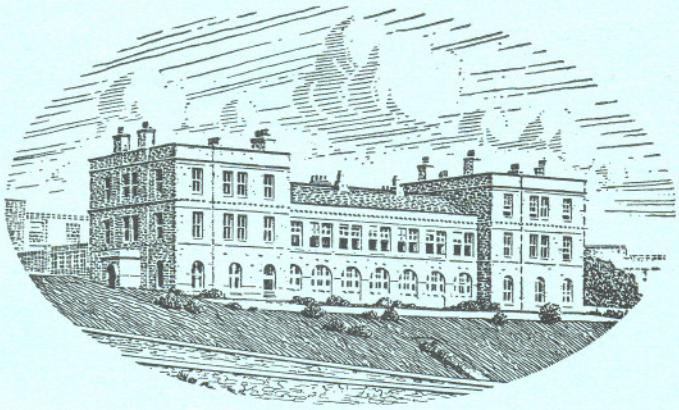
# JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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# THE ANATOMY OF THE BODY WALL AND APPENDAGES IN *ARENICOLA MARINA* L., *ARENICOLA CLAPAREDII* LEVINSEN AND *ARENICOLA ECAUDATA* JOHNSTON

By G. P. Wells

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(Text-figs. 1–21)

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## INTRODUCTION

The anatomy of *Arenicola* has often been monographed. The best-known works are those of the series with which the names of Gamble and Ashworth are associated (Gamble & Ashworth, 1898, 1900; Ashworth, 1904, 1912). Unfortunately, these accounts are not fully satisfactory. They are sometimes incorrect; they omit all reference to many points of considerable functional interest; and they lack descriptive rigour (for example, although Gamble & Ashworth, 1900, point out that the blood vessels of *Arenicola* are arranged on an obvious segmental plan, none of these works attempts to bring out the fact by adopting a nomenclature based on serial homology). Now the lugworm is an excellent laboratory polychaete, and, because of its size, abundance and hardiness (at least during the cooler months), affords suitable material for many researches. A revision of its general anatomy is therefore desirable. The following account of the body wall and appendages was undertaken as a contribution to this end; a study of the internal anatomy is in preparation.

My first intention was to limit the description to *A. marina*, the commonest species around Great Britain and the one with which I am most familiar. On reflexion, however, the decision was taken to include two other species as well. The family Arenicolidae consists (according to Ashworth, 1912, with whose classification subsequent authorities are in substantial agreement) of two

genera only, *Arenicola* and *Branchiomaldane*. The first is made up of eight species, to which Berkeley & Berkeley (1939) have subsequently added a ninth; they fall quite clearly, from an anatomical point of view, into three groups. The second consists only of a single species of small and aberrant animals. Now to describe only *Arenicola marina* would result in a work of very limited usefulness, more particularly as the species is restricted to the cooler shores of the northern hemisphere; on the other hand, by including the three species *marina* L., *claparedii* Levinsen[1] and *ecaudata* Johnston, each representing one of the sections into which the genus naturally falls, an idea can be given of the general organization and also the range of variation found in this world-wide group. I hope later to publish notes on the other species; briefly, *grubii* most nearly resembles *ecaudata*, *assimilis* is most closely related to *claparedii*, though differing from it in several important points, and the rest group themselves with *marina*.

The descriptions are based mainly on material collected by myself—*marina* at Plymouth, at Bangor, North Wales, and at Thorpe Bay on the Thames Estuary; *claparedii* at Naples, where my expenses were partly defrayed by a grant from the Challenger Society; and *ecaudata* at Plymouth. I have also a small number of *claparedii* from the Pacific Coast of U.S.A., sent, very ill-preserved, by an American dealer. By the courtesy of Mr H. W. Parker I have been allowed to examine the collection of Arenicolidae in the British Museum (Natural History); this remains, with a few additions, substantially as catalogued by Ashworth (1912).

The following study is concerned with gross morphology, not histological detail. As far as possible, some indication will be given of the functional significance of the structures described. With *marina*, the habits of the worm are well known and such interpretations can often be made. This species lives in great numbers in muddy sand flats, where the piles of sandy cylinders, its faeces, and the saucer-shaped or funnel-shaped depressions, caused by its eating away the sand below, are familiar to everybody. It sometimes occurs in less typical habitats, for example, in gravel or among stones, provided there is a certain amount of muddy material to eat. Under favourable conditions, it inhabits the same burrow for weeks or even months at a stretch, swallowing the sand at one end of the burrow and depositing it as faeces at the other. The form of the burrow, and the behaviour of the worm, have been described in detail elsewhere (Wells, 1945, 1949*b*, 1950; Newell, 1948).

[1] *A. claparedii* Levinsen is probably identical with *A. pusilla* Quatrefages. The original definition of the latter species is inadequate and conflicts with the characters of the type specimen. The type was examined by Ashworth, who identified it as an incomplete specimen of *claparedii*, atypical as to the number of nephridia. He therefore merged both species under the older name of *pusilla* (Ashworth, 1912). The great majority of later writers term it *claparedii*, and Fauvel (1927) explicity rejects Ashworth's proposal, not denying the identity of the two species, but because of the inadequacy of the definition of *pusilla* and the aberration of the type specimen.

Of *claparedii*, Ashworth (1912) wrote: 'The general habits of this species, which the writer had an opportunity of observing in Naples for some weeks, are similar to those of *A. marina*. Examples taken by Prof. A. D. Howard in Puget Sound were found generally in ordinary sandy beaches, but two larger specimens were burrowing in a coarse gravelly and rocky beach.' Describing the occurrence of *claparedii* on Vancouver Island, Berkeley & Berkeley (1932) write: 'It evidently occurs over large stretches of the sand exposed at low tide at Long Bay, judging by the enormous number of casts to be found.' Takahashi (1934) describes it as living in U- or V-shaped burrows, of depth 15–25 cm., the openings 3–10 cm. apart; in certain bottoms, the burrows of *marina* may be very like this (Wells, 1945). Now *claparedii*, while resembling *marina* in its general structure, differs in two points that one would expect to be of great functional importance; it lacks statocysts, and it lacks giant nerve fibres. The similarity of its way of life to that of *marina*, which the above citations suggest, makes these differences the more surprising. The breeding habits of *claparedii* are rather different in Canada and in Japan, according to the accounts of Guberlet (1934) and Okuda (1938).

For *ecaudata*, we have the following account by Ashworth (1912): 'It occurs in the littoral zone but chiefly in sandy, gravelly or muddy material among stones, or in clefts at the base of the rocks in the debris formed by the breaking down of the latter. A considerable amount of organic matter is generally present in the material in which the worm lives. The burrows of *A. ecaudata*...are oblique or sinuous cavities, lined with a fair amount of mucus, and situated a few inches below the surface in gravel or between rocks and stones. The castings of the worm, being composed of coarse material having little coherence, soon fall apart. The well-known signs—the sand-rope-like heap of castings and the funnel-like depression in the sand—which indicate the presence of *A. marina* on countless sandy beaches, have no good counterparts in the case of the ecaudate species, in which both the castings and the mouth of the burrow are inconspicuous among their surroundings.' Fauvel (1899*a*) comments on the occurrence of *ecaudata* in black, often foetid, sandy material between rocks at Cherbourg; the galleries are more or less sinuous and often horizontal; their walls are never yellow, as those of *marina* are. The worms are found at Plymouth in just such situations as these authorities describe, and it appears that the striking differences of structure between *marina* and *ecaudata* are paralleled by equally striking differences of habit.

## Methods

### *Preparation of worms for dissection*

Ashworth (1904) recommends that lugworms should be killed with chloroform and dissected fresh, under sea water, 'as soon as possible after they are taken from the sand'. I find that formalin material, dissected within a week or

so of killing, is very much better. Fresh worms bleed easily and freely, while in formalin material the blood sets into a firm, uniform gel, so that such operations as the removal of the whole or part of a ventricle can be performed with ease. Moreover, the septa and other membranes of fresh worms are so transparent that their relations are hard to make out. The slight cloudiness which appears in formalin material is a great improvement.

The animals used in the present study were killed in either of two attitudes, 'relaxed' or 'distended'.

*Relaxed worms*. The worms are narcotized by immersion in a large volume of $7\frac{1}{2}\%$ $MgCl_2$. The time taken varies with the size of the worm; *marina* about 10 or 15 cm. long is fully relaxed in $3\frac{1}{2}$ or 4 hr. They are then transferred to a bath of $7\frac{1}{2}\%$ $MgCl_2$ containing 4% formaldehyde. At this stage, they may show slight movements, so it is as well to do the killing in a rectangular tank, and, if necessary, to straighten the worms against the side with a glass rod. They die in a very natural configuration. The body is straight (except for a slight ventral curvature of the first few segments). The proboscis is generally withdrawn. The worms can be stored in formalin until required. The organs usually retain quite a lot of their colour for some days, and even after months of preservation, such material is easy to dissect.

*Distended worms*. The worms are narcotized as above, then distended, one by one, in the following way. A cannula is connected by rubber tubing to a funnel; the whole is filled with the Mg-formalin mixture, and the tubing is closed with a screw clamp. The level of fluid in the funnel should be 15–20 cm. above the bench. The cannula is then tied into the tail, pointing forwards; it must go into the coelome, not the gut, and the way to ensure this is to insert it into an incision made in the lateral aspect of the tail. The worm is then tumbled into a long tank of the Mg-formalin mixture, and immediately distended with the same solution, by opening the screw clamp. A surprising degree of stretch is produced, and although the resulting attitude is highly unnatural, the distension straightens out the septa and other organs and greatly facilitates the study of their relationships. The proboscis is fully extruded.

### *Preservation for museum purposes*

As many of the specimens to be found in museum collections are ill-preserved, and in very distorted attitudes, so that even their external characters are hard to make out, it may here be pointed out that worms killed in the 'relaxed' attitude, as directed above, are very suitable for museum purposes. Alcohol makes the worms rather hard, and they may easily break on handling.

### *Serial sections*

Before sectioning, the worms were killed in Mg-formalin in the relaxed attitude, then at once transferred to Susa. The following techniques were found useful:

(i) 15 $\mu$ paraffin sections, stained with haematoxylin-eosin or Hansen's trioxyhaematin followed by Mallory's phosphomolybdic acid-aniline blue-orange G mixture, and mounted in balsam.

(ii) 100 $\mu$ celloidin sections, very lightly coloured with haematoxylin and orange G, and mounted in balsam without removal of the celloidin.

