull Weak sun Dull " " Weak sun " " Dull	1 1.5 1 1 1 2 2 1	a 30.8 24.3 18.3 18.3 12.5 6.45 a	24.2 39.1 27.2 15.55 31.4 48.1 46.6 20.6	24.2 0.04 0.78 1.01 2.15 7.82 15.3 20.6	100 0.10 2.87 6.49 6.85 16.3 32.9 100
SERIES 6. 1.10.'25.								
At E1, 10 m. S.W. of Eddystone. Depth 72 m. (sounding). Light air, N.N.W. Very slight oily swell, glassy surface.	12.19 p.m. 12.31 " 12.40 " 12.53 " 1.18 " 1.35 " 1.46 " 1.58 " 2.11 "	36 37 36 35 35 34 33 32 31	Dull " " Weak sun " " " " " " " " " "	1 1 1 1.5 1.5 1.5 1.5 1.5 1.5	34.8 24.4 18.3 12.2 8.9† 34.8 6.1 1.5 a	17.4 16.0 18.3 21.3 20.4 24.5 22.5 21.1 22.4	0.094 0.47 1.45 3.97 5.77 0.132 9.28 15.0 22.4	0.54 2.93 7.92 18.6 28.3 0.54 41.2 71.2 100

line through a plotted point indicates the depth at which the anode potential of the water photometer was changed; the higher voltage being used for the deeper readings, and vice versa.

It will be observed that, with a few exceptions referred to later, the results lie tolerably well on curves, which for the shallow series cannot be distinguished from right lines. These curves are produced above the line corresponding to the water surface until they intersect the corresponding vertical lines indicating the mean values of the surface illumination for the respective series. The intercept on the surface line between a

\* Photometer resting on bottom.

† Depth chosen so that photometer window just visible.

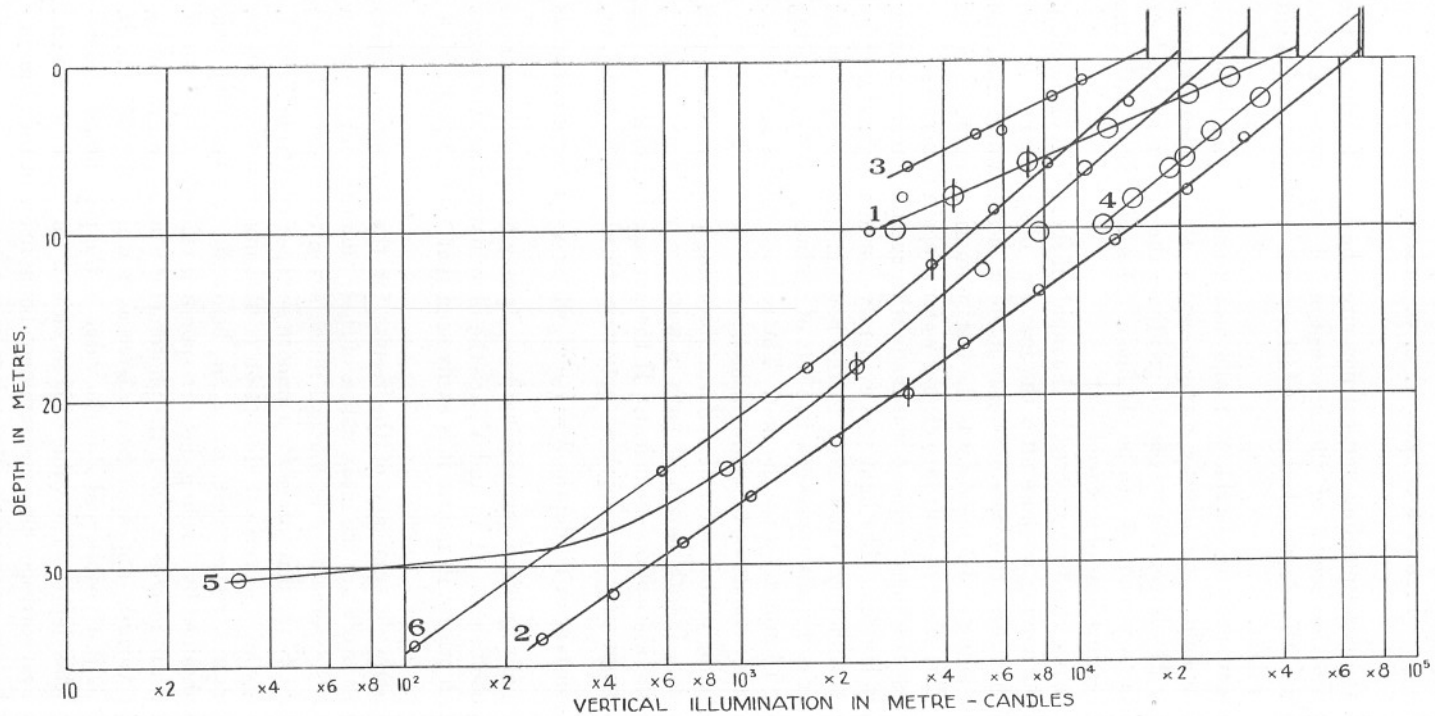


FIG. 3.

curve and the corresponding vertical measures the loss of light at the surface, while the height of the intersection of the curve and the vertical gives the depth of water which would cause an equivalent reduction in light.

It is unfortunately impossible to make measurements just below the surface as the light is so unsteady, owing to waves, that a balance cannot be effected. The larger the waves the greater is the minimum depth at which satisfactory readings can be obtained. This, of course, limits the accuracy of estimations of surface loss.

The results in series 3 are affected by the rapid off-shore drift of the ship. This involved moving in-shore after the first two observations. It will be noticed that these two were obviously made in clearer water than the rest. The reading at 4.2 metres was the last submarine measurement of the series. The effect of drift into clearer water is again noticeable.

The deepest reading of series 4 was made with the photometer resting on the sandy bottom. The light was evidently considerably reduced by a thin layer of cloudy water close to the bottom. The deepest point plotted in series 6 really represents two sets of readings, the second being made 1 hour 16 minutes after the first. The reduced results accorded so closely that they could not be distinguished.

For parallel light and water of uniform absorbing power the variation of illumination,  $I$ , with length of path in water,  $x$ , would be  $I=I_0e^{-\mu x}$ , where  $\mu$  is the absorption coefficient. If the average inclination of the light,  $\theta$ , does not vary with depth we may write this  $I=I_0e^{-\mu d \operatorname{cosec} \theta}$ , or, since  $\frac{I}{V}$  is constant at all depths,  $V=V_0e^{-\lambda d}$ , where  $\lambda=\mu \operatorname{cosec} \theta$ , and is what we actually find from our observations. It may be called the vertical absorption coefficient. If  $V_1$  and  $V_2$  are the illuminations at two points differing in depth by 10 metres it is easily seen that  $\lambda=0.23 [\log_{10} V_1 - \log_{10} V_2]$ .

Table 4 shows a summary of the results for the six series. Here  $V_a$ ,  $\alpha$ ,  $\beta$ , and  $\operatorname{cosec} \theta$  are the mean values of these quantities for the given series.  $S$  is the percentage of vertical illumination transmitted by the actual surface,  $S'$  the percentage for a smooth surface found from Table 1.  $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_3$  are the vertical absorption coefficients from 0-10, 10-20, and 20-30 metres, respectively,  $\mu_1$ ,  $\mu_2$ ,  $\mu_3$  being the corresponding true coefficients obtained by dividing the corresponding values of  $\lambda$  by  $\operatorname{cosec} \theta$ .  $D$  is the depth in metres at which the photometer window, which, owing to the matt varnish, appeared from above as a white disc 6.6 cm. in diameter, was just visible, and  $P$  is the value of the percentage  $p$  corresponding to this depth. The value of  $D$  in series 2 was found at the end of the series, no corresponding measurement being made of the illumination. In this case, accordingly,  $P$  is taken from the curve.

TABLE 4.

Series.	$V_a$ $\times 10^3$ m.c.	$\alpha$	$\beta$	$\text{cosec } \theta$	$S$ %	$S'$ %	$\lambda_1$	$\lambda_2$	$\lambda_3$	$\mu_1$	$\mu_2$	$\mu_3$	D metres	P %
1	45	43°	1	1.19	83	93.5	0.267	—	—	0.224	—	—	—	—
2	70	41°	3	1.21	90.5	96	0.148	0.163	0.164	0.122	0.135	0.136	7.0	33
3	16	31°	1	1.19	86.5	93.5	0.234*	—	—	0.196	—	—	4.2	37.3
4	68	39°	3	1.21	69	96	0.139	—	—	0.115	—	—	5.9	30.5
5	32	44°	1.5	1.19	79.5	95	0.131	0.138	0.296	0.110	0.116	0.248	—	—
6	20	34°	1.5	1.22	95	94	0.134	0.143	0.162	0.110	0.117	0.133	8.9	28.3

## DISCUSSION OF RESULTS.

The surface loss of light evidently increases with the disturbance of the water caused by wind. In series 6, with hardly any wind and only a slight swell the surface loss is about what we would expect for a smooth water, while the largest loss occurred with a strong wind in series 4. In most cases the loss is considerably less than that found by either Shelford and Gail or Klugh (6). It should be noted that, in all cases the vertical illumination,  $V$ , is referred to, the reduction in total illumination,  $I$ , being considerably larger, as already pointed out.

Shelford and Gail exposed their photo-electric cell directly to the water without any diffusing surface, since they required the utmost sensitivity in view of the considerable depth to which they worked. This unfortunately complicates the interpretation of their results for the surface loss, as the presence of a short focus diverging water lens, formed by the water between the curved surface of the cell and the surface, would strongly affect the path of the rays entering the cell. Even if the entire inner surface of the cell, other than the pupil, were coated with a uniformly sensitive layer, it is probable that some light striking obliquely near the edge of the pupil would be totally reflected, and never enter the cell. This effect would probably be increased by the presence of ripples on the surface, which would in general cause an increase in the average angle made by the light with the vertical.

Klugh gives a single result, 77%, for the light transmitted by a smooth surface in the Bay of Fundy. This is lower than most of our results though not so low as that for series 4.

As might, perhaps, be expected, the in-shore readings generally show relatively large absorption coefficients, although series 4 is an exception, in showing a small coefficient until quite near the bottom. The clearest water was found well off-shore at  $E_1$ , although the difference is not very marked.

The apparent increase of absorption coefficient with depth, which is found in all the off-shore readings may possibly be due to a lack of strict proportionality between the illumination and the current through the

\* Obtained from measurements down to 6 metres only.

Kunz cell. To test this point a specially sensitive vacuum cell is being constructed for us to replace the Kunz cell.

This explanation would, however, certainly not explain the pronounced curvature found in series 5, and it seems probable that the slight curvatures shown by Nos. 2 and 6 also represent real increases, which may be due, either to scattering, which would cause the average inclination, and hence the penetrating power, of the light to decrease with increase of depth, or to the presence in the deeper layers of matter derived from the bottom. This is certainly the explanation of the low reading obtained on the bottom in series 4, and probably that of the low reading obtained at 30.8 metres, on a very rough day, in series 5.

The absorption coefficients are all much smaller than those obtained in 1924 for the comparatively turbid waters at Cawsand Pier. The off-shore values down to 20 metres are somewhat smaller than those indicated by Shelford and Gail on p. 162 of their paper, where, however, transmission coefficients are given. Thus, in spite of the lower solar altitude, the mean of these three series gives an illumination at 20 metres, about 5.5% of that just below the surface, whereas their mean figure is 2.5% (p. 156). Thus the surface water in the English Channel off Plymouth seems to be somewhat clearer than that in Puget Sound. On the other hand Shelford and Gail worked to much greater depths than we have reached, and found a large reduction in the absorption coefficient with increase of depth, showing that the deeper water in Puget Sound is much more transparent than any water which we have met.

Klugh, using a photographic method, found, for bright sunlight in the month of August, that the light at a depth of 10 metres in the Bay of Fundy was only 1.5% of that just below the surface. As our equivalent off-shore mean figure is about 23% it is obvious that the water where he worked was much more opaque than that which we found off-shore. His results, however, are very similar to those which we obtained in 1924 at Cawsand Pier.

The results may also be compared with those of Knudsen (7), who, using a spectro-photographic method in water 9 metres deep in Nyborg Fjord, found a mean value 0.30 for the vertical absorption coefficient for light of wave length 4500 A.U. This is intermediate between the values for our 1925 in-shore measurements and our 1924 measurements at Cawsand Pier.

The figures for the depth and percentage of surface light at which the photometer window is just visible are of some interest in connection with the large number of observations that have been made with Secchi's disc, although they are not strictly comparable with the latter, since the photometer window is only about one-third the diameter of, and is probably not so white as the disc. Apparently the limit of visibility is

reached when the vertical illumination has been reduced to about one-third of that above the surface. This appears to be nearly independent of the actual value of the surface illumination over a wide range. The vertical illumination required to see the disc was naturally least in calm water.

In this connection it is of interest to record the fact that the German diver who went down in the new diving apparatus to look for Submarine M 1 was able to see a slender rope at 5 metres distance at a depth of 40 metres between 4 and 4.30 p.m., on November 25th, a dull overcast day with a rough sea. Captain G. C. Damant, R.N., who kindly communicated this to us, is of the opinion that the water in this locality, off Start Point, Devon, to the east of Plymouth, was exceptionally clear as judged by his own experience as a diver. The surface conditions were apparently somewhat similar to those for our series 5, and the total depth of water was also about the same, but the surface light must have been very much less, possibly about 3000 metre candles. The remarkable visibility suggests that the water near the bottom was not as much obscured by matter in suspension, as in our series 5. Assuming the clear water conditions of our series 6, and extrapolating to 40 metres, the vertical illumination would be 0.25 per cent of that at the surface. Thus we would expect the vertical illumination on this occasion to have been of the order of 10 metre candles. Since, however, the weather had been rough previously and the diver was actually on the bottom the illumination may have been considerably less.