(iii) 300 $\mu$ celloidin sections, mounted unstained in glycerine jelly without removal of the celloidin.

In general, and especially when dealing with the front end of the worm, the horizontal plane is more useful than the sagittal.

### *Special methods*

Polarized light is invaluable for working out the arrangement of the muscles. It can be used on sections, or on such objects as pieces of the body wall of distended worms, spread out flat and cleared. To avoid the necessity of turning the slide on the stage, which makes the working out of complicated muscular networks rather tricky, I have mounted two Polaroid disks, 7 in. in diameter, on a common vertical axle. One goes above, and the other below, the stage of my binocular microscope; by turning the axle, the plane of polarization of the light can be rotated without disturbing the specimen.

Spectacular preparations of the vascular system can be made by choosing unpigmented or lightly pigmented worms, distending them, then rapidly dehydrating the whole worms and clearing them in benzyl alcohol, in which they are kept.

When studying the movements of living worms, they should be placed in glass tubes; a suitable arrangement for this purpose was described elsewhere (Wells, 1945).

## The Main Regions of the Body

*Arenicola* shows very clearly the tendency, which generally appears in sedentary polychaetes, to differentiate the chain of fundamentally similar segments, of which their body consists, into distinctively specialized regions.

The common lugworm, *A. marina*, has 19 segments with parapodia (rarely 20), and, although these segments show certain local specializations (gills restricted to segments vii–xix, nephridia restricted to iv–ix, etc.),[1] they are all built on a very evident metameric plan. These 19 segments together occupy the middle of the body and form a comparatively unspecialized region from which the two extremities stand out in marked contrast. Anterior to the first chaetigerous segment, there is a short, bluntly conical region, composed of the prostomium and one or two segments which have lost their appendages—one according to Lillie (1905), and two according to Ashworth (1904, 1912). The whole of this region is welded into a functional and structural unit, mainly in connexion with proboscis activity, and its metamerism is hard to make out.

[1] Roman numbers are used to identify particular segments.

At the hinder end of the body is the conspicuous 'tail', again composed of segments which have lost their appendages, and apparently lengthening continually backwards, in young animals at least, from reserve segments at its base (Fig. 1 A). We may therefore describe the body of *marina* as differentiated

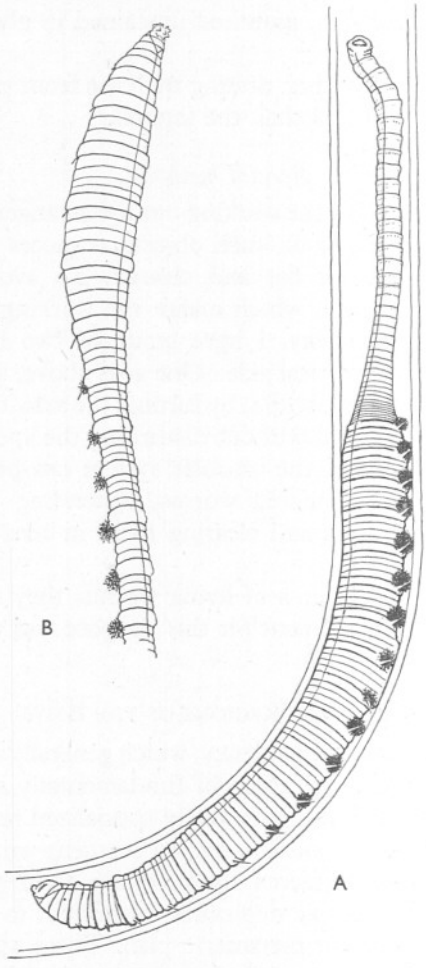


Fig. 1. *Arenicola marina*. A, a healthy individual lying, head downwards, in a glass observation tube. Most of the chaetigerous segments are pressed, laterally and ventrally, against the walls of the tube, but are separated from it by a narrow space on the dorsal side. Waves of swelling, which occlude this space, are travelling gently headwards and so driving water through the tube; one such wave is passing the 5th and 6th gills. B, the 'clubbed' attitude, which often appears in moribund specimens.

into three very distinct regions—an achaetous anterior region, or 'head', a chaetigerous middle region, or 'trunk', and an achaetous posterior region or 'tail'. The middle region shows various subsidiary differentiations, with

regard to the distribution of gills, nephridia, etc., among its component segments.

The body of *claparedii* resembles, in all the above respects, that of *marina*. In *ecaudata*, the differentiation between 'head' and 'trunk' occurs as in the other species, but the specialized third region appears, at first sight, to be lacking. The worm has a great number of segments and the parapodia and gills continue as far as, or nearly as far as, the hinder extremity. There are, however, indications of a differentiation corresponding to, though less profound than, that between 'trunk' and 'tail' in the other species (p. 37).

The above method of describing the regional organization of *Arenicola* differs from that generally adopted in the literature. Audouin & Milne Edwards (1834) wrote of *marina* as 'composé de trois portions assez distinctes: l'une antérieure, ordinairement renflée et ne portant pas de branchies, une moyenne, étroite et branchifère, et une postérieure, apode'. The anterior region, in this account, includes the 'head' and the first six chaetigerous segments. The majority of subsequent writers, down to the present day, have adopted this method of subdividing the worm. Ashworth (1904) instructs his students to 'note the shape of the worm; its division into an anterior abranchiate chaetigerous portion, middle branchiate chaetigerous region and posterior achaetous and abranchiate tail'. Fauvel (1927) describes *marina* thus: 'Région antérieure à 6 segments uncinigères abranches. Région abdominale a 13 sétigères, branchifères. Région caudale achète et abranche de longueur variable, fragile.' The gills have also been used to characterize the regions of *ecaudata*. 'Le corps', wrote Fauvel (1899*a*) of this species, 'se divise en deux parties: 1° la région anterieure ou thoracique qui comprend le prostomium, le segment buccal, un segment post-buccal achète et 15 ou 16 segments pourvus de parapodes et de tores uncinigères mais abranches; 2° la région abdominale dont tous les segments portent des parapodes et des branchies sauf parfois les 1 à 7 derniers qui sont abranches mais toujours sétigères.'

It seems to the writer, that the method of subdividing the body with reference to the gills is rather misleading. Of the various divergent specializations which differentiate the segments of *Arenicola* from each other, some are extremely constant and fixed in position, not only from individual to individual but also from species to species. Such, for example, are the persistence of septa i, iii and iv of the middle region as the well-known 'diaphragms', or the elaboration of the vessels of the (vanished) septum vii to form the ventricles, closely applied to the gut and separating its oesophageal from its gastric part. Others, on the other hand, fluctuate; for example, the nephridia are always restricted to a limited number of segments, but the number and position along the body of the segments concerned varies, not only from species to species but also to some extent from individual to individual. When seeking for criteria of regional differentiation, one should clearly choose characters of the former kind; yet the distribution of the gills, which so many

authorities use, is of the latter. In the 'caudate' species, i.e. in all those with an achaetous 'tail', the most anterior gill is typically on segment vii, and the division between abranchiate and branchiate regions therefore coincides with the position of the hearts and boundary between oesophagus and stomach. In the so-called 'ecaudate' species (*ecaudata* and *grubii*), the most anterior gill lies several segments farther back, though the cardiac and enteric differentiations remain at the same level as before. Even in the caudate species, including *marina*, 'the first gill is almost invariably small, and in a considerable percentage of examples, is reduced to minute proportions or is absent' (Ashworth, 1912). The same is true of *ecaudata*. Evidently, the boundary between abranchiate and branchiate regions is by no means a rigidly fixed one, and when more constant intersegmental differentiations are available, there is no justification for subdividing the body on the basis of the distribution of the gills. The division into 'head', 'trunk' and 'tail', described above, is undoubtedly the most profound of the local specializations exhibited by *Arenicola*, and is merely obscured by throwing together the 'head' and the first few 'trunk' segments into an 'anterior abranchiate chaetigerous portion'.

In conclusion, a word may be said about the 'renflée' and 'étroite' of Audouin & Milne Edwards' description, cited above. One sometimes finds lugworms in which the first half a dozen or so segments are distended and the rest of the trunk is narrowed by contraction of the circular muscles. The worm as a whole is therefore club-shaped (Fig. 1B). One never sees this attitude in vigorous, healthy worms, but only in dead or moribund specimens. It is very common in worms which have been badly collected, for example, in a hot, overcrowded jar. I believe its assumption to be an irreversible process, and a sign of approaching death; if any of the worms in my stock tanks exhibit it, they are thrown away before they die and foul the water.

The point would be hardly worth mentioning, were it not that 'clubbed' worms have appeared very often in the literature. The 'renflée' and 'étroite' in Audouin & Milne Edwards's description, together with their Pl. 8, fig. 8, show unmistakably that their worms were in the 'clubbed' attitude. Grube (1851) also refers to the anterior part of the body as 'mehr oder minder aufgebläht'. More recently, a beautifully drawn figure of a 'clubbed' worm was published by Cunningham & Ramage (1888) and reproduced in the well-known *Handbuch* of Kükenthal-Krumbach (Hempelmann, 1934, p. 191). A striking example is to be found in the *Cambridge Natural History* (Benham, 1896, p. 333). In healthy worms, however, or in those prepared by the Mg-formalin method, no trace of 'clubbing' can be seen. When we bear in mind, first, that the part of the body which distends in this abnormal attitude is also the pre-cardiac or 'anterior abranchiate' part, and, secondly, that many of the early authorities based their descriptions on specimens thus distorted, we may infer that the 'clubbed' attitude has some responsibility,

historically, for the idea that the boundary between abranchiate and branchiate regions represents a differentiation of major importance.

## The Body Wall and Appendages

The account of the body wall follows the division of the body as a whole into three regions, as explained in the last section. The general plan of the body wall, common to all the regions, will be described first.

### THE GENERAL STRUCTURE OF THE BODY WALL

The body wall is divided externally into *annuli*, separated by *interannular grooves*. The position of the nerve cord is marked externally by a conspicuous, pale *ventral groove*, in *marina* and *claparedii* but not in *ecaudata*.

The body wall consists of the following layers: (i) epidermis, (ii) subepidermal connective tissue, (iii) circular muscle, (iv) a layer of intermuscular connective tissue, which is brought out prominently by the aniline blue of Mallory's triple stain, (v) longitudinal muscle, (vi) coelomic epithelium. A series of oblique muscles, of the usual polychaete type, is generally present (Fig. 2). The body wall is richly vascularized, and one can generally see in sections that the blood vessels lie in tubular spaces; these are extensions of the coelome, penetrating into the body wall.

The *circular muscle layer* is interrupted by a radial partition of connective tissue at each interannular groove (Fig. 5C–E, p. 17). According to Lillie (1905), the circular muscles develop very much later than the longitudinal in *A. cristata* Stimpson—a species very similar to *marina*.

If one takes a piece of body wall from a distended specimen, clears it, spreads it flat on a slide, and then examines it between crossed polaroids, rotating the slide relative to the plane of polarization, one finds that the whole of the musculature at any given point on the body wall, both circular and longitudinal, blacks out in the same position. This means that the musculature of the general body surface consists *only* of these two series of fibres, whose molecules are orientated truly at right angles to each other. There can be no diagonal or spirally running fibres, as occur, for example, in several Oligochaeta.

The fibres of the *longitudinal layer* are grouped, in *marina* and *claparedii*, into a great number of longitudinal columns, each covered by coelomic epithelium. These columns branch and anastomose with their neighbours, and form a conspicuous and characteristic background when one dissects either of these species (Fig. 3A–C). In *ecaudata*, on the other hand, the body wall presents a smooth appearance internally; the longitudinal layer is covered over by a continuous peritoneal sheet which is only occasionally perforated or grooved to accommodate a blood vessel (Fig. 3D).

In all species, certain *lines of separation* can be traced in the longitudinal layer, which are important anatomical landmarks. They are usually evident in

dissections, and are especially obvious in distended material. They appear, in *ecaudata*, as longitudinal clefts in the layer, and in *marina* and *claparedii* as deep grooves between adjacent muscle columns, across which anastomoses seldom or never occur. The lines are (Fig. 2): (i) the *ventral line*, in which the nerve cord (*n.c.*) lies; (ii) the *nephridial lines* (*neph.l.*), at the level of the nephridiopores; (iii) the *notopodial lines*, (*notop.l.*), through which the inner ends of the notopodia protrude into the body cavity; and (iv) the *dorsal line*

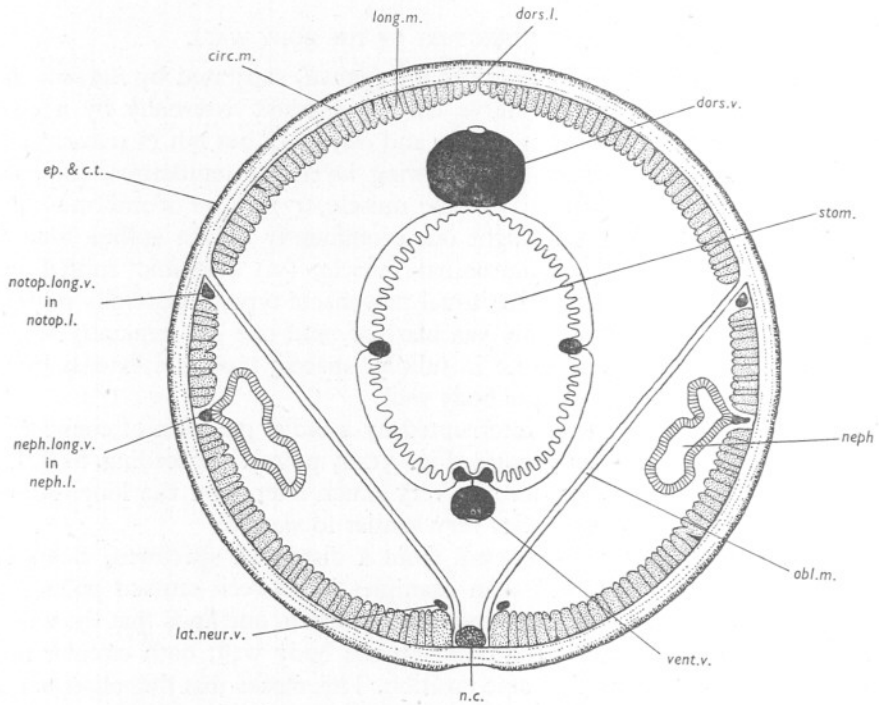


Fig. 2. *Arenicola marina*. Transverse section of an ordinary annulus, drawn from a section slightly anterior to the eighth chaetigerous annulus. For explanation of the lettering on the figures, see list on p. 44.

(*dors.l.*), into which the dorsal mesentery, where present, is inserted. The ventral, notopodial and dorsal lines are always present, and may perhaps divide the longitudinal musculature into functionally distinct fields. The nephridial lines are more variable; they are evident along the whole length of *ecaudata*, and in the trunk, but not the tail, of *marina*. In *claparedii*, they can be made out only in the immediate neighbourhood of the nephridia.

The *ventral nerve cord* is rounded in section and without segmental enlargements. It gives off a pair of interannular nerves in each interannular groove; these nerves run round the body to unite dorsally and so form a hoop enclosing

the body. They lie in the connective tissue partitions which divide the circular muscle layers in the interannular grooves (Fig. 5C–E, *interann.n.*). There is also a special outflow of nerves in each chaetigerous annulus, details of which have not yet been traced. The cord itself consists of a deep (dorsal) fibrous part and a superficial (ventral) ganglionic part. A giant fibre system is present in *marina* and *ecaudata*, but not in *claparedii*. Details of the giant fibre system

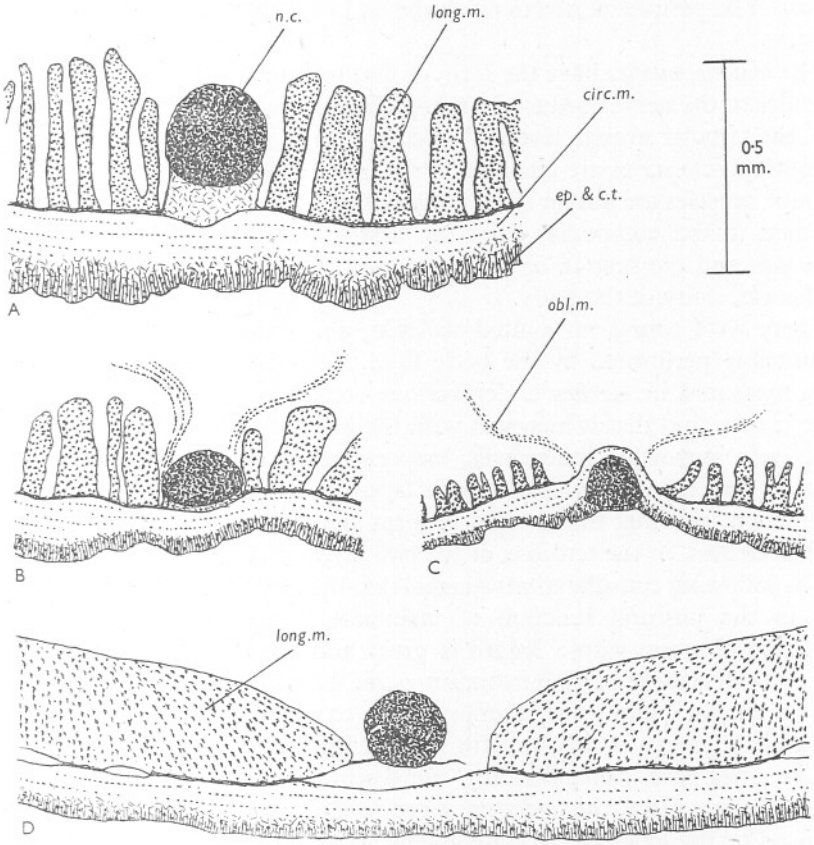


Fig. 3. Transverse sections through the body wall of ordinary annuli, in the region of the ventral nerve cord. A, *marina*, segment iii; B, *marina*, segment xviii; C, *claparedii*, segment xiv; D, *ecaudata*, segment xii. Lettering as on p. 44.

are given by Gamble & Ashworth (1898, 1900), by Ashworth (1904) and by Nicol (1948).

The position of the nerve cord relative to the layers of the body wall varies from species to species. The most primitive condition is presumably that found in *claparedii*, where it lies superficial to the circular muscle layer and in intimate relation with the epidermis (Fig. 3C). In the other two species, the

cord lies deep to the circular muscle layer.[1] In *marina*, it is separated from the circular layer by a pad of connective tissue, staining conspicuously blue with the aniline blue in Mallory's triple stain, and thicker in the anterior segments of the body than farther back (Fig. 3 A, B). In *ecaudata*, this pad is absent, and an extensive coelomic space separates the cord from the circular muscle (Fig. 3 D). The cord is held in position by a membranous sheet running laterally to the longitudinal muscle layer, and perforated in many places to allow blood vessels to pass. The peripheral nerves reach the body wall by way of this membranous sheet.

The *oblique muscles* have the form of flat, translucent strips. They run from the sides of the nerve cord to the notopodial line, where their fibres enter, and join, the circular muscle layer. Particularly thin, thread-like members of the oblique muscle series are attached to the inner ends of most of the notopodia. Oblique muscles are absent from the heads of all species, and (except for those attached to the notopodia) from the first 3 trunk segments of *marina* and *claparedii* and the first 16 or 17 of *ecaudata*. Thereafter they continue to the hinder extremity of the body.

There is of course no jointed skeleton, and the main skeletal function is presumably performed by the body fluid. The pressure in the coelome has been measured in *marina* under various conditions by Chapman & Newell (1947); they find that it increases with the level of activity of the worms and, in actively burrowing individuals, may exceed 30 cm. of sea water. We may suppose that in active animals, both layers are in a state of sustained tonic contraction, and that the changes of form are produced by local increases, or local decreases, in the tensions of the two layers.

The following considerations suggest that the circular layer plays the greater part in the postural function of maintaining internal pressure. Suppose a cylindrical worm whose length is great and the thickness of whose body wall is small compared with its radius $r$ cm. Let the pressure in its body fluid be $P$ g. wt./cm.$^2$, and let it be entirely due to the tensions in the circular and longitudinal layers, which, as with surface tension, we call $S_C$, $S_L$ g. wt./cm.