#### SUMMARY.

1. A description is given of some measurements of the penetration of light into sea-water carried out near Plymouth in the autumn of 1925 by means of photo-electric cells, the current through the cell being measured by a method, previously described, which is not affected by the motion of the ship.

2. The absorption coefficients found for off-shore waters down to 30 metres are smaller than the average of those found by several recent observers in various localities, but considerably larger than those found by Shelford and Gail for the deeper waters of Puget Sound. The coefficients tend to increase with increase of depth, and are generally larger for in-shore waters. The clearest water, 20 miles out in the English Channel, gave an absorption coefficient 0.110 for the upper 10 metres, 0.117 for the second, and 0.133 for the third. This water, with glassy surface, transmitted 0.54% of the vertical illumination to 34.8 metres, 28.3% to 8.9 metres, at which depth a white disc was just visible, and 71.2% to 1.5 metres.

3. The loss of light caused by surface reflection was not so large as has been recorded by some other workers, but varied from 5-31% according to conditions; the least loss was with glassy water and a grey sky, the greatest was with a fresh N.W. wind causing waves to break, viz. "white horses," without much swell.

In conclusion we wish to express our sincere gratitude to Dr. Allen, Director of the Marine Biological Laboratory, for the laboratory and marine facilities which have rendered this work possible; to Prof. W. E. Thrift, of Trinity College, Dublin, where most of the laboratory work was carried out, for laboratory facilities and the loan of valuable apparatus; to Prof. Joly for the loan of further apparatus; and to the Committee of Science of the Royal Dublin Society for their kind permission to make use of blocks from a paper in the Society's Scientific Proceedings.

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# On Lunar Periodicity in Spawning of normally grown Falmouth Oysters (*O. edulis*) in 1925, with a comparison of the spawning capacity of normally grown and dumpy Oysters.

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With 7 Figures in the Text.

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## INTRODUCTION.

In a report on a survey of the oyster beds in the Fal Estuary (1) it was shown that even in the depleted condition of those beds 42% of the stock of oysters consisted of a type of oyster called dumpy. The percentage of these dumps is slightly greater, about 45%, in the *small* oysters, which are not allowed to be taken from the beds. It was pointed out in that



report that it would be worth while finding out whether this type of oyster is useful or not for breeding purposes : if dumpy oysters do not spawn in reasonable numbers in comparison with normal oysters, it would benefit the dredgemen to be allowed to take them for sale ; if they are good spawners, then—assuming, as there is reasonable ground for doing, that the spawn under favourable conditions will produce young oysters—the dumpy oysters, which remain on the grounds to a greater age than the normally grown ones, form a fairly stable spawning stock, for supplying spat in the future. In this case it is strongly advisable to keep on the grounds as many as possible of the dumpy forms.

#### COMPARISON OF THE CHARACTERS OF NORMAL, DUMPY, AND SLIGHTLY DUMPY OYSTERS.

The difference between dumpy and normally grown oysters is shown in the diagrams drawn to scale and given in text Figs. 1 and 2. The characters of the shells of dumpy oysters are as follows :—

(1) In outline a dumpy shell is roughly rhomboidal or of an elongated lozenge shape, while that of a normal shell is roughly circular.

(2) The shell is narrow, the antero-posterior axis (length) being constantly shorter than the ventro-dorsal (height). In a sample of 100 shells measured the relations length to height to width were 50 : 59 : 19 respectively. In normal oysters the ratio, length to height, is 1 to 1, or rather more than 1 to 1, whereas in the sample of dumps cited the ratio is 1 to 1.18.

(3) The shells are relatively very wide, i.e. the distance between the middle of one valve and the middle of the other—across the mantle space—is relatively great ; in samples of dumpy and normal shells of about the same shell area, the width of the dumpy to the normal will be of the order of 2 to 1.

(4) The lines of growth on dumpy shells are very close together and numerous (see Bell, 2, Plate XII, Fig. 3), and although no definite experimental observation is available, it seems obvious that shell-growth occurs in most of these forms very slowly for the following reasons :—

- (a) Their abundance on the grounds from year to year, even when there are only low stocks of “brood” to contribute towards an increase of dumps, and when over-fishing is occurring.
- (b) The new growth at the end of the growing season—judged purely arbitrarily, but by practical experience of the difference between new and old shell in appearance, texture and super-added marine growths or their absence—is apparently very small and of the order of a mean increase in length at the median ventral edge of 6 to 8 mm. (See Fig. 2.)

(5) The umbo of the shell projects dorsally to the hinge so as to form a pronounced beak, and is especially well marked in the lower (left) valve. In normal forms the beak is very slightly developed.

(6) The space in the tightly closed shell (shell-volume) is much greater in relation to the size of the shell (shell-area) than in normally grown oysters. This is really a definite way of expressing the fact that dumpy shells are wider than normal ones; the width of a shell being very difficult

FIG. 1.

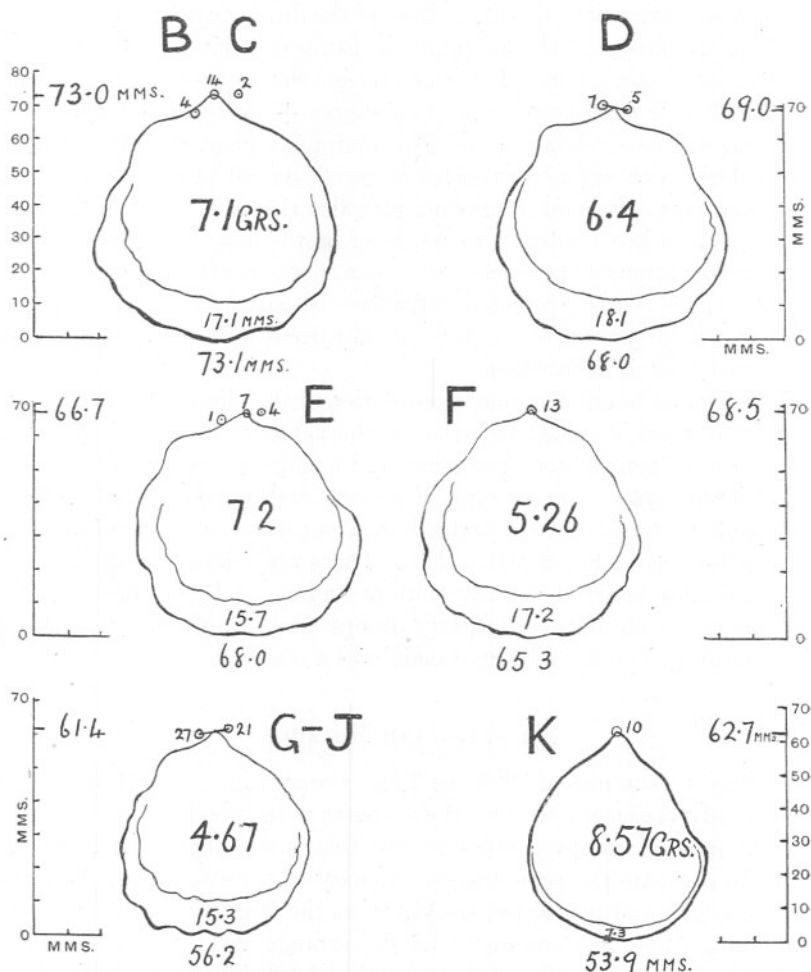


FIG. 1.—Diagrams of groups of well-grown oysters (except K) of similar size, showing average shape and size (length by height) plotted to scale, and correlated average weight of fish in grams and approximate average increment of shell-growth in 1925. (Turnaware Bar, Fal Estuary, Nov. 17, 1925.)

B and C, 20 large normals; D, 12 medium normals;  
 E, 12 medium normals; F, 13 medium normals;  
 G.H.I.J. 47 small normals; K, 10 good biconvex dumps.

to define in figures. For example, 11 Mylor Bank dumps (2.12.25) with an average length by height 60.0 by 70.02 mm., had an average shell-space capacity of 15.27 c.c., while 8 Mylor Bank normal (2.12.25) had the corresponding figures of  $76.4 \times 72.1$  mm. and 11.27 c.c. average capacity.

(7) The shell valves of dumps, especially the lower (left one), tend to be chambered, and are on the average attacked more by *Polydora* and *Cliona*; a fact which may merely mean that the shells are older than those of the average normal ones existing on the beds.

There are differences also in the flesh of the dumpy oysters as compared with normal ones; (a) the weight of the fish is not only greater than that of equal sized normal ones, but is greater in relation to shell-space, which we have noted is an expression of shell-area + shell-width. (Details of the work will be given later.) (b) The anatomical characters are different particularly with regard to reserve material, details of which cannot be discussed here. It is an interesting fact also that the "fish" of dumpy oysters shows less tendency to be green or to show greenness—due to copper absorption by the leucocytes—than that of normal oysters.

Thus there is a deep-seated difference between dumpy and normal oysters, which appears to be, but may not necessarily be, due to a mere difference in shell metabolism.

It was found in practice that a proportion of the dumpy oysters showed some characters intermediate between characteristic dumpy and normal forms, having generally a longer shell and a shape nearer the normal, and being intermediate also in type of growth and width of shell. These intermediate forms were examined in a separate category and called *slightly dumpy* (see Fig. 2, OP, p. 203). There was seldom any difficulty in distinguishing between slightly dumpy and normal, but it was often difficult to decide between slightly dumpy and dumpy, for this reason the dumpy oysters are discussed mainly as a whole.

#### MATERIAL AND METHODS.

During the summer of 1925 the Truro Corporation (River Committee) courteously consented to supply the writer with weekly samples of 100 normal and 100 dumpy oysters not less than a size of about 2 inches, in order to compare the reproductive capacity of the two kinds. Samples were dredged and forwarded weekly from the beginning of July to the end of September in accordance with this arrangement. At the beginning of the dredging season (in October) samples of oysters were bought (for the Marine Biological Association) directly from the dredgers by the writer and afterwards samples were again sent on by rail. Normal and dumpy oysters were taken in the same hauls of the dredge or—when the sample of normal was taken before the total of dumpy required was collected—by

row-boat dredging over the same ground or sail-boat dredging over the same ground until about 100 dumps were collected.

The results of the examination of the samples are shown in Table I on page 205. The samples were examined on the day of arrival and the recording completed mostly during the following day. Sick oysters were isolated at once in dishes as soon as found, and examined first: most of the sick oysters could be detected at or soon after the opening of the box in which they were consigned. In all samples except

FIG. 2.

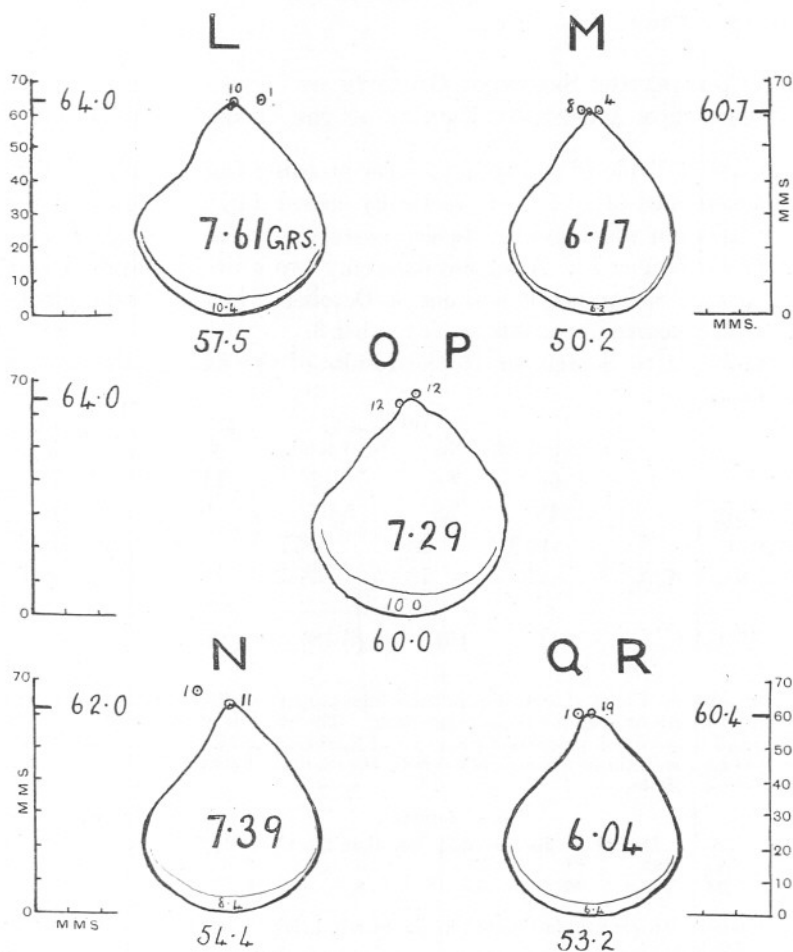


FIG. 2.—Diagrams of groups of dumpy and slightly dumpy oysters of similar size, showing average shape and size (length by height) plotted to scale, and correlated average fish-weight in grams, and approximate average increment in shell-growth in 1925. (Turnaware Bar, Fal Estuary, Nov. 17, 1925.) L, 12 dumps; M, 12 smaller dumps; N, 12 slightly dumpy approaching dumpy; O and P, 24 larger slightly dumpy; Q and R, 20 smaller dumpy.

a few, macroscopic and microscopic examination was used to find the pure ripe females, as well as those spawning. Later it was found possible to pick out the ripe females by eye and low power lens examination only with, however, an occasional error; some pure males and most hermaphrodite forms have the same opaque chalky appearance as the body of the ripe females, but in the case of the males a slight cut in the body is sufficient to disclose the clumps of ripe spermatozoa to an eye behind a low-power lens. For the purpose of this paper it will be sufficient to notice here briefly only the ripe and ripening females along with the spawning females.