Now imagine a plane dividing the worm transversely. If no change of shape is taking place, the hydrostatic pressure acting over the area of section is balanced by the longitudinal muscle tension round the circumference, and we have

$$\pi r^2 P = 2\pi r S_L \quad \text{or} \quad S_L = \tfrac{1}{2} P r. \tag{i}$$

[1] Ashworth (1904) writes of *marina*: 'In some specimens the cord in the tail and in the last chaetigerous segment lies only just below the epidermis.' I find, on examining serial sections of the tails of seven worms, that the cord lies deep to the circular muscles in all but one. In the single exception, the cord seems in some sections to lie as in *claparedii* while in others it is embraced by the circular muscle, the latter running both superficial and deep to it. This is much the smallest worm of the seven (tail diameter 1·1 mm.) so the appearances may represent a migration during development from the primitive to the final position. This specimen has the cord deep to the circular muscle in the chaetigerous segments.

Now imagine the worm divided by a longitudinal plane passing through its long axis. This time, the pressure is balanced by the circular muscles, and, if the length is $l$ cm., we have

$$2rlP = 2lS_C \quad \text{or} \quad S_C = Pr. \tag{ii}$$

Combining (i) and (ii)

$$S_C = 2S_L. \tag{iii}$$

How far do these considerations apply to a real *Arenicola*? In the first place, the muscle layers have a measurable thickness; this is, however, not great compared with the radius and its effect will be to apply a small correction to the quotient 2 in equation (iii). Secondly, the oblique muscles may have a postural function; they are, however, very thin, and absent from a fairly considerable stretch of the body in *ecaudata*; and we may note, in passing, that septa and mesenteries are lacking over most of the trunk in all species. Thirdly, the body fluid is not the only skeleton. Isolated branchiate segments of *marina*, lying in a watch-glass of sea water, often undergo regularly rhythmical changes of shape, not perhaps very extensive but perfectly visible and corresponding in timing with the waves that traverse the body, when water is being pumped through the tube. This observation shows that there is a certain amount of elasticity in the body wall itself, though it seems probable that this factor plays only a minor role in the intact worm. Finally, there is the skeletal function of the surrounding mud. The movements of *marina* in glass tubes have been studied by various authors (Just, 1924; van Dam, 1937, 1938; Wells, 1944, 1945), and will be treated in a later section. For the present, we need only note that there appears to be an inverse relation between the degree of activity of the worm and the proportion of its surface which makes contact with the tube. At one extreme, it may be completely at rest: in this posture, the body is short and thick and presses against the tube with its whole surface; thus the relationships discussed above obviously do not apply. At the other, it is creeping actively forwards or backwards: the body is extremely elongated and at all points away from the tube, except that waves of swelling run along it, grip the tube, and so act as fixed points; here, as the waves follow each other fairly rapidly, the trouble lies in the assumption that no change of shape is taking place.

Evidently, equation (iii) is not to be taken as precise. It may, nevertheless, point in the right direction. Lugworms kept in glass tubes often show a regular alternation of rest and rhythmic activity. The resting worms are short and thick, and the onset of an activity outburst is accompanied by lengthening and narrowing of the body (Wells, 1949*a*). Spontaneous activity is also associated with an increase in internal pressure (Chapman & Newell, 1947). The phasic responses to stimulation are suggestive in this connexion. A nocuous stimulus may produce sudden shortening of the head or tail, or curving of the body (Just, 1924)—results evidently due, in the main, to

longitudinal muscle contraction. If a worm is creeping into a tube, and an attempt is made to pull it out backwards, it expands its front end very abruptly to grip the tube, a movement which suggests circular muscle inhibition. The data as a whole suggest that, in an active worm, the circular muscles are fairly highly contracted and the longitudinals less so; the phasic acts, whether reflexly or spontaneously produced, are mainly, at least, in the sense of longitudinal contraction and circular inhibition.

Fox (1949) has pointed out that the muscles of *Arenicola* contain haemoglobin, but does not discuss whether there is any inequality of distribution between the muscle layers. For the other pigments of the body wall, the works of Fauvel (1899*b*) and Lignac (1945) may be consulted.

The epidermis is richly provided with unicellular gland cells. The skin secretes mucus, which is used, in *marina*, to impregnate the wall of the burrow and keep it firm (Osler, 1826; Linke, 1939). The mucus of *ecaudata* is particularly copious, as anyone who has handled the living worm is aware. If specimens of *marina* are kept in the laboratory, the water comes to contain 'belts' of greyish mucus, of about the same diameter as the worms; these belts are sometimes seen round their bodies; they appear to be passed slowly headwards and to be a means of getting rid of such unwanted residues as the breakdown products of old chaetae. When handled, the lugworm produces a fluorescent, greenish yellow secretion, which stains the fingers and is also rather irritating.[1]

## THE MIDDLE REGION ('TRUNK')

As the middle region of the body is in many ways the least specialized of the three, it will be taken first.

### *Arenicola marina*

The trunk of this species consists of 19 segments (in exceptional individuals, 20). They exhibit a certain amount of structural and functional divergence. Each segment includes several annuli, of which one, the *chaetigerous annulus*, is larger than the others and bears the parapodia and gills. The chaetigerous annuli are shown white in Fig. 4. The boundaries between segments are given internally by septa, or, where the septa have disappeared, by the septal blood vessels. The septal planes correspond approximately, though not quite exactly, to the second groove behind each chaetigerous annulus: in other words, the penultimate annulus of each segment is chaetigerous.

Typically, any two chaetigerous annuli are separated by 4 ordinary annuli, so that the number of annuli per segment is 5. In the first 3 segments, however, the number of annuli is reduced. The first has 2, the second 3 and the third 4, except that in a 'laminarian variety', described by Gamble & Ashworth (1898), the third has 3. The fourth, and all subsequent trunk

[1] The worm as a whole has a characteristic fragrance, especially when laid open. After he had worked on it for some years, it produced strong allergic symptoms in the writer (catarrh, asthma); this was put right by a course of injections.

segments, have 5 each. The rule, that the chaetigerous annulus is penultimate, holds for the anterior segments in spite of this reduction.

Ashworth gives no attention to the possible systematic usefulness of these numbers. It is true of all *Arenicola* species, that the majority of the trunk segments have 5 annuli, and that some degree of reduction occurs at the front

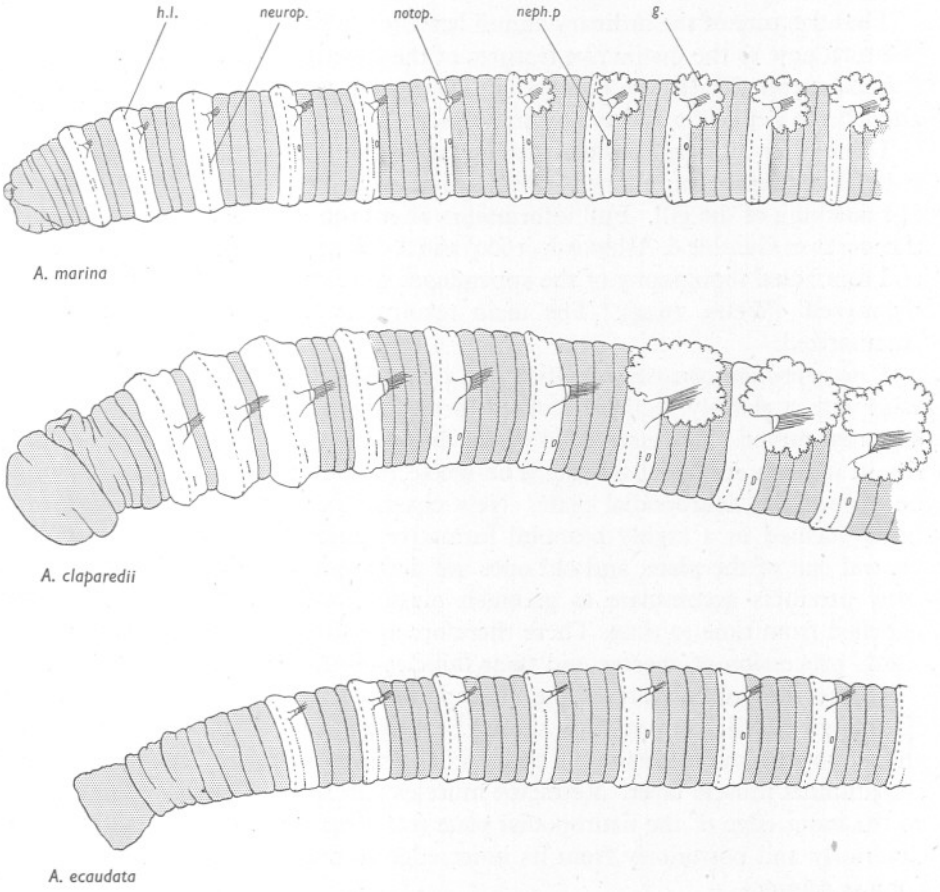


Fig. 4. Lateral views of the front ends of the three species, to show the annulation and the characters of the chaetigerous annuli and appendages (white). The proboscis is withdrawn in the *marina* and extended in the other two. Lettering as on p. 44.

end. The extent of this reduction is not always the same, and I find that each of the species now under examination has a fairly constant and characteristic annulation formula, which holds for all the range of material which I have been able to examine (p. 2).

The most convenient way of describing the reduction is to use serial Roman figures for the chaetigerous annuli, and to put between them, in Arabic

figures, the numbers of intervening ordinary annuli. Thus the typical formula for *marina* is:

i.2.ii.3.iii.4.iv.4.v ...

While the 'laminarian variety' is:

i.2.ii.2.iii.4.iv.4.v ...

The structure of the ordinary annuli has already been sufficiently described. We turn now to the distinctive features of the chaetigerous annuli. These are: (i) the neuropodia, (ii) the notopodia, (iii) the parapodial girdles, (iv) the gills, and (v) the nephridia and nephridiopores.

The earlier authorities were mainly interested in the characters supposed to be of systematic importance—the detailed form of the chaetae, and the mode of branching of the gill. Full information about these points is to be found in the works of Gamble & Ashworth (1900) and Ashworth (1912). The musculature and functional topography of the appendages were described, for *marina* only, by myself (Wells, 1944). The main results for that species will now be summarized.

A *neuropodium* consists essentially of a single dorsi-ventral row of chaetae, each with a sharply inclined rostrum projecting from the body surface and a gently curved shaft embedded in the body wall (Fig. 5A, B). Each chaeta lies in its own epithelial follicle. The whole row of chaetae and follicles may be termed the neuropodial plate. New chaetae and follicles are continually being formed in a highly basophil formative region (Fig. 5A, *form.*) at the ventral end of the plate, and old ones are destroyed at the dorsal end, where their products accumulate as greenish masses (*dest.*). These are somehow expelled from time to time. There therefore appears to be a continual dorsalwards procession of chaetae and their follicles along the neuropodial plate.

To see the musculature of the neuropodium, longitudinal sections, cut at right angles to the body surface, should be studied (Fig. 5C). The inner end of the neuropodium projects into a cavity, cut off from the general coelome by the longitudinal muscle layer. Retractor muscles run from the longitudinal layer to the outer edge of the neuropodial plate (*ret.m.neurop.*), and protractors run anteriorly and posteriorly from its inner edge to the neighbouring body wall (*prot.m.neurop.*).

The neuropodia of the more anterior segments are very short dorsi-ventrally, but they lengthen from segment to segment until, from segment x or xi backwards, they extend from a point slightly above the nephridial line to the side of the nerve cord (Fig. 4).

I know of no published description of the movements of the neuropodial chaetae. They could obviously be protracted to some extent by the protractors, and withdrawn again by the retractors, if the substance of the annulus is sufficiently flexible. I am, however, inclined to guess that another movement is more significant. Simultaneous contraction of the posterior protractors and

anterior retractors would tend to incline the chaeta as a whole, so that its inner end would move backwards relative to its outer; at the same time, owing to the form of the chaeta and the position in which it normally lies in the neuropodial plate, it would rotate so that the rostrum points forwards (Fig. 5 A, B). Similarly, the anterior protractors and posterior retractors could turn the rostra backwards. The usefulness of this movement, in facilitating the ratchet or gripping function of the neuropodia when the worm is creeping along the tube, needs hardly to be stressed.

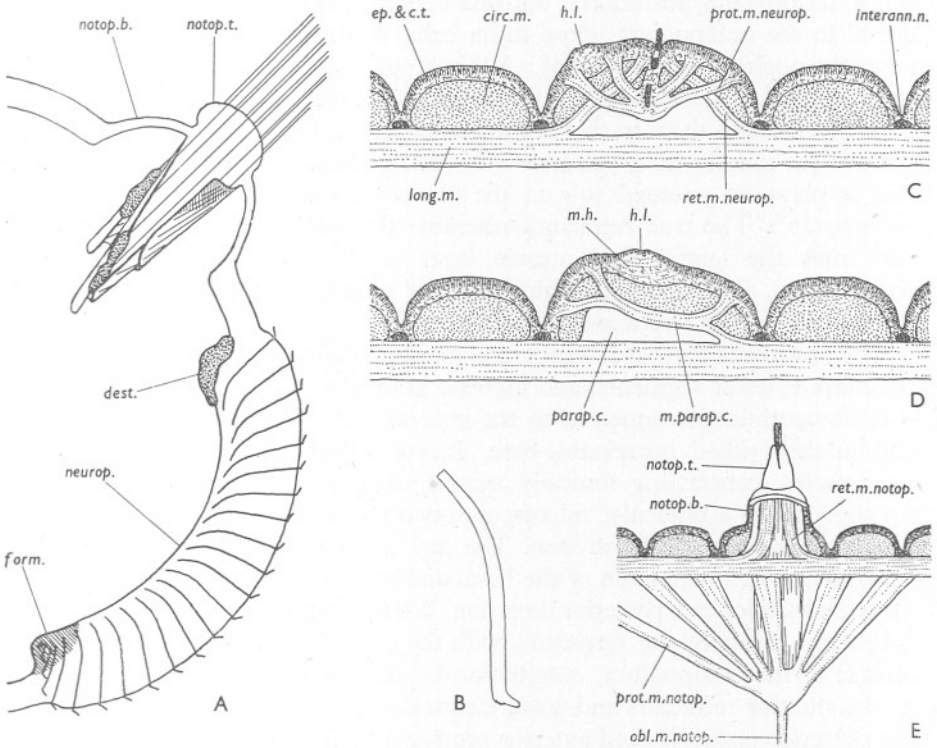


Fig. 5. *Arenicola marina*. Diagrams of the parapodia. A, the essential structure of a notopodium (above) and a neuropodium (below). B, a neuropodial chaeta. C, longitudinal section through one of the hinder neuropodia, at right angles to the body surface. Two ordinary annuli are also included. D, sagittal section through one of the first three chaetigerous annuli, near the mid-dorsal line. E, the muscles of a notopodium, exposed by a longitudinal cut through the body wall passing through its base. Lettering as on p. 44.

A *notopodium* can be regarded as a modified neuropodium. In external view, a dorsi-ventrally flattened tip (Fig. 5 A, E, *notop.t.*) can be distinguished from a thin-walled, evaginable base (*notop.b.*). The chaetae are very long and emerge from the tip in two closely applied, parallel rows. To derive a notopodium from a neuropodium, the plate must be supposed to have duplicated itself into two plates lying close side by side like two leaves of a book, and then the inner

corners of the double plate to have been folded and rolled forwards, giving the inner end of the whole a somewhat scroll-like appearance (Fig. 5A). The resulting structure is complicated and not easy to visualize. Full details of the notopodium and its musculature were given elsewhere (Wells, 1944).

The inner end of the notopodium protrudes through the longitudinal muscle layer into the general body cavity. The protractor muscles radiate from this end to the surrounding body wall (Fig. 5E, *prot.m.notop.*). Most of these run anteriorly and posteriorly, but one or two are inserted on the body wall dorsal to the notopodium, close to its base, while others spread ventrally as far as the nephridial line (Fig. 6). A thin strand of muscle generally runs from the inner end of the notopodium to the side of the nerve cord, and this has often been described as the retractor of the notopodium. It is evidently a member of the oblique muscle series; and, as it is quite often absent, we cannot suppose that it plays an essential role in the movements of the podium. (Fig. 5E, *obl.m.notop.*). The true retractors resemble those of the neuropodium; they run from the longitudinal muscle layer to the notopodial tip (Fig. 5E, *ret.m.notop.*). There are also thin sheets of muscle sheathing the notopodial plates, and running between their inner ends.

The notopodia further resemble the neuropodia in that they are smallest in the more anterior segments, and increase gradually in size posteriorly.

A notopodium is connected to the general body wall only by the muscles and the thin-walled, invaginable base. It must therefore be held in position by its muscles, contracting tonically against each other. If a living worm is watched under a binocular microscope, two types of movement of the notopodium can very readily be seen. The first is retraction and protraction, i.e. invagination or evagination of the base, and the second is the direction of the tip in an anterior or a posterior direction. We may conjecture that invagination is brought about by the retractors, with the possible assistance of the oblique muscle of the notopodium, evagination by the protractors, anterior pointing by the anterior retractors and posterior protractors, and backward pointing by the posterior retractors and anterior protractors. A high pressure of the body fluid will tend towards evagination. From the arrangement of the muscles, it would also be possible to swing the tip dorsally and ventrally, and perhaps to rotate the podium on its own long axis, but I am not aware that such movements have been witnessed or described.

The *parapodial girdle* is a name now proposed to cover a group of special features of the chaetigerous annulus to which I drew attention elsewhere (Wells, 1944). These features are best seen in a sagittal section through one of the first three segments, somewhere near the dorsal line (Fig. 5D). The chaetigerous annulus stands out at once in such a section, because it contains a conspicuous cavity, the 'parapodial canal' (*parap.c.*). This canal runs right round the annulus, and is separated from the general body cavity by the

longitudinal muscle columns, and by a connective tissue sheet on which they rest. It communicates with the general cavity only at the notopodial, nephridial and ventral lines (Fig. 6). Outside the parapodial canal is a special longitudinally directed musculature, arching in the main from the front to the rear half of the annulus, but also running into the longitudinal layer posteriorly ('muscles of the parapodial canal', Fig. 5D, *m.parap.c.*). If now one looks at the surface of one of these annuli, one sees that it is girdled by a pale line, usually elevated as a slight ridge (Fig. 4, *h.l.*); this is the 'hinge line' and under it, in the subepidermal connective tissue, a series of fine, antero-posteriorly running muscles can be detected ('muscles of the hinge', *m.h.*). All of these structures run right round the annulus, except only for the ventral line, where it is crossed by the ventral groove.

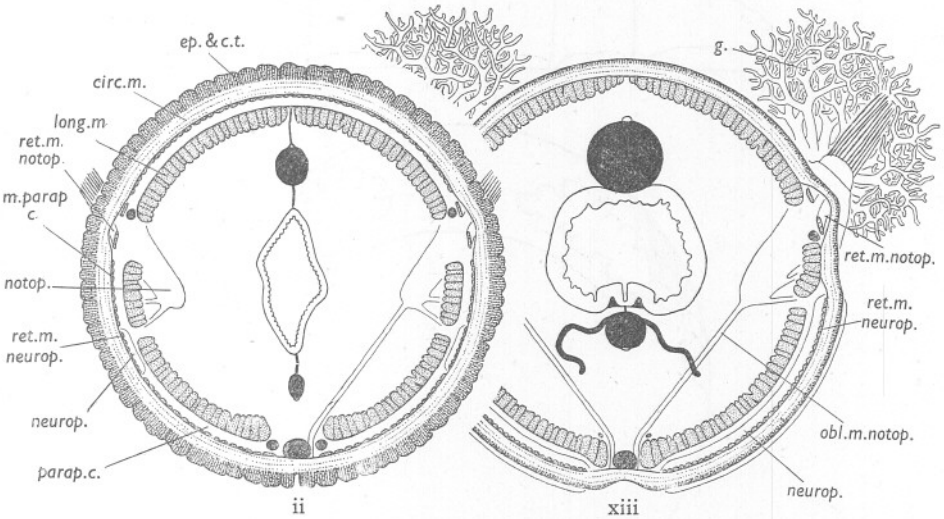


Fig. 6. *Arenicola marina*. Transverse section through chaetigerous annuli ii and xiii. The worm was transected in front of the appendages, and drawn with a binocular: the appendages are therefore seen just beyond the plane of section. Compare Fig. 2. Lettering as on p. 44.

We have already seen that the neuropodia and notopodia are small in the more anterior segments, and increase in size as one passes backwards. Just the opposite is true of the parapodial girdle (Fig. 4). The hinge line approaches more and more closely to the front of the annulus in segments iv–viii, and at the same time the parapodial canal and the two special musculatures decrease in importance and move with it. At first sight, each of these chaetigerous annuli looks rather like two; the front part is raised and swollen by the parapodial girdle, while the hinder part is flatter, like the rest of the body wall. Finally, from segment ix onwards, the parapodial girdle disappears altogether from the dorsal part of the annulus.