THE COMPARATIVE SPAWNING CAPACITY OF NORMAL AND DUMPY OYSTERS FROM A GENERAL REVIEW OF THE OBSERVATIONS MADE.

A glance at Table I\* will show that the breeding had begun in the first sample examined (July 1) and practically ceased during September; the last occasion on which two white-sick oysters were found in one sample being on September 16. After this date only two white-sick oysters were taken, one on September 30 and one on October 8, but occasional black-sick oysters occurred to as late as November 3.

From July 1 to September 16 the results of the examination of the three types are:—

	No. Examined.	White-sick.		With embryos more than 2 days old.	
		No.	% of total.	No.	% of total.
Normal	1368	88	6.43	113	8.27
All Dumps	1243	63	5.07	90	7.24
Dumpy	945	45	4.77	63	6.67
Slightly dumpy	298	18	6.05	27	9.07
Totals	2611	151	(5.78)	203	(7.80)

\* The samples of normal oysters included a large proportion of small, that is less than  $2\frac{1}{2}$  inches in length or height, but also some large. The samples of dumpy oysters were mostly small with a small proportion round about legal size, i.e.  $2\frac{1}{2}$  inches. All the earlier samples and many of the others were measured; the results of the examination of samples 1 and 4 are as follows:—

	No.		No. of normal.			No. of dumpy.		
	N	D	above $2\frac{3}{8}$	above $2\frac{1}{2}$	less than $2\frac{1}{2}$	above $2\frac{3}{8}$	above $2\frac{1}{2}$	less than $2\frac{1}{2}$
July 1	84	89	21	37	26	8	17	64
July 22	94	106	31	55	8	19	25	62

The average new growth (estimated as increase in height) July 1 normal=10 mm.; dumpy=7.6 mm.

The average new growth July 22 normal=11.1 mm.; dumpy=5.7 mm.

Note. Among a small number of individuals, a few dumps with a big shoot of say 10 to 15 mm will increase the average to a relatively high figure. The age of the normal oysters may be estimated to be mainly 4 to 5 years, but ranging from 3 to 7 or 8. The age of the dumps is not determinable, but is probably on the average 2 to 3 years higher.

The years new growth is shown representatively in Figs. 1 and 2, pp. 201 and 203.

TABLE I.

Results of the examination<sup>1</sup> of weekly samples of approximately 100 normally grown and 100 dumpy oysters for spawning individuals and pure ripe females (normal-only) from the Truro oyster beds, Fal Estuary, during 1925. (Including one sample on August 11 from the Falmouth North Bank, north of the Cross Road Channel.)

N.=normal; Sl. D.=slightly dumpy; D.=dumpy. I=Stage I, or with embryos to about two days old; II=Stage II, with larvæ mainly shelled or more than two days old.

Date of dredging, 1925.	Locality of dredging.	No. examined.			No. with spawn.						No. of pure ripe ♀'s N. (only)	% pure ripe ♀'s N. (only)	Percentages.									
					Totals.			N.		Sl. D.			D.		All D.		N.		Sl. D.		D.	
		N.	Sl.	D.	I.	II.	I.	II.	I.	II.	I.	II.	I.	II.	I.	II.	I.	II.	I.	II.		
July 1	East Bank (Watering)	94	0	89	7	1	0	0	8	0	8	0	24	25.5	7.45	1.06	0.00	0.00	9.00	0.00	9.00	0.00
" 8	Turnaware Point	119	31	71	18	10	3	4	5	3	8	7	27	22.7	15.14	8.40	9.68	12.9	7.05	4.23	7.85	6.87
" 15	East Bank	118	14	64	12	27	2	2	1	1	3	3	17	12.7	10.17	22.88	14.28	14.28	1.56	1.56	3.85	3.85
" 22	East and Mylor Banks	89	12	100	5	6	1	2	12	2	13	4	17	19.1	5.62	6.74	0.83	1.66	12.00	2.00	11.61	3.57
" 30	Turnaware Point	93	53	53	2	5	2	3	3	4	5	7	20	21.4	2.15	5.38	3.78	5.67	5.67	7.56	4.72	6.61
Aug. 5	Turnaware P. & East Edge	91	29	79	0	5	0	3	0	6	0	9	14	15.4	0.00	5.50	0.00	10.34	0.00	7.60	0.00	8.33
" 10	Falmouth North Bank	113	10	51	11	8	0	2	3	9	3	11	20	17.3	9.74	7.00	0.00	20.00	5.88	17.64	4.92	18.00
" 11	East Edge	104	29	77	10	9	2	1	1	1	3	2	18	17.9	9.62	8.67	6.90	3.45	1.30	1.30	2.83	1.89
" 18	East and Mylor Banks	99	39	65	4	5	5	2	4	3	9	5	13	13.1	4.04	5.02	12.84	5.12	6.16	4.62	8.65	4.81
" 26	Mylor Bank	132	23	52	4	11	0	3	2	11	2	14	12	9.1	3.03	8.34	0.00	13.04	3.85	21.2	2.67	18.66
Sept. 3	Turnaware Point	108	19	90	12	1	3	1	4	10	7	11	8	7.4	11.14	0.93	15.80	5.27	4.45	11.12	6.43	10.12
" 9	East Edge	98	15	86	1	21	0	2	2	10	2	12	5†	5.0†	1.02	21.40	0.00	13.34	2.33	11.64	1.98	11.86
" 16	Turnaware Point	110	24	68	2	4	0	2	0	3	0	5	4	3.73	1.82	3.63	0.00	8.37	0.00	4.42	0.00	3.27
" 23	Turnaware Point	126	15	58	0	1	0	1	0	0	0	1	8	6.35	0.00	0.80	0.00	6.67	0.00	0.00	0.00	1.37
" 30	Mylor Pool (Bank)	158	5	47	0	0	0	0	1	0												
Oct. 1	Turnaware Point and Shore	0	0	75	0	0	0	0	0	0	0	1	12	7.6	0.0	0.0	0.0	0.0	0.42	0.42	0.41	0.41
" 2	Turnaware Point and Shore	0	0	116	0	0	0	0	0	1												
" 7	Turnaware Point and Shore	83	0	104	0	0	0	0	0	0	1											
" 7	East Bank	98	11	146	0	0	0	0	0	0	0	1	12	4.7	0.75	0.75	0.0	0.0	0.0	0.29	0.00	0.27
" 8	Mylor Pool (Bank)	87	14	89	1	1	0	0	0	0												
" 14	Turnaware Point	112	17	98	0	0	0	0	0	3												
" 14	East Edge	105	8	134	0	0	0	0	0	0	0	3	16	4.76	0.0	0.0	0.0	0.0	0.0	0.35	0.0	0.31
" 14	Mylor Pool (Penarrow)	128	12	56	0	0	6	0	0	0												
" 17	Mylor Pool (Penarrow)	3	2	60	0	0	0	0	0	0												
" 19	Turnaware Point (Shore)	167	50	143	0	0	0	1	0	0	0	1	4	2.35	0.0	0.0	0.0	1.94	0.0	0.0	0.0	0.39
" 27	Mylor Bank	107	23	71	0	0	0	0	6	1												
" 27	East Bank	86	33	82	0	0	0	0	0	0	0	1	7	3.63	0.0	0.0	0.0	0.0	0.0	0.60	0.0	0.48
Nov. 3	East Bank and Edge.	104	26	81	0	0	0	0	0	0	0											
" 3	Turnaware Point	112	83	76	0	0	0	1	0	0	0	1	9	4.17	0.0	0.0	0.0	0.62	0.0	0.0	0.0	0.38
" 10	East Bank	83	34	85	0	0	0	0	0	0												
" 11	Mylor Bank	99	39	63	0	0	0	0	0	0	0	0	7+6†	3.85-7.13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
" 17	Turnaware Point	114	44	48	0	0	0	0	0	0	0	0	0-0	0.0-0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
" 17	East Bank	100	35	66	0	0	0	0	0	0	0	0	4+3†	4.26-7.47	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

\* Number calculated, as all the oysters in the sample could not be examined microscopically.

† Ripening females.

<sup>1</sup> See the footnote on the bottom of page 204 for further details of the characters of the samples.

It is thus seen that whereas the normally grown oysters on the whole total yielded 6.43% white-sick and 8.27% black-sick, on the whole total of dumps only 5.07% white-sick and 7.24% black-sick were taken. These percentages are not those of oysters spawning out of the total on the grounds, but merely those of the oysters examined, some of which would already have spawned before being dredged. It will be shown later that more than 100% of the normals spawned during 1925, and as the dumps were only slightly inferior in spawning capacity nearly every dump must have spawned at least once also in 1925.

Although the dumps are now seen to be not so good as the others for spawning purposes, yet they are only slightly inferior. There can remain no doubt, therefore, that dumps are valuable for breeding inasmuch as a high proportion yield larvae like normal individuals. We have no means at present of ascertaining the survival values of the larvae of the two types of oysters, and, on the other hand, no substantial reason to doubt that the larvae of both types are healthy and will produce spat equally well under favourable conditions.

It is worthy of note that the slightly dumphy group are more like the normal in their spawning capacity, and that of the 1922 normal and 2149 dumphy oysters examined after September 16 the normal gave only 1 white-sick and 2 black-sick, and none after October 8; the slightly dumphy 3 black-sick only, but one as late as November 3, and the dumphy one white-sick and 3 black-sick, one of which was taken as late as October 27. The last 810 oysters, examined November 10 and 17, gave no spawning oysters, so that it may fairly be stated that the end of the spawning season has been thoroughly investigated. Reference to this part of the work will be made later. During the whole season 3290 normal and 3392 dumphy oysters were examined, making a total of 6682, nevertheless, the number is not regarded as too high for the kind of problem being examined. It may be remarked that other characters than spawning were noticed in these later oysters in order to avoid wastage of material.

## PERIODICITY IN THE SPAWNING HABITS.

### FAVOURABLE WEATHER FOR SPAWNING IN 1925.

The method of examining weekly samples of oysters throughout the summer of 1925 has resulted in showing that among the whole population, but especially among oysters growing shell normally, there is an undoubted, although slightly irregular, periodicity in the spawning, and that the maximum spawning occurs at about the time of full moon. This is well shown in Figs. 3 and 4, pages 210 and 211. It is, however, equally clear that among the dumphy oysters spawning is not so regular. (See Figs. 5, 6 and 7.)

As is well known the summer of 1925 was more than normally warm and therefore favourable for the spawning of oysters. It will probably be many years before such a favourable summer will occur again ; and since the temperature remained high enough over at least most of the summer to permit oysters to spawn at such times as they were ready, an opportunity occurred of observing whether there exists any tendency for rhythmical breeding in this mollusc. No one has previously demonstrated rhythmical breeding in the oyster, although the ancient naturalists, as Philpots (3) and recently Fox (4) have shown, stated that oysters were fat at full moon and " empty " at new moon, while Tarentines are stated to hold the same belief at the present day. (See also page 221.)

DESCRIPTION OF THE TRURO OYSTER BEDS AND DISCUSSION REGARDING  
THE BIOLOGICAL SIMILARITY OF THE POPULATION EXAMINED.

The main Truro oyster beds of the Fal Estuary lie between the Fal-mouth Harbour proper and the Fal River, in a lake, or widening of the Estuary, in which the main channel, 14 to 9 fathoms deep, crosses the lake diagonally, while shallow banks occur on the south-west to west, and east to north-east sides of the channel. (See 5.) There is an eddy tide on both sides of the main channel. The general hydrographical conditions of the lake are not known, but from the general similarity of the East and West Banks, it is believed that such hydrographical and biological differences as may occur in the waters over the two banks would not be significantly different on the whole in their influence on the spawning habits of the oysters. There is, however, reason to believe that oysters in the Channel itself might be significantly different from those on the adjacent banks, and some samples were obtained from the East Edge, a locality where the East Bank slopes at a depth of 2 to  $2\frac{1}{2}$  fathoms towards the Channel proper. The localities from which samples were taken are :—

- (1) East Bank, with depths of about 0 to  $1\frac{1}{2}$  fathoms at low water.
- (2) East Edge, at depths of  $1\frac{1}{2}$  to  $2\frac{1}{2}$  fathoms shelving towards the Channel.
- (3) Mylor Bank and Pool, similar to the East Bank, but on the west and south-west side of the Channel.
- (4) Turnaware Point and Bar, the northerly continuation of the East Bank which juts out to form a bar, and is partially exposed at low spring tides.

It was found in practice difficult to obtain all the material from one place, as efficiency in dredging varies with exposure to different strong winds. Ideal material would, however, be obtained from the same place,



but periodicity in breeding was not contemplated when the research was begun.