Now, on comparing C, D and E in Fig. 5, it will be seen that there is a considerable degree of resemblance between the musculatures of the notopodium, of the neuropodium, and of the parapodial canal. The two former can be regarded as derived, in part at least, from the latter. The cavity in which the inner end of the neuropodium lies is clearly a part of the parapodial canal (Fig. 6), and by analogy the invaginable notopodial base can also be so derived. In other words, the parapodial girdle persists in the hinder segments, but only in connexion with the notopodia and neuropodia. The hinge line can be seen, running down the front of the neuropodium, on many of the hinder segments, but it fades as one passes back, and is usually quite invisible on the last four or five.

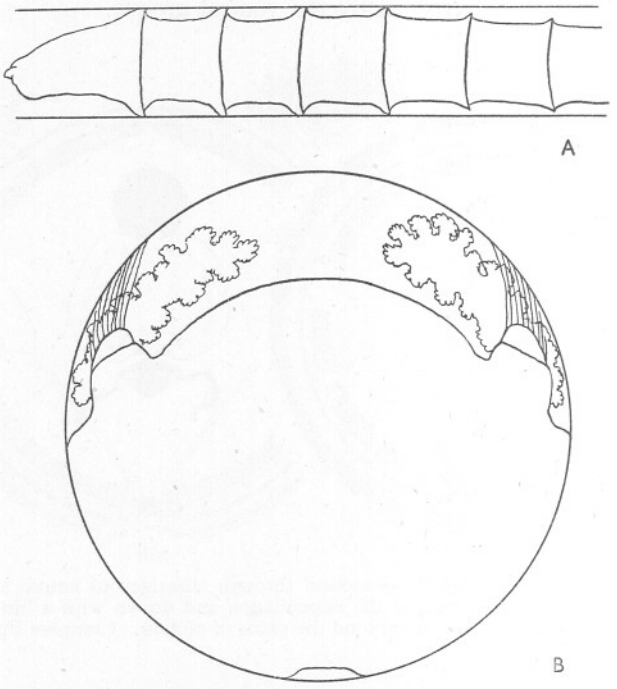


Fig. 7. *Arenicola marina*. A, the elevation of the anterior chaetigerous annuli. B, diagrammatic section of a worm circulating water through a tube, as in Fig. 1A.

There is no doubt at all about the importance of the parapodial girdle of the more anterior segments as a motor apparatus. If a *marina* is put into a large funnel of sea water, with the lower end of the stem closed with rubber tubing and a clamp, the worm usually burrows down into the stem, and the movements of the more anterior chaetigerous annuli can then be watched. At one moment they lie flat; then they are suddenly raised, and apparently distended, into the form of sharp, backwardly directed flanges; then they drop again (Fig. 7A). The whole apparatus seems to act as a single unit, i.e. all of the 'parapodialized'

annuli, and the whole periphery of any one of them, rising and falling together, though the movements are most evident in the first three segments, in which the responsible structures are best developed. The movements are used in burrowing, to grip the sand and help to draw the worm in, and also, apparently, for certain other purposes, such as the drawing of surface sand down into the head end of the burrow (Wells, 1944).

The *gills* are hollow, branched, contractile outgrowths of the body wall, borne by the chaetigerous annuli just behind the notopodia, and present on every segment from vii onwards (Fig. 4). The most anterior gill is smaller than the rest and may be lacking altogether on one or both sides. For details of the mode of branching of the gills, the works of Ashworth (1904, 1912) may be consulted.

The sphinctered *nephridiopores* open just behind, and very slightly below, the upper ends of the neuropodia, on segments iv to ix inclusive. According to Goodrich (1946) the 'nephridium' of *Arenicola* is a nephromixium and includes an ectodermal component which should logically be described with the rest of the body wall; it will, however, be included with the internal anatomy, which the writer hopes to describe in a later paper.

We turn now from the various components of which the body wall of the trunk consists, to the plan of the region as a whole. It can be divided, on structural grounds, into the following three sections (Fig. 4):

(i) Segments i, ii, iii. Gills absent. Neuropodia and notopodia small and apparently unimportant. Parapodial girdles massively developed round the whole circumference of the chaetigerous annuli.

(ii) Segments iv to viii. Graded, transitional.

(iii) Segments ix onwards. Gills present. Neuropodia and notopodia well developed. Parapodial girdle absent, except in connexion with the neuropodia and notopodia.

Now this structural differentiation is very nicely paralleled by a physiological one. The movements of *marina* were first studied in detail by Just (1924), who pointed out that the first three or four segments (the boundary is not absolutely sharp) stand in functional contrast to the rest. His observations have been confirmed and extended by others (van Dam, 1937, 1938; Wells, 1944, 1945). In burrowing, in forwards or backwards creeping, and in the driving of water through the burrow, waves of swelling travel along the trunk. These waves may go in either direction and their form varies with the particular type of movement that is being carried out. At all times, however, they concern the hinder 15 or 16 segments, and (though the amount of worm they involve varies to some extent with the type and vigour of the movement) they are seldom, if ever, shown by the first three. Proboscis activity, on the other hand, is brought about by the integrated action of the proboscis itself, of the body wall of the head, and of the body wall of the first three trunk segments.

If a worm is watched quietly pumping water through a glass tube (Fig. 1), the ventro-lateral surfaces may be noticed, over most of the trunk, to be pressed tight against the tube; a space remains, however, between the dorsal surface and the tube, and the gills spread out into this space. Waves of swelling travel along the dorsal surface, occluding the space and so driving water through the tube; the gills contract as the waves approach and expand again as soon as they pass. A rather conjectural cross-section of a worm in the act of irrigation, based on watching worms in glass tubes from the side, is drawn in Fig. 7B. The problem at once arises, of how the close pressing of the flanks against the tube is achieved. The only possible answer, I think, is by means of the notopodial protractors. It will be seen from the drawing, that the contact could be maintained if the notopodia were pressing outwards and upwards. Meanwhile, the head and first few segments (which are not concerned in the irrigation waves, and in which the notopodia are poorly developed) arch away from the side of the tube (Fig. 1).

In active creeping, as Just (1924) described, the notopodia exert a ratchet action, being directed backwards for headward locomotion, and forwards for tailward locomotion. We may fairly safely guess that the neuropodial rostra play a similar role. When swimming, the worm travels tail first, with lateral waves of great amplitude travelling headwards along the body, while the notopodia are directed headwards and held close to the body surface. The podia are never used as oars or paddles, or even as punt poles; they are bracing and anti-slip devices.

It seems, then, that the neuropodia and notopodia are adapted to assist in those wave movements which are the concern of the hinder segments, and it is in those segments that they are best developed. The first few trunk segments are specialized, partly to help in the extrusion of the proboscis by driving their contained body fluid forwards (Just, 1924) and partly for the flanging movement described above. The great development of the parapodial girdles which the latter function involves appears to carry with it a reduction in the size of the neuropodia and notopodia, and the disappearance of the gills. It is indeed striking, in a view of the whole worm, that the gills appear just as the parapodial girdles leave the dorsal faces of the chaetigerous annuli (Fig. 4).

*Arenicola claparedii.*

The general organization of the body wall of the trunk is the same in the other two species as in *marina*; it is therefore only necessary to note divergences.

An immediately obvious feature of *claparedii* is the enormous development of the first three chaetigerous annuli (Fig. 4). In the living worm, the movements of these annuli are like those of *marina* in type, but very much more powerful and impressive. The anatomical features which distinguish these annuli are correspondingly well developed. At the same time, this expansion has entailed

a great reduction in the ordinary annuli of the anterior segments. I find the following formula, in my Neapolitan specimens:

i.1.ii.1.iii.3.iv.4.v ...

The hindmost of the 3 annuli between iii and iv is generally much smaller than the others. Some of the American specimens at the British Museum have a second annulus between ii and iii; it is however always very small and may

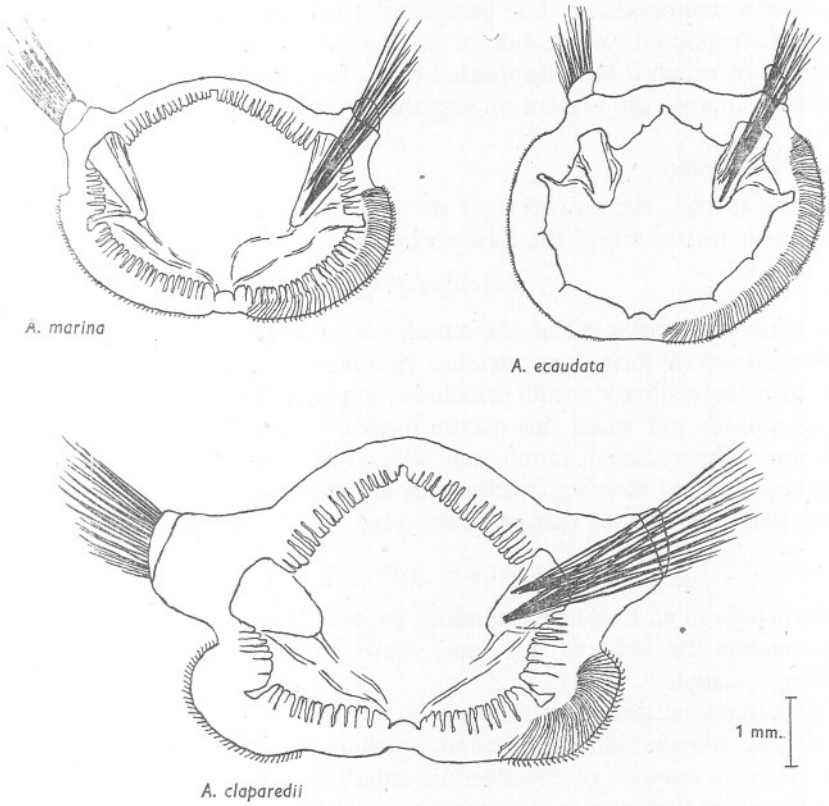


Fig. 8. Drawings, all to the same scale, of chaetigerous annulus xvi in each of the three species. Drawn from cleared specimens of the isolated annuli. The full extent of the chaetae is shown on the right, the projecting portions only on the left.

not extend round the whole circumference of the worm. In others, chaetigerous annulus iii hangs forwards in such a way that a minute ring might be present but hidden. We seem to be concerned here with an annulus in process of disappearance; and the variations described below for *ecaudata* support the idea that it is always immediately in front of the chaetigerous annuli that reduction occurs.

In a posterior direction the parapodial girdle is seen to leave the dorsal surface after segment vi—so, although the girdle is better developed than in *marina*, it embraces rather fewer segments.

The notopodia are more massive in *claparedii* than in *marina*, and so are the individual notopodial chaetae. The neuropodia are short in the more anterior segments and lengthen posteriorly, but they never approach the ventral line as closely as in *marina* (Fig. 8). Even in the hinder segments, the ventral ends of the neuropodia are separated by a distance about equal to the length of a neuropodium. The parapodial girdle extends from the lower end of the neuropodium to the side of the ventral groove, even in those hinder segments in which it has disappeared from the dorsal surface.

Nephridiopores are present on segments v to ix inclusive.

*Arenicola ecaudata*

In this species, the reduction of the ordinary annuli of the more anterior segments is least marked, the formula being:

i.3.ii.4.iii.4.iv.4.v ...

In many specimens, all of the annuli are prominently developed, and the truth of the above formula is obvious. In others, however, there is a tendency to reduce the ordinary annuli which lie immediately in front of the chaetigerous annuli, and when this occurs it affects all of the first three or four segments. The reduced annuli may in extreme cases be so small, and so overhung by the following chaetigerous annuli, as to be invisible on surface inspection. The formula then appears to be:

i.2.ii.3.iii.3.iv.4.v ...

Nevertheless, in all examples examined by myself, a sagittal cut with a razor blade reveals the hidden rings, and shows that the formula is in fact as previously stated.

The parapodial girdles of this species are rather poorly developed, as the low degree of reduction of the annuli perhaps suggests. The hinge lines lie near the front margins of chaetigerous annuli i–iii, instead of bisecting them as in the other two species. The various components of the parapodial girdle are all present, but they are small, and all localized in the front part of the annulus. In a posterior direction these structures get gradually less and less well defined, until they can no longer be made out on the dorsal surface, as from about segment xiv. In other words, although less well developed than in the other species, they concern about twice as many segments. Now the most anterior gill, in *ecaudata*, is typically on segment xvi; as in *marina*, this gill is generally small and sometimes absent. The whole arrangement evidently confirms the idea, already suggested by the other two species, that the gills and the parapodial girdles tend to exclude each other from the dorsal surface.

The notopodia are relatively smaller, and more dorsally placed, than in the other species (Fig. 8). The neuropodia are exceedingly long, extending from the side of the nerve cord to a point well above the nephridial line. In the more anterior segments, far from being short (as in *marina* or *claparedii*), the neuropodia of *ecaudata* are best developed, and reach from the ventral line to the bases of the notopodia (Fig. 4).

Nephridiopores are present on segments v to xvii.

## THE ANTERIOR REGION ('HEAD')

The 'head' is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus (Fig. 4). Its segmentation is largely obscured, in the adult, by its profound functional modifications. It consists of the prostomium and a second large portion which, to quote Ashworth (1912),

> in most adult specimens of *Arenicola*, is divided by encircling grooves into three or four (or more) rings. There are good reasons for stating that this is composed of the peristomium and a body segment which is without chaetae in the adult. In post-larval stages of *A. marina* and *ecaudata*, the region between the prostomium and the first ordinary chaetiferous segment is subdivided by a groove into two parts. The anterior and usually rather smaller portion is undoubtedly the peristomium; it never bears chaetae, but the paired statocysts may be seen near its anterior margin. The posterior of the two parts is, in the post-larval stages which the writer has examined, achaetous, but a chaeta has been observed in this segment, in either *A. marina* or *A. ecaudata*, by Professors Ehlers, Benham, Mesnil and Fauvel, a fact which demonstrates that this is a true segment. Evidence confirmatory of this interpretation is afforded by the arrangement of the giant nerve cells. In later post-larval stages in which the annulation is making its appearance, the peristomium and the segment in question become subdivided into secondary rings.... The composition of this region is probably constant throughout the family.

Except for the important study of the statocysts by Ehlers (1892), previous writers on this region have mainly confined themselves to cursory accounts of its external features, and discussions of its segmental homology. Many interesting features, especially the musculature, have received little or no attention. The following account omits the proboscis, and certain special structures (e.g. the retractor muscle) associated therewith. I hope to describe them, with the internal anatomy in general, at a later date.

### *Arenicola marina*

Apart from the absence of parapodia, the most noteworthy specializations of the body wall of the anterior region may be grouped under the following headings: (i) the mouth, (ii) the prostomium and nuchal pouch, (iii) the central nervous system, (iv) the metastomial muscle, and (v) the statocysts.

At the *mouth*, which is terminal, the layers of the body wall continue on to the eversible proboscis. The latter organ is partly extruded in Figs. 9 and 10.

The *prostomium* may be completely withdrawn into the *nuchal pouch*, which lies behind it. The general relations of these structures can be seen in Figs. 9–13. The pouch (*nuch.p.*, Figs. 10B, 13) opens by a crescentic slit just above the prostomium (*prost.*); its roof is thin and flexible; its floor is the prostomium itself. The latter organ, when fully exposed, has roughly the form of an

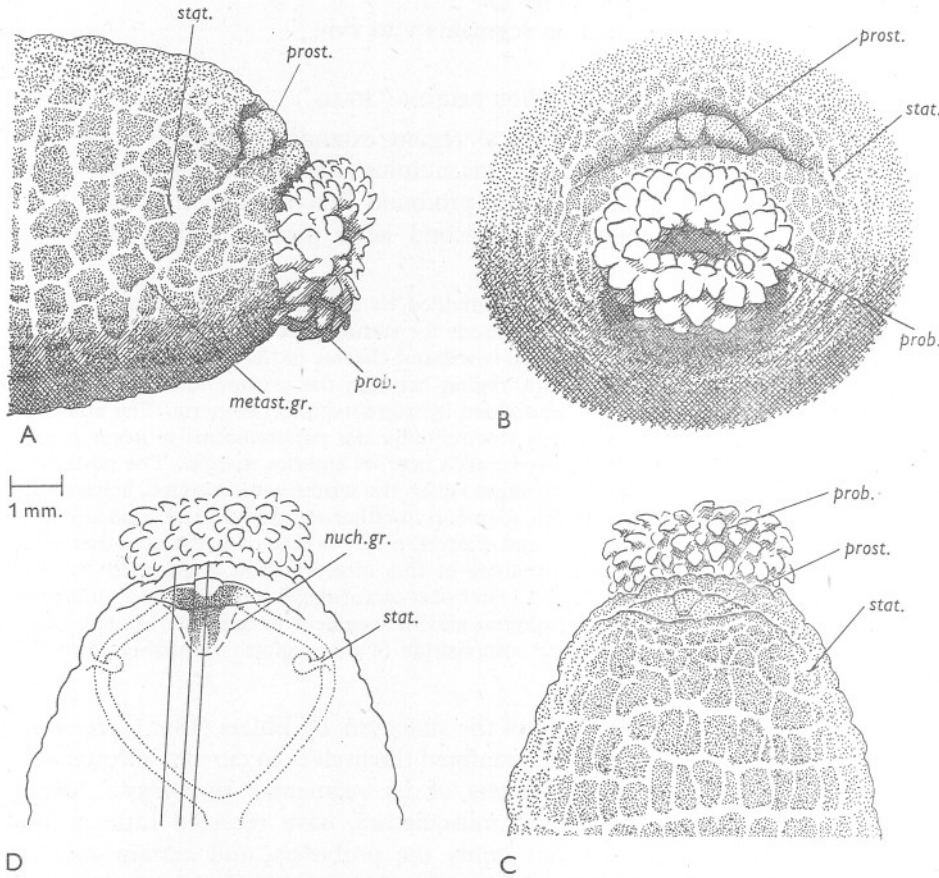


Fig. 9. *Arenicola marina*. Lateral view (A), anterior view (B) and dorsal view (C) of a specimen killed in the relaxed attitude by the Mg-formalin method. D, outline of the dorsal view, with the positions of the brain and oesophageal connectives included; that part of the brain which adheres to the dorsal surface of the prostomium is stippled; the nuchal groove is shown as a dashed line; the ruled lines give the positions of the sections in Fig. 12. Lettering as on p. 44.

isosceles triangle with its apex directed backwards; its dorsal face is impressed by a shallow Y-shaped groove (Fig. 10A). The worm must, however, be dissected if the whole prostomium is to be seen. In preserved material, it is always more or less completely overlapped by the dorsal lip of the nuchal pouch, so that one sees only its anterior margin; this is trilobed, owing to the

fact that the arms of the dorsal, Y-shaped groove continue down the anterior face of the prostomium. Between the prostomium and the mouth is a strip of body wall, which Ashworth (1912) terms the 'upper lip'.

The nuchal pouch as a whole may be regarded as a blind in-pushing of the epidermis and subjacent connective tissue, passing through the circular and longitudinal muscle layers. In sections, a large amount of transversely running muscle can be seen immediately ventral to the prostomium. Its position and course suggest that it is circular muscle; in fact, however, as will be shown below, it is made up of certain specialized muscles, derived, largely at least, from the longitudinal layer (the metastomial muscle, and the dorsal muscle of

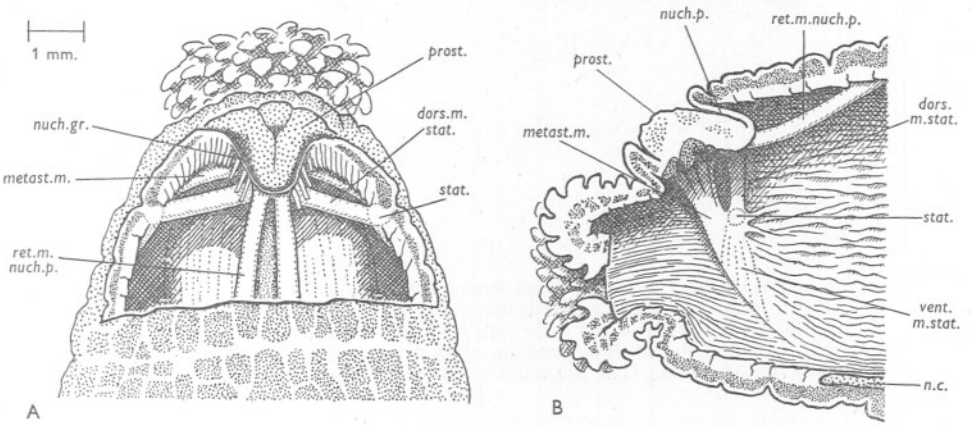


Fig. 10. *Arenicola marina*. A, dorsal dissection of the animal of Fig. 9; part of the body wall and the thin roof of the nuchal pouch have been removed. The front part of the dorsal vessel (stippled) can be seen between the retractors of the nuchal pouch. B, lateral dissection of another worm to show the coelomic aspect of the body-wall muscles of the right side; the animal has been bisected in the median plane and the gut and blood vessels have been removed. The ventral muscle of the statocyst is seen as a series of fine strands (dotted lines) running ventrally across the face of the metastomial muscle. Lettering as on p. 44.

the statocyst). The columns of the longitudinal layer pass by the sides of the nuchal pouch, and those immediately adjacent to it send slips which are inserted on its walls and help in its retraction. The chief part in retraction, however, is played by a paired muscle, the retractor of the nuchal pouch, clearly derived from the longitudinal layer, and running from the hind end of the pouch to a point on the body wall, about half way between the prostomium and the first chaetigerous annulus (Figs. 10 and 13, *ret.m.nuch.p.*).