One sample of oysters was especially obtained from the Falmouth North Bank (in the grounds under the administration of and supplied by the courtesy of the Falmouth Corporation [Harbour Committee]) for the critical second week in August. That Bank is a continuation of Mylor Bank, but runs off towards the Cross Road Channel in slightly deeper water. It may be expected that in its nearer position to the open sea, the Falmouth North Bank would have a slightly higher mean salinity with correlated hydrographical variations than situations higher up on the Mylor Bank, and as the nature of the bottom is harder there would occur also a biological difference, but whether these differences would be significant in their effect on spawning cannot be stated. It was actually found that the normal oysters taken from the ground were remarkably similar to those taken at the same time from the East Edge, but that there was an astonishing difference in the dumpy oysters from the same two localities. It would appear, therefore, that the normals had spawned similarly at about full moon in these two localities, but that whereas the dumps from the waters of the Falmouth Bank also spawned at the same time as the normals, those on the East Edge did not.

With regard to the Truro samples, the critical ones taken about full moon on July 8 and September 3 were from off Turnaware Point, and that of August 5 mainly from the same locality; while of those taken in the weeks after full moon, the sample taken on July 15 was from the East Bank, and those of August 11 and September 9 were from the East Edge. Thus, the corresponding samples at the critical periods of full moon and the week after are either from the same place or a locality very near.

On the whole there is little reason to believe that the oysters on the grounds sampled did not form a fairly homogeneous population with regard to general biological environment; on this basis, therefore, and until the contrary can be shown, the weekly samples may be taken to be representative of an approximately uniform population.

If, on the other hand, a different point of view be taken, and the results obtained be considered, then the orderly rhythmical breeding period shown by the normal oysters in two out of the three months—and the variation in the middle month of August, apparently due to the sudden cold spell of weather at that time, is really also confirmatory of what we know of the oyster in relation to temperature change—may be regarded as confirming the view—but not proving—that the samples were representative of an approximately homogeneous population with regard to spawning behaviour. If, however, it is a fact that normal oysters everywhere spawn *chiefly* at full moon, proof will soon be forthcoming in the future from populations undoubtedly dissimilar in other respects.

## THE SPAWNING OF THE NORMAL OYSTERS.

The results of the examination of the samples may now be discussed as shown in the graphs in Figs. 3 to 7. In Fig. 3, page 210, are shown the total percentages of normal oysters spawning each week throughout the summer (thick line). In the months of July, August and September the peaks of the graphs occur in the week after full moon, at which time those oysters which spawned in the full moon period will have embryos mainly a week old, but more than two days old. If oysters spawn during say five days of the full moon period a smaller percentage in spawn may be expected in a sample taken at or in the days preceding full moon than later, but, since oysters retain their embryos for certainly a week, a sample taken a week after full moon will contain all those oysters which spawned round about the period of full moon, and the percentage will be a maximum, or higher than in samples taken a week earlier. There can be no doubt that this is the explanation of the occurrence of the peaks of the graphs in the week after full moon. It is worthy of note that there is also a small peak in the week after the full moon in October. Thus Fig. 3 seems to show that there is clearly a regular periodicity in the breeding of the oysters and that a maximum of spawning occurs round about the days of full moon. The writer has shown elsewhere (6), however, that white-sick oysters, i.e. oysters with very young embryos, must be interpreted with care, that they may in fact be forced spawners. A long experience in inspecting recently dredged oysters and examining the state of development of the embryos carried by such, leaves no doubt that the mere disturbance due to dredging or lying about in the sun, or being crowded in a bag out of water, may cause individuals to spawn prematurely, if such are ripe, or even nearly ripe. For this reason the percentages carrying embryos up to about two days old (about the stage of the ciliated trochosphere) and those carrying embryos more than two days old (shelled larvæ) are shown separately in Figs. 4 and 5. In Fig. 4, p. 211, which shows the normal oysters with embryos, there is seen to be a high percentage of recently spawned oysters at full moon in July and September, but the highest percentage in August falls in the week after full moon; on the other hand, the highest percentage of oysters with embryos two days to a week old falls in the week after the full moon in July and September, but in August there are two peaks, one after the full and one after the new moon period. Further, in July and September the percentage of oysters with recently extruded embryos falls off rapidly from full moon and fairly rapidly also in August from the week after full moon. Similarly the percentage of oysters with old embryos falls off rapidly in July and September at a similar rate to that of oysters with young embryos; in August, however, there are

FIG. 3.

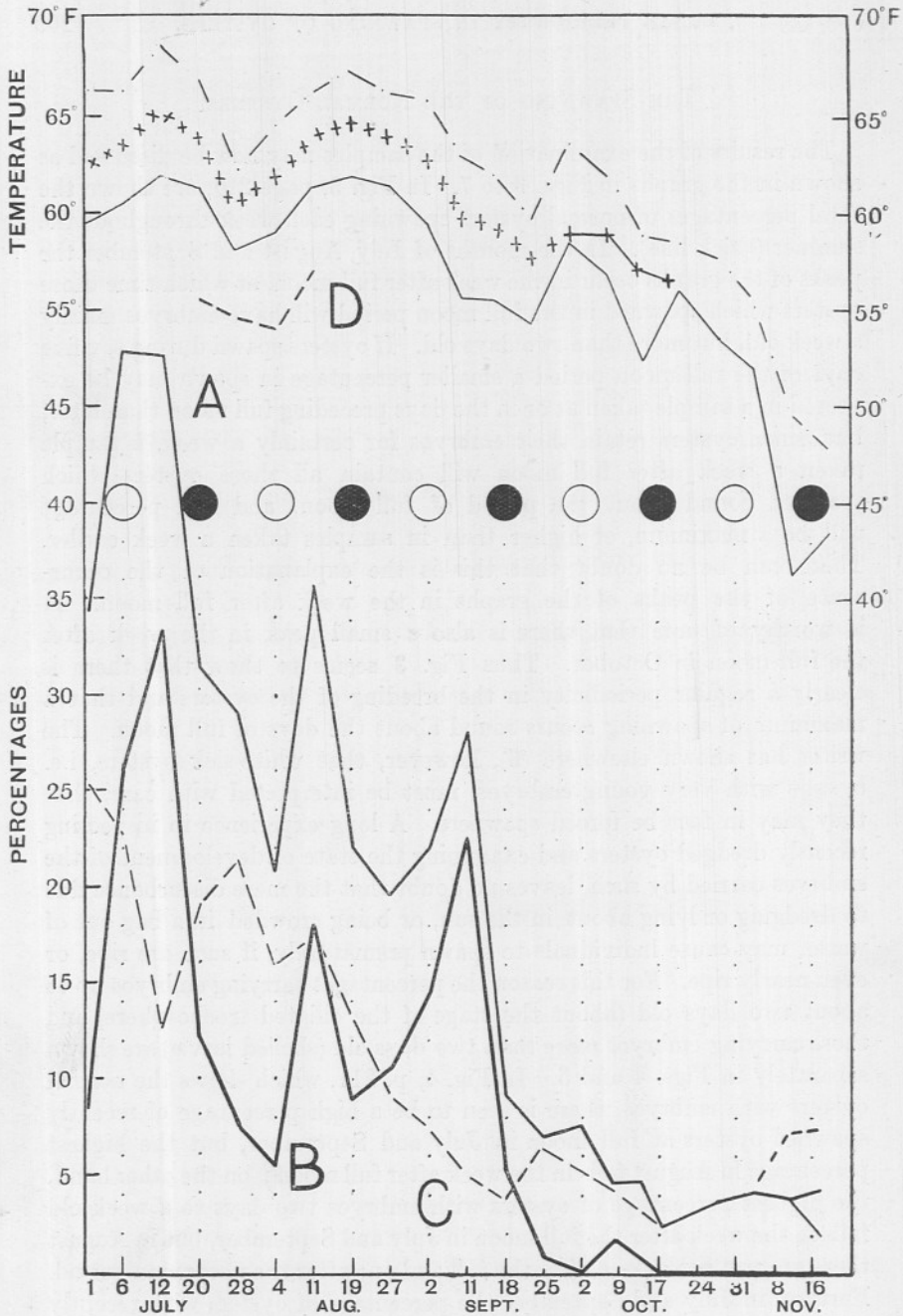


FIG. 3.—Graphs showing the weekly percentages of

(A) total female oysters (B+C), (B) total spawning oysters, (C) total pure ripe but unspawned females in relation to the moon's phases among oysters with normally grown shells from the Truro beds. Fal Estuary, 1925 (age estimated at mainly 4 to 5 years, but extending probably from 3 to 7 or 8).

The thick broken line branching from the graph A at the end of October shows the increasing percentage of recognisable ripening females. The graphs at the top of the figure show mean maximum (dots and dashes) and mean air temperature (continuous line) at Falmouth, with the approximate mean sea-temperature over the oyster beds indicated by crosses.

At D are given the mean minimum air temperatures round the period of the August full moon.

again two peaks, but with a minimum value towards the September full moon. The analysis given in Fig. 4 confirms the result shown in Fig. 3, but points to a disturbance of the indicated rhythm by something occurring at the beginning of August. It is an interesting fact that at full moon and round about the period of full moon spring tides in August there occurred a cold spell of weather (see Fig. 3 D.) while on August 5 (at full moon) a minimum temperature of  $51.2^{\circ}$  F. and a rainfall of 31 mm. was recorded at

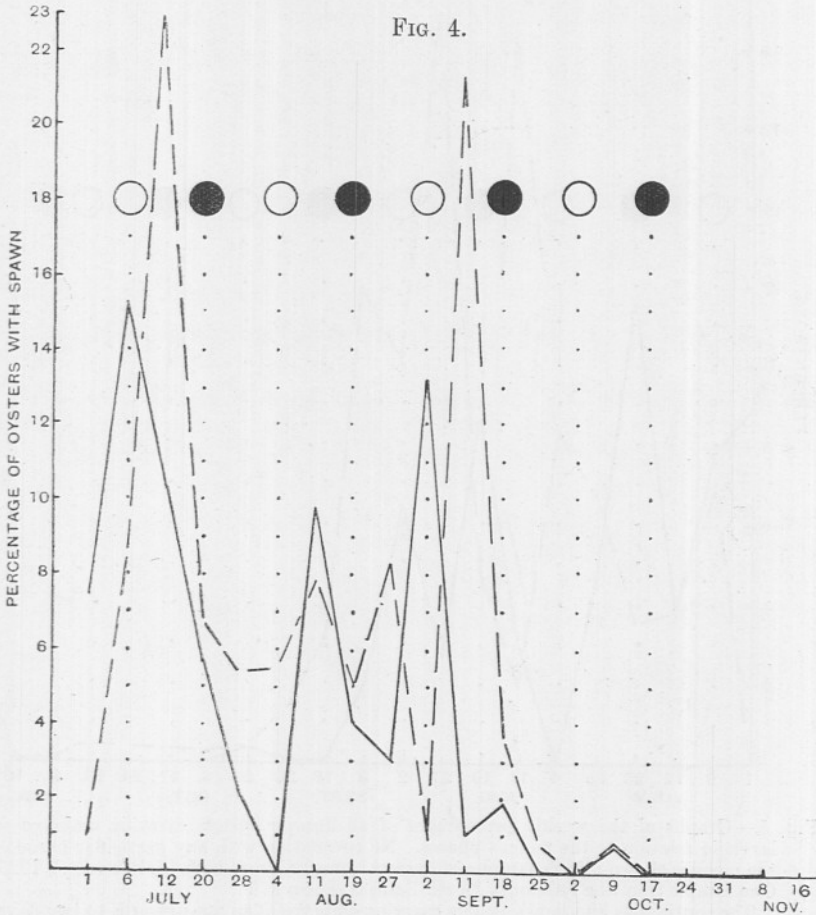


FIG. 4.—Graphs showing the weekly percentages of oysters carrying embryos or larvae in relation to the moon's phases, indicating an irregular correlation between lunar periodicity and breeding phenomena; from samples of oysters with well-grown shells from the Truro oyster beds (Fal Estuary), 1925.

The continuous line shows oysters carrying embryos of an age upwards to about two days.

The broken line shows oysters carrying embryos mainly fully shelled or older than about two days.

Full moons are shown by the circles, and new moons by the filled-in circles, here and in Figs. 5, 6, and 7.

Falmouth. (See 7a and b, Monthly and Weekly Weather reports of the Meteorological Office.) Unfortunately there are no sea-temperature records available for the Falmouth oyster beds, or the sea near the oyster beds, to correlate with the spawning conditions observed from July to October, 1925, but the mean maximum air and mean air for Falmouth (7a) is shown

FIG. 5.

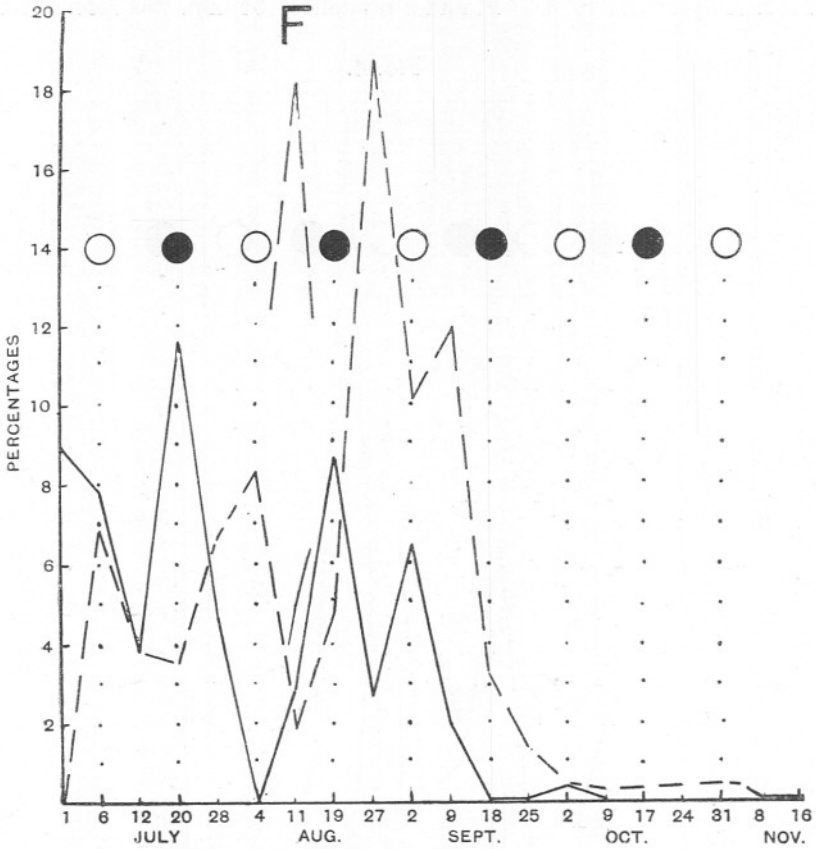


FIG. 5.—Graphs of the weekly percentages of all dumpy oysters carrying embryos or larvæ in relation to the moon's phases. No correlation with any particular phase of the moon is shown: from samples of oysters from the Truro beds (Fal Estuary), 1925. One sample from the Falmouth North Bank is shown at F.

The continuous line shows oysters carrying embryos of an age upwards to two days.

The broken line shows oysters carrying embryos mainly fully shelled or older than about two days.

in Fig. 3 along with a few sea observations made on the beds by the writer in October. From this information it is possible to obtain an approximate indication of the sea-temperature over the oyster beds, for the writer has shown (8), and in unpublished work, that whereas in the deeper water at the mouth of the Thames Estuary mean sea follows mean air-

temperature almost exactly but with a lag period of a fortnight, at situations higher up the estuary in shallower water mean sea-temperature rises above mean air with a decreasing amount of lag, and on the oyster beds in 1 to 2 fathoms :—

(1) From April to September mean sea-temperature may be from 2 to 5° F. above mean air, whether the preceding period has been warm as in 1921, or somewhat cold as in 1922.

(2) Mean sea-temperature remains above mean air-temperature for the greater part of the year ; fluctuation in the relative values of sea- and air-means may occur in the winter months.

(3) Low-water means are higher than high-water means from about May to September, and lower or about the same from November to March.

(4) Sea-temperature monthly means vary directly with air-temperature means without any lag.

The temperature variation over the Truro oyster beds may be predicted to be somewhat similar to those occurring over the Whitstable beds, but attaining neither the higher nor the lower values of that region, because of the influence of the Channel water. Therefore, with regard to the low-water temperature in the August tides on the Truro beds, although the temperature might be reduced to a very low figure, especially at midnight at full moon on August 5, it is not possible to estimate a probable figure in view of the absence of temperature readings from the grounds at some date near that period. It is certain, however, that during the August full moon tides there would be a sensible drop in the water-temperature, especially at low water. This conclusion is of great interest in connexion with the detection of the direct stimulus which produces spawning, namely, that there occurred a sudden drop in the temperature at the time a general spawning was due, which was followed by an irregular spawning in the month of August, with, however—

- (1) a maximum of recently spawned normal oysters in the week after full moon (see Fig. 4) apparently delayed one week.
- (2) two maxima for oysters with embryos about a week old in the week after full *and* new moon, that is after the spring tides.

The occurrence of an abundant spawning in the full moon period of September following the irregular month of August is of special interest in connexion with the problem of the proportion of the whole population spawning in one season, and with the probability that while one section of the population is spawning another proportion is ripening.

## THE SPAWNING OF THE DUMPY OYSTERS.

Before discussing further the causes of the irregular periodicity observed in the spawning of the normal oysters, it is necessary to consider the spawning behaviour of the dumpy oysters, which is shown in Figs. 5, 6, and 7. Fig. 5, p. 212, shows the weekly percentages with embryos two days old, and those with embryos more than two days to about a week old, Fig. 6 compares the percentages of normals and dumps with the older

FIG. 6.

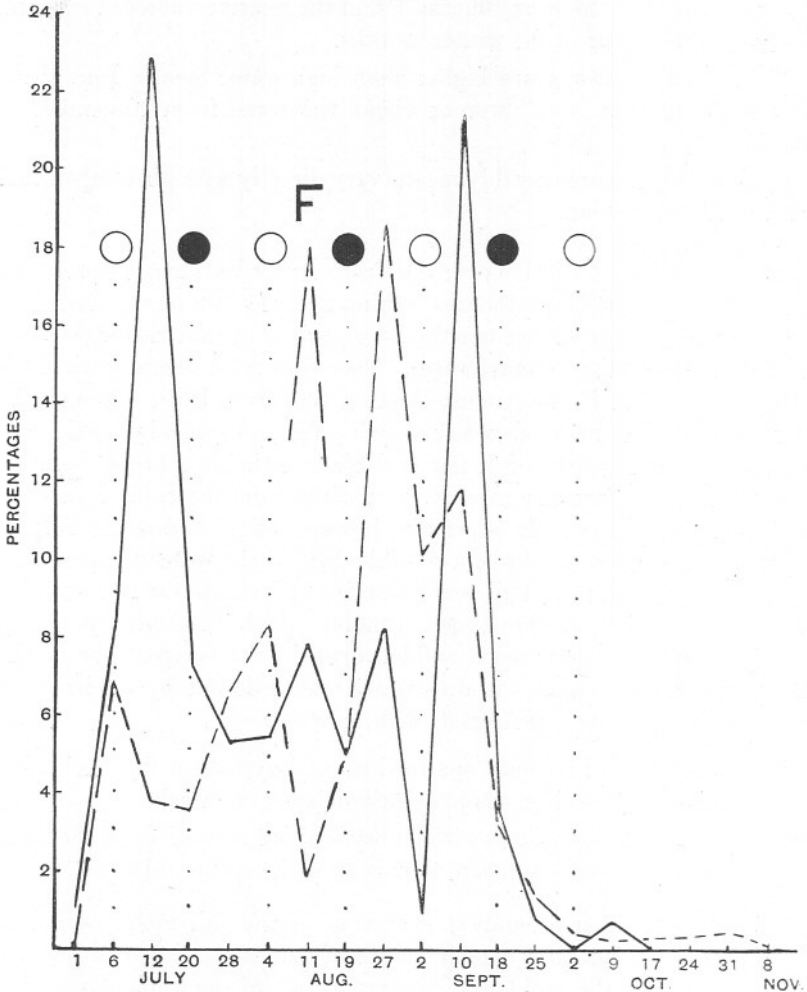


FIG. 6—Graphs comparing weekly percentages of normal (continuous line) and dumpy oysters (broken line) carrying embryos mainly fully shelled or more than about two days old; from the Truro beds (Fal Estuary), 1925. One sample from the Falmouth North Bank is shown at F.

embryos, and Fig. 7 compares the total in spawn of both normal and dumps. In Figs. 5 and 6 the results of the examination of the dumps from the Falmouth North Bank are also shown at F. A glance at Fig. 5, p. 212, shows that the spawning of the dumps is entirely irregular as compared with the normals. The graph of percentage of oysters with young embryos (unbroken line) shows three peaks, two at *new* and one

FIG. 7.

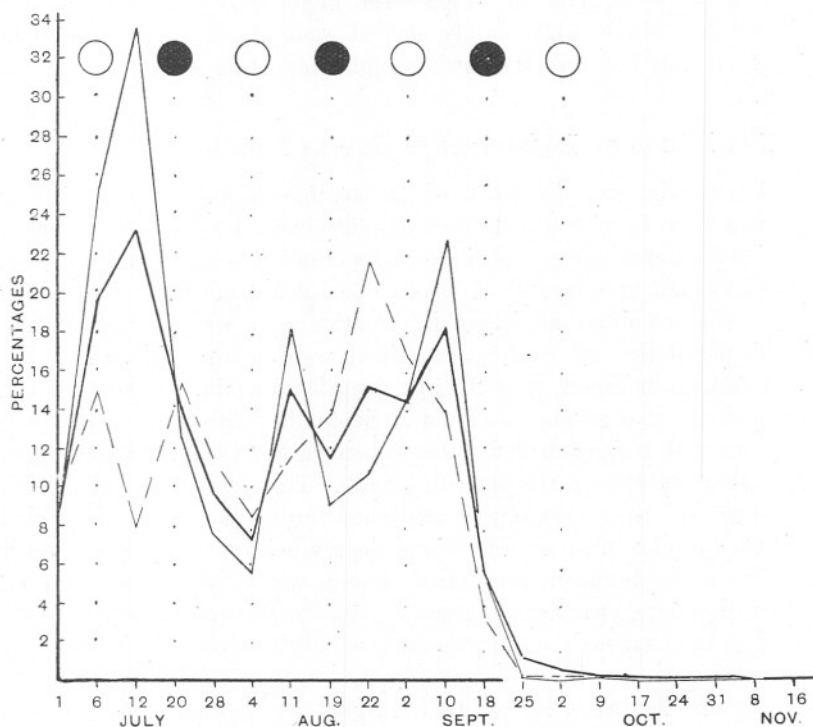


FIG. 7.—Graphs comparing the weekly percentages of all normal and all dumpy oysters spawning, and the percentage spawning in all samples of all kinds combined (Truro oyster beds, Fal Estuary, 1925).

The thick line shows percentages spawning of all samples of all kinds (including the sample from the Falmouth North Bank) combined, the thin line shows percentage of all normal spawning, the broken line the percentage of all dumpy spawning.

at full moon, while the graph of percentage with older embryos (broken line) shows peaks at full moon (twice), the week after full moon (twice), and one high peak after new moon, while from Fig. 7, broken line, in which the total percentage of dumps spawning is compared with the normal and the whole population, it is seen that of the three maxima, one is at full, one at new moon, and one the week after new moon.



It is clear, therefore, that the spawning of the dumpy oysters is quite irregular, whether the total spawning be considered or the percentage spawning with advanced embryos at the time of examination. Thus, besides the abnormality of dumpy oysters in shell metabolism, it is seen that they are also abnormal in their spawning behaviour as compared with normal individuals. Although generally speaking the dumps are irregular in spawning, the sample of dumps from the Falmouth North Bank in the week after the August full moon gave the high figure of 18% of individuals with mainly shelled embryos, indicating that the dumps on that bed had spawned in high proportion about August full moon.

#### THE PERIOD OF INCUBATION OF OYSTER LARVÆ IN THE SEA.

Before passing to a discussion of the possible causes of the periodicity observed in the spawning of the normal individuals, it will be convenient to examine further the graphs of percentages of normals in spawn in relation to the known facts of the rate of development of the embryos. In this way it is possible to obtain additional information as to whether the samples of the population of oysters examined were comparable. Let the results shown in Fig. 4, page 211, be considered again. The maximum values of the two graphs in July and September differ, the percentage of oysters with mainly shelled embryos being greater than that of oysters with young embryos in the preceding week. This difference is explicable on the ground that spawning is continued during the full moon period after the samples taken on July 6 and September 2 were dredged, and it has also to be borne in mind that among white-sick oysters may be some which have spawned unnaturally, due to disturbance on or after dredging, but that such oysters would generally be ripe ones on the point of spawning.

If now the disturbed conditions in August be ignored, it will be seen that the graph of oysters with old embryos follows significantly closely the graph of oysters with young embryos with a lag period of one to about one and a half weeks. From this it may be inferred, if the members of the population are approximately similar, that oyster embryos develop to the shelled stage and are expelled by the parent in a period of one to one and a half weeks. As it can be shown that the larvæ do develop to the shelled stage in about a week at summer temperatures, there is, therefore, an additional reason for the assumption that the population of oysters examined was in fact approximately uniform in spawning capacity. It is a difficult matter to obtain the actual age of the embryos of oysters, as the beginning of spawning can only be rarely observed, but the age can be obtained approximately by noting the approximate age, to within 12 to 24 hours, of oysters with young spawn and observing the subsequent rate

of development, as in the following experiments carried out by the writer.

(1)	July 29, 1920. Segmentation stages (age ca. 24 hrs.)	Aug. 3, 1920. Embryos shelled and black	ca. 6 days	Temperature. 59.2° to 65.5° F. mainly 63° to 64°
(2)	July 30, 1920 Trochosphere stages (age ca. 48 hrs.)	Aug. 4, 1920. Embryos shelled and black	ca. 6 days	Temperature. 59.2° to 65.5° F. mainly 62.5° to 64.0°
(3)	ditto (age ca. 48 hrs.)	ditto and black	ditto	ditto mainly 62.5° to 64.0°

In these cases the embryos were taken from the parent and placed in shallow dishes in a tank in the Plymouth laboratory.

Späreck records a similar case (9, p. 31) of an oyster with eggs in segmentation stages (up to 24 hrs. old) 20 July, and swimming larvæ 25-26 July, in six to seven days, and two other similar cases (loc. cit. p. 46). We now know, therefore, from experiments, that oysters will usually reach the black-sick stage about one week after spawning. This result confirms the more important field observations of Mr. Louis French who, during a great many years experience as a practical oyster producer at West Mersea, Essex, has observed that black-sick oysters may be found on the beds generally about one week after white-sick ones are found, and that settled spat may be expected in warm weather ten days to a fortnight after the first black-sick oysters are seen. Generally, settled spat may be taken in fair numbers in normally warm weather about one month after the first batch of white-sick oysters is seen, as the writer has several times had the opportunity of verifying on the beds.

Apart from direct observations on successive batches of oysters taken from beds in the sea, it will be difficult to obtain reliable information on the *normal* period which oyster larvæ pass in the mantle cavity of the parent, but valuable observations on the matter may, however, be expected from the large scale tank experiments being carried out by the English Fisheries Department at Conway, where large numbers of oysters are probably allowed to remain undisturbed during the incubation of their young. If incubating oysters are disturbed they are liable to behave abnormally and throw out their young even in very early stages of development. There is need for far more extensive and precise information about oyster embryos and larvæ than exists at present. (See also Späreck 9, p. 46.)

We have seen, therefore, that if the normal oysters examined from the Falmouth grounds be assumed to be representatives of a similar population, then the period which oyster young pass in the mantle cavity of the parent is about one to one and a half weeks (at a temperature unknown); on the other hand, practical experience and experiments point to a period of one to two weeks as the period of incubation of oyster young, and

thereby confirm the assumption that the Falmouth normal oysters were in fact an approximately uniform population with regard to spawning capacity and behaviour.

#### DISCUSSION ON THE PROBABLE CAUSES OF THE PERIODICITY IN THE SPAWNING OF THE OYSTER.

As it has now been shown that spawning in normal oysters is periodical and that a maximum of spawning certainly occurred about full moon on the Fal Estuary beds in 1925, while, on the other hand, it is clear that dumpy oysters spawn irregularly, it is possible to discuss the probable causes of the rhythmical character of the normal spawning. In order, however, to explain satisfactorily why the oyster tends to spawn at full moon, it would be necessary to show how such a time for spawning *fits in with the general relation of the oyster to its environment over the whole of its life history*; while in order to find out the immediate cause of spawning, it will be necessary to examine critically the spawning habits of oysters under different conditions in different localities in relation to all probable predisposing factors, such as :—

##### I. Tide : variation in height, accompanied by—

- (a) increase and decrease of pressure at successive high and low tides.
- (b) increase and decrease of temperature generally at successive low and high tides.
- (c) increase and decrease of salinity generally at successive high and low tides.
- (d) increase and decrease of other more recondite hydrographical factors, such as pH.

At spring tides the rate of change in the above factors will generally be greatest, so that decrease of pressure, increase of temperature and to a less extent decrease of salinity will act together.

##### II. Moonlight : variation in intensity and duration.

Maximum values will occur about new moon spring tides.

##### III. Food : variation in the amount of (a) available food material, and/or (b) food-intake in the tidal or bi-lunar cycle.

Food may be most abundant and feeding most active during neap tides, but this is not known with accuracy, but in view of the rapid development of the sex-elements (6 and 9) these factors are undoubtedly important.

##### IV, Temperature : absolute variation.

There can be little doubt that a temperature of about 60° F. constitutes the lower limiting value for breeding in the oyster.

- V. Sunshine: the variation in duration and intensity of which should not be neglected in a study of an estuarine form: maximum values *on the beds* would tend to occur at spring tides.
- VI. Undetected factors, such as may have operated in the course of evolution, and may or may not now be determinable.

On the Falmouth beds—and in the South of England—low spring tides fall at about midday and midnight, and as is well known the greatest springs occur in the summer time, on the full moon tides. Therefore, the range of variation in I, a, b, and c, and probably d, is greatest at full moon tides, but is also great at new moon tides. II has its highest value at full and lowest at new moon tides, while III, a, and probably III, b, are greatest at neap tides, but these are unknown (see 14). IV will normally produce its greatest effect on the spring tides of full and new moon, but is subject to fluctuation, while V would again tend to have maximum values in shallow water and at low water springs full and new moon.

Now, since dumpy oysters showed a tendency to breed in numbers on both new and full moon tides, as did the normals on the August new moon tide, it would appear that those factors telling principally at the spring tides are chiefly concerned as stimuli causing the oyster to spawn. Thus, it may well be that the rapid rate of change in pressure accompanied by increased temperature at spring tides is sufficient stimulus to cause spawning. On this view it follows that spawning at the full moon tide may be a mere coincidence, and it will be interesting to see what will happen in 1926 when the times of the month at which full and new moons occur will practically have changed places as compared with 1925. It may be that moonlight or other factors are concerned, but unless the whole of the factors concerned can be obtained and correlated it is unlikely that a critical resolution of the probable stimulus or stimuli can be effected. It is more likely that critical information on the probable stimuli causing spawning will be obtained from a simultaneous study of populations of oysters in widely different localities, or even geographical regions, especially if a locality could be found where full and new moon tides have practically the same range of rise and fall.

#### ON THE FREQUENCY IN AND PROPORTION OF THE OYSTER POPULATION SPAWNING.

The monthly rhythm in the spawning of the oyster may be, and probably is, connected with the period required for the maturation of the gonad. Spärck has recently given experimental data showing that three males rapidly passed into ripe females in from one week to a fortnight

(9, p. 31) in the summer months. Fox (10) has observed rapid development of eggs in sea-urchins comparable with that seen by Spärck in oysters. The present writer has recorded one case (6) of an oyster spawning as a female, changing into a male, and yet again spawning as a female six weeks after it was last noticed in a male condition.

There is need for extensive experiments on these lines, but some information on the problem may be culled from Figs. 3 and 4. The maturation of the gonad, however, comprises in the case of females, not only a development of oogonia into ripe eggs, but a period of active feeding to enable the necessary reserves to be accumulated to nourish the developing eggs. It is proposed to discuss this matter fully later, but reference may be made to Fig. 3, p. 210, which gives the analysis of the samples of normal oysters for pure ripe females which did not spawn in the weekly batches examined. The percentage of unspawning ripe females added to the total percentage spawning gives the total percentage of females in each sample. The percentage of ripe unspawning females falls off on the whole from a high figure at the beginning of the season to a low figure at the end, but persisted in a small percentage into the winter period. In the same way the total percentage of females shows a gradual falling off through the summer, but the increases observable in the full moon week or the week after are only explicable on the assumption that there is a rapid development of females round about the period of full moon. It is therefore a reasonable assumption that the weeks following full moon constitute a period of preparation of potential females for maturation at about the time of the next full moon, and that in 1925 such a maturation occurred in *fair* numbers of individuals in the months of June, July, and August, while there is even a small rise at the end of September. At the beginning of the winter an indication of an increase in the percentage of ripening females is shown in Fig. 3, p. 210, and on February 18, 1926, a sample of oysters was found to have the high percentage of 31.7 *recognisable* ripening females. There is therefore no doubt that at the end of the spring of 1926, the percentage of ripe females will have risen again to the high figure shown in Fig. 3 (nearly 50%) occurring on July 1, 1925. Thus it is clear that the maturation period of the majority of female oysters must occur in the winter and early spring.

The writer has now obtained by experiment a reasonable number of oysters which have been shown to experience four changes of sex in a period of twelve to thirteen months, but in view of the results shown in Fig. 3, it is probable that in a summer like 1925 four changes of sex may occur in one and the same season. Indeed assuming, as we now have reason to, that the constituents of the oyster population were similar, it can be shown that more than 100% of the oysters spawned

as females, a result which means that some oysters spawned as females twice, with the corollary that they must have experienced also two phases of maleness. Let only the samples taken during the weeks after full moon in July, August, September, and October be considered, then respectively 33, 18, 22, and 1.5% were taken carrying embryos, giving a total of the population—disregarding all other samples and those breeding before July—of 110% breeding as females. In the same way it can be shown that at least 100% of the dumps must also have spawned. The actual figure might be very much higher than this, and a large proportion of the population must, on the assumption made, which we have seen is reasonable, have spawned twice as females. This result is surprising, perhaps, but not at all unreasonable in view of what is known of the breeding of other marine animals.

#### OTHER MARINE ANIMALS SPAWNING AT OR NEAR FULL MOON.

Fox (4) found the Suez sea-urchins (*Centrechinus setosus*) [*Diadema*] to breed at full moon, and one and the same individual to breed in successive full moons, but in these sea-urchins there is no known change of sex. The occurrence of breeding in marine animals in relation to varying phases of the moon is also discussed at length by Fox, who notes that in no case has a satisfactory explanation been offered of an apparent relation between some phase of the moon and breeding in various types of marine animals, including worms, molluscs, sea-urchins and a fish. In most cases the influence of the tides in connexion with the moon is suspected, but in the locality where the Suez sea-urchins occur, Fox showed that there is actually more tide at new than at full moon. It would seem reasonable, therefore, to investigate more fully the possible influence of moonlight itself, even though this factor does not appear on the surface to be essentially concerned. When the case of the oyster has been more fully investigated, it will be possible to make definite experiments on a large scale, as the oyster is a sedentary animal and amenable to experimental work.

#### ANCIENT NATURALISTS ON THE CONDITION OF THE OYSTER IN RELATION TO THE MOON'S PHASES.

It is fitting to conclude this paper with quotations long ago culled by Philpots (3, pp. 44-52) from the writings of the ancient naturalists. Pliny states "that generally speaking (oysters) increase in size with the increase of the moon" and similar quotations are given from Lucilius, Manilius, Horace, and Cicero (loc. cit., p. 50), while a quotation of Annianus is given with reference to the condition of oysters after full moon, namely, "the moon is now in truth waning, and on that account the oyster, like

other things, is lean and void of juice." Fox (4) gives also similar quotations from Aristotle and others. It is a fact of great interest that Fox began his successful investigation of breeding in the Suez sea-urchins as a result of hearing the belief widely held at the present day in the East of the effect of the moon on not only certain marine animals, but also certain vegetables. An interesting general discussion is given by Fox. Philpots also observes (loc. cit., p. 51) that Faber (11) records that even at the present day the Tarentines declare that oysters are "fattest during the full moon." In view of what has been described above in the case of Fal Estuary oysters, we may now reasonably expect a demonstration of a maximum spawning of—at least, normal—oysters in the Tarento beds in the south of Italy and elsewhere at about the time of full moon.

#### THE ECONOMIC ASPECT OF THE RESULTS OBTAINED.

The economic aspect of some of the results noted above has been partly dealt with (12), and it has already been shown that cultch can be laid much later in the year than is customary with a prospect of an economic return in a collection of late spat. It has been shown that on the oyster beds in the Thames Estuary spat caught later in the year than July had grown to a size of upwards to  $1\frac{1}{4}$  inches by the following July, and that spat taken as late as August in the poor year of 1923 attained a good shape and a size of upwards to one inch by the following July *in the sea*. In a warm year, therefore, and indeed also in normal years, it follows that since a maximum of spawning may be expected at full moon tides, the cultch should not be laid in one great batch, but should be laid in separate batches at intervals of about one month, beginning in the week after the first full moon at which a normal spawning occurs. In this way can be prevented a great waste of cultch by its becoming slimy or unclean from overgrowth. Where cultch is cheap a batch may be sprinkled over the grounds in a warm summer, even in September, especially on the Fal Estuary beds, with a prospect of an economic return in settled spat. In this connexion it is of interest to record that during visits to the Truro beds in October, 1925, the writer found on a fair proportion of shells of recently dead oysters tiny spat only a few millimetres in diameter, which had probably settled during the month of September. Mr. J. W. Tabor sends information by letter that he also found similar tiny spat on the beds off Whitstable late in the year 1925.

The observation of Mr. French (see p. 217) that settled spat may begin to fall *in the sea* ten days to one fortnight after the first black-sick oyster is seen on the beds—Hagmeier (13) obtained similar results in pit experiments—is of great value in estimating the correct time to put out in the sea the first batches of cultch, and as it has been shown above that a maximum number of black-sick oysters is likely to occur in the week

after full moon, the fall of spat may be expected to begin normally on the following new moon tides. On economic grounds it is advisable, however, that extended observations on spawning in relation to the moon's phases should be carried on over a series of years to test fully the probability of a maximum spawning occurring at any fixed period. In this way cultch can eventually be laid intelligently and with a greater prospect of an economic return, and a replenishment of our oyster beds with spat.

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#### ACKNOWLEDGMENTS.

Acknowledgment is due to the Truro Corporation (River Committee) for supplying oysters during the summer for the observations on spawning; and to the Falmouth Corporation (Harbour Committee) for a sample of oysters in August; and the writer is especially indebted to Professor P. R. Awati for assistance in examining the first four samples from Truro; to Mr. Louis French for permission to quote his valuable field experience, and in many ways to the Directors of the Tollesbury and Mersea Native Oyster Company.

#### SUMMARY.

During 1925 dumpy oysters spawned in a high proportion on the Fal beds, and although not such heavy breeders as normal oysters, they are undoubtedly valuable in forming a stable spawning stock for replenishing the beds in the future.

Nearly every normal and dumpy oyster above a size of 2 to  $2\frac{1}{2}$  inches produced at least one batch of spawn in 1925. Since dumps increase in proportion on the beds as over-fishing occurs, they form a natural breeding reserve for repopulating the beds in favourable years, as there is no adequate reason to suppose that the larvæ of dumps are unhealthy. Weekly samples of oysters examined closely during the summer of 1925 for the percentage of spawning females and ripe but unspawned females show—

- (1) that the population as a whole gave maximal percentages in spawn in the weeks after the July and September full moons.
- (2) that normal oysters showed three maximal percentages in spawn in the weeks after the July, August, and September full moons.
- (3) that dumpy oysters spawned more irregularly.

A certain amount of spawning occurred at other times than full moon.

There is good reason to believe that the population of oysters sampled is an approximately uniform one in spawning behaviour. Hence there is little doubt that oysters showed a marked tendency in the Fal Estuary in 1925 to breed rhythmically at about the time of full moon.



The summer of 1925 was very favourable for the spawning of oysters, except for a short spell of cold weather in early August, and spawning was subjected to relatively little interference for English weather conditions.

An analysis of the spawning oysters into those with young embryos and those with mainly shelled larvæ brings out the fact statistically that oyster larvæ under natural conditions are retained in the mantle cavity a period of only 1 to 1½ weeks from the date of their extrusion as fertilised eggs from the parent. This observation is in concordance with extended field observations and experimental evidence of the attainment of the black-sick stage by an oyster in 5 to 7 days from the date of spawning.

The probable causes of spawning at full moon are discussed, and of the immediate stimuli likely to produce spawning decrease of pressure with increase of temperature at low water are considered the most likely factors, without, however, excluding other factors which cannot be fully investigated in the absence of data. It is pointed out that a full explanation of spawning at full moon must explain this phenomenon in relation to the main facts of the life-history of the oyster.

Ripe females decreased in numbers during the summer from about 50% to about 5%, while recognisable ripening females increased in the following autumn and winter from about 4% to more than 30% already in February.

The chief period for maturation of females is in the winter, but a proportion may mature also in the summer.

It is shown that on the assumption that a uniform population was sampled all through the summer, the normal and to a less extent the dumpy oysters must have spawned in fair numbers twice as females—and consequently once and possibly twice as males during the course of the summer. Attention is drawn to statements by Aristotle and Pliny and other ancient naturalists, and by Tarentines at the present day on the correlation between the condition of Mediterranean oysters and the moon's phases, and the probability of truth in these statements as the result of the observations recorded above.

The extended spawning season here demonstrated adds weight to experiments carried out by the writer with late cultch, showing that economic returns may be expected from layings of cultch made far later in the year than is the custom.

Proof of a maximum spawning time, as at full moon, if confirmed over a period of years, would allow the oyster-producer to lay cultch at the correct time to catch a maximum of spat with a minimum of waste cultch, and waste oyster larvæ.

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## Modification by Habitat in the Portuguese Oyster *Ostrea (Gryphæa) angulata*.

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AND

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*Professor of Zoology, Royal Institute of Science, Bombay.*

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With 1 Figure in the Text.

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WHILE working on the beds in the River Blackwater, Essex, a collection of Portuguese oysters, which had been dredged along with native oysters (*O. edulis*) from the river and creeks, was seen at a glance to show a distinct average difference in shape from the usual type of Portuguese oyster. The ordinary Portuguese oyster as seen exposed for sale is usually imported when quite small, or occasionally well-grown, and relaid on English beds at or above low-water mark to grow and fatten. Orton\* has shown by definite experiments on the same beds that the Portuguese oyster spawns and spats in English waters in favourable (hot) weather. There can be no doubt, therefore, that the Portuguese oysters dredged had grown in situ from larvæ which had developed in the waters of the river and creeks. In Portugal and France the Portuguese oyster is stated to occur at and just below low water springs (see Bashford Dean, Bull. U.S.F.C. XI, 1891 (1893), p. 368), and is apparently hand collected at the present day for export purposes.

A difference in shape in native oysters is very common, but Bell and others have so far found it a very difficult matter to correlate any particular shape with a particular environment. Indeed, Bell stated, in a letter, that each locality seems to have its own type of shell-growth in the native oyster. Such a difference as that noted above in the Portuguese oyster was therefore deemed worthy of some attempt at expression.

In the present paper, which can only be regarded as a preliminary study, the lengths of the oysters, measured to the nearest millimetre, have been collected in centimetre groups, and correlated with the corresponding shell-heights, and an average shell obtained from plotting the results to scale. (See Fig. 1, p. 229.)

\* *Nature*, Vol. 110, August 12, 1922, p. 213.

Three samples of oysters were used for the diagrams given in Fig. 1.

(1) Through the courtesy of Mr. J. M. Tabor it was possible to obtain two lots, each of 100, of Portuguese oysters imported September and October, 1925, from the Tagus beds, Portugal. A glance at Fig. 1 thick-lined figure shows that the sample examined was a uniform one; the actual centimetre averages of one lot are as follows, the others being similar :—

No. of Individuals.	Length.	Height.
2	27.4 mm.	48.5 mm.
49	37.4 mm.	60.5 mm.
54	42.7 mm.	64.2 mm.
2	53.0 mm.	74.0 mm.

(2) Mr. J. M. Tabor also kindly supplied on October 28 a sample of about 100 *Gryphæa*, which had been imported from Portugal in March, 1925, and relaid at about low water neaps at Brightlingsea to grow and fatten during the summer. The measurements of this sample are as follows :—

No. of Individuals.	Average Length.	Average Height.
10	46.4 mm.	89.8 mm.
61	54.9 mm.	91.3 mm.
29	62.4 mm.	93.0 mm.

The average shape of this sample is distinctly longer than that of the usual Portuguese, therefore the difference to be observed between this sample and that dredged from deep water is the more noteworthy.

(3) The sample dredged at West Mersea, River Blackwater, gave the following averages :—

No. of Individuals.	Average Length.	Average Height.
1	26 mm.	52 mm.
2	37.5 mm.	54.5 mm.
12	46.4 mm.	61.8 mm.
28	53.0 mm.	61.7 mm.
13	63.9 mm.	76.5 mm.
4	74.5 mm.	80.25 mm.
1	80.0 mm.	80.0 mm.

It is interesting that the longer specimens in this sample approached an equal length and height, thus resembling the native oyster. The approximate average ratios of length to height in the three samples are 1 to 1.65, 1 to 1.69, and 1 to 1.17 respectively. In large *Gryphæas* from the natural habitat on the shore, the ratio as judged by existing illustrations (see Bashford Dean, Bull. U.S.F.C. X, 1890 (1892), figs. 3, 4, p. 363) is probably 1 to 2 or more. There is thus a considerable difference between the shells from above tide-mark from those dredged below tide-mark.

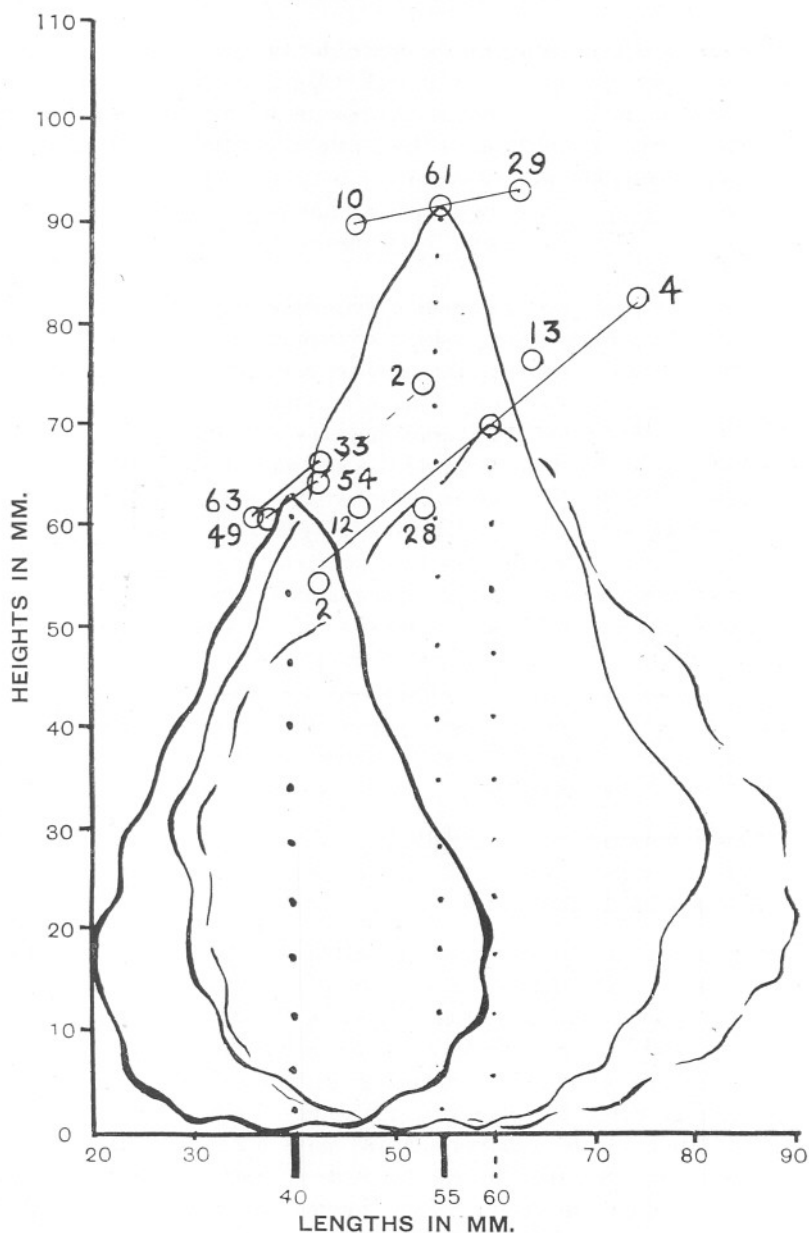


FIG. 1.—Scale-diagrams of Portuguese oysters (*G. angulata*) showing mean variation in shape with variation in habitat (above and below low-water mark).

A. Thick-lined form from Portugal.

B. Thin-lined form from Portugal, March, 1925 with English summer growth, 1925, above low-water mark.

C. Broken-lined form dredged from the Blackwater beds from below low-water mark in about 2 to 4 fathoms.

The diagrams show the average heights correlated with the average lengths in centimetre groups, and the approximate mean of all the measurements in each case.

No explanation can at present be offered for the occurrence of a broader shell in deeper water; and although cross-fertilisation between the Portuguese and native oysters is not impossible, it does not seem that the deep-water forms are hybrids, as the genital products of the two species are totally dissimilar, and those of the deep-water individuals are like the Portuguese in all respects: neither has any other character than shape of the deep-water forms been observed to be different from a normal Portuguese.

Since *G. angulata* has now been shown to exhibit a difference in the length-height ratio according to depth of habitat, it will be interesting to know whether an analysis of the measurements of other shelled forms living at different depths show a similar varying ratio.

It was possible to find the average increase in height of growth of the second sample of *Gryphæas* during the summer of 1925, as the *Tagus* oysters on arrival in this country are green and retain their greenness to a great extent, while the new English shell-growth is white with pretty patterns of blue-black and reddish-brown stripes. In this way it was found that the average increase in height of the sample relaid in March, 1925, to October 28, 1925, was 35 mm. The sizes of the shells as they were in March, 1925, were also recorded, and are plotted in Fig. 1 on the line 63-33; it is seen that the two samples of young Portuguese imported in March and October, 1925, were practically similar in mean size.

The sexes were examined in the different samples with the following results shown as percentages:—

	♀	♂	♄
Newly imported, September, 1925	11.9	18.4	69.7
Relaid March-October, 1925	60.0	36.0	3.0
Dredged Blackwater	88.3	11.6	0.0

These figures of sex percentages are perhaps worth recording, but are based on too small a number of individuals, or, in the case of the newly imported sample, examined after subjection to entirely abnormal conditions, to render it worth while discussing them. It is of interest to note that the growth of males and females in 1925 was approximately of the same average value, namely, 35 and 35.8 mm. respectively, while that of the few individuals of neuter sex was only 29.0 mm. on the average. The newly imported small *Gryphæas* were in poor condition, probably owing to a large proportion having recently spawned. Fattening in *Gryphæa* consists in this country almost entirely in development of the sex-elements in the gonad, in contradistinction to the native oyster where fattening begins by a laying down of reserve products, mainly glycogen, and is followed by development of the gonad. Thus, Portuguese oysters which had recently spawned would be mainly neuter and in poor condition, that is, not "fat."

## Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

### Hermaphroditism in the Portuguese Oyster.

By **Ikusaku Amemiya.**

*Nature*, No. 2921, Vol. 116, 1925, p. 608

The Portuguese oyster (*Ostrea (Gryphæa) angulata*) has been studied by many investigators, but no one has ever recorded the occurrence of hermaphroditism in this species, so that it was believed that the sexes were strictly separate. However, the writer found two hermaphrodite specimens in a batch of seventy-five individuals at the Plymouth Laboratory, where they had been kept alive in a sea-water tank in the open air for some time before their hermaphroditism was noticed. Eggs and sperm which were found in the same tubule exhibited no differences in their nature as compared with those taken from normal dioecious specimens. The writer is inclined to suggest that possibly there exists some relation between nutritive conditions and hermaphroditism in the oysters whose sexes are normally separate.

I. A.

### The Ocean regarded as a Pasture.

By **W. R. G. Atkins.**

*Marine Observer* Vol. II, October, 1925, pp. 162-164.

This is a semi-popular account of work on the estimation of the phytoplankton crop by the measurement of the changes in alkalinity and in phosphate content experienced by sea-water each year.

W. R. G. A.

### The Variation with Depths of Certain Salts utilised in Plant Growth in the Sea.

By **W. R. G. Atkins and H. W. Harvey.**

*Nature*, 1925, Vol. 116, p. 784.

Samples received from the R.R.S. *Discovery* were analysed for hydrogen ion concentration, phosphate, nitrate and silicate from surface to 3000 metres. All the constituents mentioned were found to increase with depth. The first 50 metres from the surface contained no phosphate and but little nitrate.

W. R. G. A. AND H. W. H.



**The Comparative Morphology of the Caecal Gland (Rectal Gland) of Selachian Fishes, with some reference to the Morphology and Physiology of the Similar Intestinal Appendage throughout Ichthyopsida and Sauropsida.**

By **Doris R. Crofts, M.Sc., F.Z.S.**

*Proc. Zool. Soc., 1925, Part I, pp. 101-188.*

*Macroscopic Features, Histology and Embryology.*

The gland is present in the twenty-seven genera of Selachian fishes examined. *Chimæra* probably has the original form—longitudinal glands, opening by separate orifices, situated in the wall of the commencement of the post-valvular intestine.

*Shape and Size.*—Vary much, but are similar in related genera. The size bears no relation to the length of duct or to the feeding habits. Slight seasonal and sexual variation may occur.

*Ducts.*—Short and simple in primitive Euselachians and in Batoids, but greatly specialised in Galeoidei and Squaloidei, where the duct orifice progresses nearer the spiral valve during ontogenesis.

*Mesentery.*—There are two types of gland suspension.

(a) by the gonad mesentery with lymphoid tissue packed near the gland.

(b) by independent mesentery.

*Suggestions concerning Physiology.*

A double significance is probable :

(a) The viscid liquid discharged from the gland lumen has some doubtful effect on the intestinal lumen and seems most important in Galeoidei and Squaloidei, where arrangements convey the liquid towards the spiral valve.

(b) Some blood function is suggested by :

(i) The marked vascularity and importance of the blood vessels of the gland.

(ii) The intimate relation of the glandular tubule cells with the blood and the frequent migration of leucocytes with these cells.

(A delicate lymphatic plexus follows the main blood vessels and the tubules are well supplied with nerve endings.)

(iii) Simple lymphoid tissue varies in quantity in the glands in different genera. *Heptanchus* and *Mitsukurina* have definite lymphoid follicles.

The endodermal origin of the gland and the forward direction of its fluid in many genera make a urinary function unlikely.

The presence of lymphoid tissue supports the view that the gland is the homologue of the caecal appendage of other vertebrates.

D. R. C.

### The Development and Relationships of the Myxosporidia.

By J. S. Dunkerly.

*Quart. Journ. Micr. Sci.*, Vol. LXIX, 1925, pp. 185-216.

1. The structure and development of a new quadricapsulate species of Myxosporidian (*Agarella gracilis*) belonging to the family Chloromyxidae and found in the testis of the Dipnoan fish *Lepidosiren paradoxa* is described.

2. Attention is drawn to the interrelationships of parasitic Chloromyxidae correlated with interrelationships between their hosts in the groups Dipnoi, Elasmobranchii, and Amphibia.

3. The life-cycle in Myxosporidia is discussed, especially the origin and relationships of the spore-forming nuclei and cells in the pansporoblast, and it is suggested that physiologically the spore of a Myxosporidian is a multicellular unit analogous with the infusoriform embryo of the Mesozoan Dicyema, although the Myxosporidia exhibit Rhizopodan relationships and Mesozoa are probably derived from ciliated ancestors.

4. Although it is not suggested that Myxosporidia represent a direct link between Protozoa and Metazoa, they may indicate a physiological reason for the origin of a soma, i.e. as a protective accessory to germ-cells. The Mesozoa show a similar process occurring in a non-related line of organisms.

J. S. D.

### Land Mollusca on the Mewstone.

By A. E. Ellis.

*Journ. Conchology*, XVII, 1924, pp. 187-8.

In March, 1924, a comparison of the land mollusca on the Mewstone with those on the adjacent mainland was made. Thirteen species were recorded on the island, and twenty-one on the coast near Wembury. *Lauria cylindracea* and *Clausilia rugosa* were more abundant on the Mewstone than on the mainland, while *Helix aspersa*, *Arion hortensis*, *A. ater*, *Agriolimax agrestis*, *Cochlicopa lubrica*, and *Trichia hispida* were frequent on the mainland, but absent from the Mewstone. The Mewstone specimens of *Helicella caperata* were much larger and more variable than those on the coast, most of the *Oxychilus alliarius* were var. *viridula*, which was absent from the mainland, and nearly all the *Goniodiscus rotundatus* were var. *subrufula*. The differences are chiefly attributed to isolation, environmental factors being much the same on the Mewstone and mainland.

A. E. E.

**The Larval development of some British Prawns (Palaemonidae). II. Leander longirostris and Leander squilla.**

By Robert Gurney, M.A., F.Z.S.

*Proc. Zool. Soc.*, 1924, pp. 961-982.

In the Palaemonidæ there are normally five larval stages only. Four of these stages are described for *L. longirostris* and three of them for *L. squilla*. The occurrence of a larva of *L. longirostris* at Plymouth is particularly remarkable, as the parent form only occurs in England in the Norfolk rivers—so far as is known.

Some account is given of early post-larval growth and the changes in the proportional length of the joints in the second legs.

A comparison of the larvæ of British Palaemonidæ is made with the object of affording means for their identification in plankton.

Attention may be drawn to an error on p. 977 where text figure 11 represents the 1st post-larval stage of *L. squilla* and not stage 5.

R. G.

**Report on Examination of Raft and Test Pieces at Plymouth, November, 1923.**

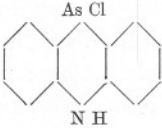
By C. R. Harington, Ph.D.

**Remarks on Dr. Harington's Report.**

By G. Barger, M.A., D.Sc., F.R.S.

*Fifth Interim Report of Sea Action Committee of Institution of Civil Engineers*, 1925, pp. 13-17.

Examination of the raft and test pieces of wood put out at Plymouth in September, 1920, revealed a considerable degree of destruction by *Teredo* and *Limnoria*; many of the test pieces had disappeared completely, and those which remained were all more or less severely attacked. The only surviving test pieces were those which had been treated with creosote to which had been added (a) 2.2 % carbazole, (b) 2.2 % dinitronaphthalene, (c) 2.2 % chlorodinitrobenzene, and detailed examination of individual pieces indicated that the relative efficiency of these substances is in the order in which they are named. The protective effect of chlorodinitrobenzene was also observed in parallel tests at Lowestoft, although in the latter place carbazole, in lower concentration, was not found to be effective. The Lowestoft experiments indicate that the

arsenic compound "D.M."  is the most efficient sub-

stance yet tried, and the similarity in chemical constitution between the latter substance and carbazole is of interest.

C. R. H.

**Hydrography of the English Channel.****By H. W. Harvey, M.A.***Rapport Atlantique*, 1924. *Copenhagen*, 1925.

A summary of the results and the interpretations based upon them, which have been obtained by various workers who have studied the Hydrography of the English Channel. Observations made in the area upon the effect of water movements, temperature, salinity distributions and estuarine conditions upon the fauna and flora have been collected together, and a bibliography giving references to sixty-four original papers is appended.

H. W. H.

**Notes on *Hoplitophrya* (*Anoplophrya*) *brasili* (Léger and Duboscq), an Intestinal Ciliate of the Polychaete Worm *Cirratulus*.****By C. C. Hentschel, B.Sc.***Parasitology*, Vol. XVII, No. 3, pp. 217-220, *May*, 1925.

This paper records a few points of interest concerning the astomatous ciliate found in the intestine of the Polychaete Worm *Cirratulus* (*Audouinia*) *tentaculatus*. This form was described by Léger and Duboscq in 1904 under the name of *Anoplophrya brasili*. These authors apparently did not observe the true nature of a small papilla at the anterior end of the ciliate, the possession of which precludes the inclusion of this form in the genus *Anoplophrya*. It is therefore provisionally placed in the genus *Hoplitophrya*. The paper also includes some remarks on the function of this papilla as a thrusting organ, by means of which the ciliate pushes its way through the intestinal débris. The geographical distribution is wide, it being recorded from France, Plymouth, the Shetland Islands, and also (from *C. grandis*) from Woods Hole, U.S.A.

C. C. H.

**Studies on the Comparative Physiology of Contractile Tissues. I. The Action of Electrolytes on Invertebrate Muscle.****By Lancelot T. Hogben.***Quart. Journ. Exp. Physiol.*, XV., 1925, pp. 263-312.

The influence of electrolytes on the rhythm and tone of muscular tissues of various crustacean and molluscan organs is recorded.

(a) The Crustacean heart: In this section the effects of removal and of excess of calcium in presence of varying amounts of potassium are analysed: the influence of Ca, Sr, and Mg compared and contrasted with

that of Ba, and the behaviour of the crustacean heart with reference to potassium, rubidium, caesium and hydrogen ions is also discussed.

(b) The Molluscan heart: The relation of potassium and magnesium to the cardiac rhythm of *Pecten* and *Helix* is dealt with especially.

(c) Musculature of the Molluscan gut. The crop muscle of *Aplysia* is treated fully from the same standpoint as in § (a).

L. T. H.

### **The Dinoflagellates of Northern Seas.**

**By Marie V. Lebour, D.Sc., F.Z.S.**

*Published by the Marine Biological Association, 1925.*

The purpose of this monograph is to offer an up-to-date survey of northern marine dinoflagellates with, as far as possible, a figure or figures of each species, for the most part original, but, in the absence of available specimen copies from various authors, using Paulsen's "Peridinales" in "Nordische Plankton," 1908, as a basis for literature. Most of the synonymy is referred to this work, an up-to-date bibliography being added. Each species is described, figured, and brief notes given as to its distribution. A short introduction deals with general morphology, nutrition, and habits, further details being given with the descriptions of species. An appendix at the end of the book offers suggestions for collecting, examining, and preserving Dinoflagellates, and it is hoped that the work will be useful for the amateur microscopist as well as the trained naturalist.

M. V. L.

### **The Action of Adrenaline on the Perfused Fish Heart.**

**By A. D. Macdonald.**

*Quart. Journ. Exp. Physiol., XV, pp. 69-80.*

The action of ions on the perfused elasmobranch heart as investigated by Mines is confirmed and extended. Adrenaline produces, in such dilutions as 1/100,000.

1. An initial and often striking inhibition of the normal rhythmical contractions.
2. A subsequent increase in amplitude which may be, but is not invariably, associated with appreciable acceleration.
3. An increased tolerance to hydrogen ions.

This response and that to related drugs is discussed in terms of permeability to and variations in the concentration of ions in the perfusing solution.

A. D. M.

**The Early Development of *Astropecten irregularis*, with Remarks on Duplicity in Echinoderm Larvae.**

By **H. G. Newth, A.R.C.Sc., D.I.C.**

*Quart. Journ. Micr. Sci.*, Vol. LXIX, 1925, pp. 519-554.

A small culture of *Astropecten* larvæ was reared to the age of three weeks. Metamorphosis had not then begun. Two larvæ were found which showed duplication of internal and external characters. A consideration of these, and a critical review of previous work on double monsters among larval Echinoderms, lead to the provisional conclusion that the various kinds of larval duplicity (among which is to be included enantiomorphy or *situs inversus*) do not imply, and are not dependent for their appearance upon a latent bilateral symmetry in the normal larva. They are due either to interference with the metabolism of the egg, or to inhibition of growth during or immediately after gastrulation.

H. G. N.

**An Amphoteric Substance in the Radula of the Whelk (*Buccinum undatum*).**

By **C. F. A. Pantin and T. H. Rogers.**

*Nature*, Vol. CXV, 1925, pp. 639-640.

Gives an account of differentiating amphoteric from other substances in the chitin of the radula of *Buccinum*. The method consists of forming metallic salts with the proteins present: the presence of the metal is subsequently detected by its common colour reactions. The method is essentially based on the work of J. Loeb upon proteins.

C. F. A. P. AND T. H. R.

**Depth Recording with Plankton Nets.**

By **F. S. Russell.**

*Nature*, Vol. CXV, pp. 603 and 604, April 25th, 1925.

A brief account is given of the use with the stramin ring-trawl of a graphic depth-recording instrument, kindly loaned by the Admiralty. The factors controlling the depth at which the net will fish are discussed, and illustrations of the tracings of the path of the net through the water as recorded by the instrument are reproduced.

In order that collections made from day to day may be the more comparable the speed of towing should be kept as nearly as possible the same: attempts can be made to do this by adjusting the angle of entry of the warp into the water in order to keep it constant: this can be effected

by varying the number of revolutions of the ship's screw. Under the varying weather conditions, however, it is on occasion extremely difficult to keep the net fishing at one level throughout the duration of the haul: records show that at such times the path followed by the net through the water is very wavy, the upper and lower limits often being several fathoms apart.

Results point to the necessity of the employment of a graphic depth-recording instrument when studying the vertical distribution of plankton organisms (or even their horizontal distribution) with large tow-nets such as the ring-trawl.

F. S. R.

**Haemocyanin, Part I. The Dissociation Curves of the Oxyhaemocyanin contained in the Blood of some Decapod Crustacea.**

**By Ellen Stedman and Edgar Stedman.**

*Journal of Biological Chemistry, XIX, p. 544 (1925).*

Using the Van Slyke manometric method for the estimation of blood gases, it has been shown that the hæmocyanin contained in the blood of *Maia*, *Palinurus*, *Cancer*, and *Homarus* combines reversibly with oxygen, and hence is capable of exercising respiratory functions in a manner analogous to hæmoglobin. The oxyhæmocyanin dissociation curves as determined on the serum of the above four species were found to be identical. The hæmocyanin is about 85 per cent saturated at an oxygen tension of 20 mm. and a temperature of 15°. The dissociation curve resembles that of oxyhæmoglobin in showing a point of inflexion.

E. S. AND E. S.

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