My impression is that retraction of the nuchal pouch never occurs as an isolated act, but only when the anterior end as a whole is shortened and thickened, as part of the general movement. There are no protractor muscles. Extrusion of the proboscis is presumably due to the pressure of the body fluid, and occurs, I believe, whenever the head as a whole lengthens and narrows, and at no other time. Fig. 11, drawn from preserved specimens, illustrates

two configurations within the range that can be seen in the living animal. When the living worm assumes the extended attitude, the roof of the nuchal pouch evaginates and can be seen as a crimson transverse ridge, just behind the prostomium.

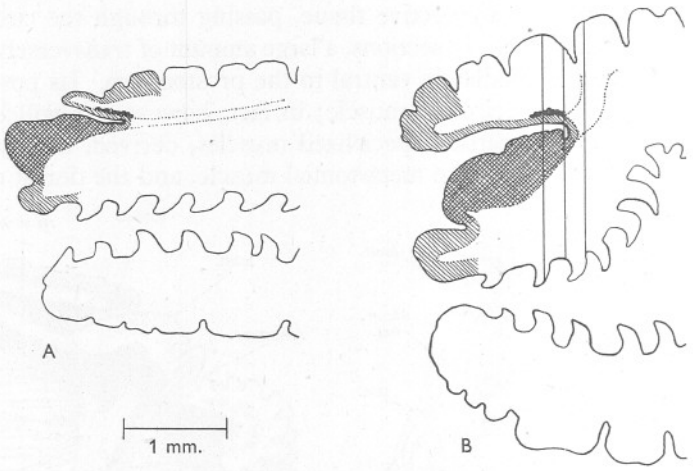


Fig. 11. *Arenicola marina*. Median sagittal sections of specimens killed as follows: A, in Mg-formalin; B, in Bouin without previous narcosis. The ruled lines in B give the planes of the sections in Fig. 13. Part of the body wall is shaded to show its thickness, and the prostomium is cross-hatched. The position of the retractor muscle of the prostomium is given as a dotted outline. The proboscis is fully withdrawn in both specimens.

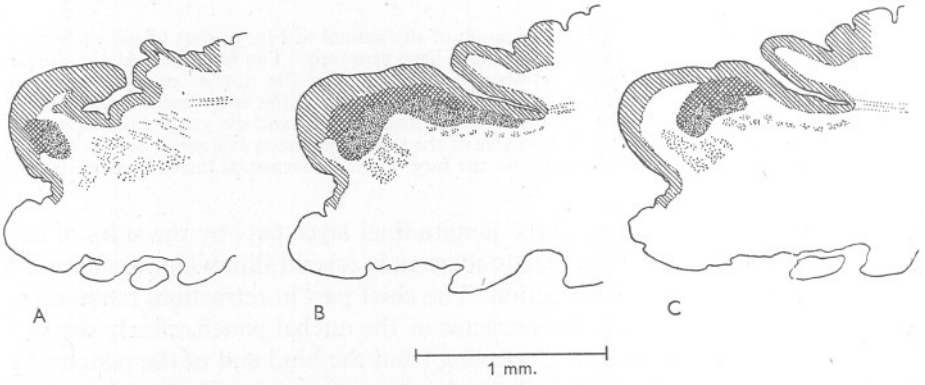


Fig. 12. *Arenicola marina*. Sagittal sections of a Mg-formalin specimen, corresponding approximately to the ruled lines in Fig. 9D. The proboscis is fully withdrawn. The superficial (ganglionic) part of the brain is cross-hatched, and the deep (fibrous) part is closely stippled. Section C is median.

The hinder part of the roof of the nuchal pouch bears a curious vascular plexus, shown black in Fig. 11. This marks what is evidently an important structural differentiation of the roof. In the region of the plexus, the roof consists of a very deep columnar epithelium without a subjacent muscular

layer. Elsewhere, it has a shallower epithelium and a thin circular muscle layer, continuous with the circular muscle layer of the general body wall. Now in the other two species, as we shall see, the prostomium cannot be retracted, and its hinder margin is marked by a nuchal groove, whose epithelium is very deep, ciliated and presumably sensory. This evidently corresponds to the hinder, vascular part of the roof in *marina*. The non-vascular part, present only in *marina*, is simply attenuated body wall, and it is this which converts the whole region into a pouch and makes retraction of the prostomium possible.

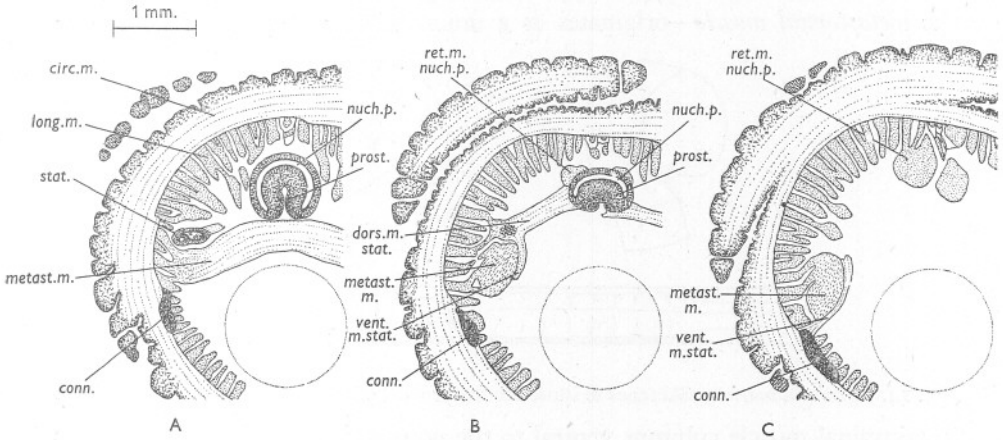


Fig. 13. *Arenicola marina*. Three transverse sections, corresponding approximately to the ruled lines in Fig. 11B, of a specimen killed in Bouin. The sections are equidistant and 0·2 mm. apart; the most anterior is on the left. The dotted circle gives the position of the gut. Lettering as on p. 44.

The general plan of the *central nervous system* of the head is shown in Fig. 9D. The ventral nerve cord continues forwards for a short distance on to the head; it then divides to give rise to the connectives, which run obliquely upwards and forwards to the prostomium. Just as the course of the ventral cord is marked externally by the ventral groove, so that of the connectives is marked by the more or less evident metastomial grooves (Fig. 9A, *metast.gr.*). The connectives resemble the ventral cord in consisting of a superficial ganglionic and a deep fibrous part, and in lying deep to the circular muscle layer (Fig. 13, *conn.*). When they reach the lateral corners of the prostomium, where the nuchal pouch pushes through the circular layer, the ganglionic part of the connectives enters into intimate relation with the epidermis. The nerves now expand somewhat and, remaining in close contact with the epidermis, pass up the front face of the prostomium to reach its dorsal side. Here they run backwards for a short distance to meet each other in the median plane. From their point of union, a pair of massive nerves runs back to the nuchal groove. That part of the central nervous system which lies in the prostomium,

in intimate relation with the epidermis, is generally termed the brain. Its form can be seen in Figs. 9D and 12. For the fine structure of the brain, see Gamble & Ashworth (1900).

The shallow grooves, which divide the anterior margin of the prostomium into three lobes and trace a Y on its dorsal face, give the line along which the brain adheres to the epidermis. The body wall is therefore thick under these grooves. At the sides of the prostomium, and in its median anterior lobe, the body wall is thin and the coelome comes near the surface (Fig. 12).

Immediately dorsal to the connectives, over the more ventral part of their course, lies the largest special muscle in the body wall of the worm. This—the *metastomial muscle*—originates as a union of contributions from all the

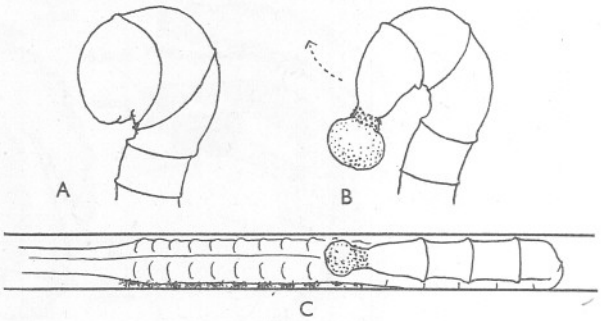


Fig. 14. *Arenicola marina*. Sketches to illustrate the process of reversing in the tube (see text).

longitudinal muscle columns ventral to the notopodial line. It runs forwards and upwards, following the general course of the connectives, until it reaches the level of the statocysts; it then leaves the inner face of the longitudinal layer and crosses the body cavity, just below the brain, to continue into its fellow of the opposite side (Figs. 10, 13, *metast.m.*).

This muscle was first described by Ehlers (1892), who said that it was inserted on to the prostomium. It is briefly mentioned by Gamble & Ashworth (1898) and by Ashworth (1904), who regard it as a retractor of the prostomium. Its true anatomical relationships, however, show that it cannot play that role. Its actual function is quite different, and very important. The lugworm sometimes reverses itself, either in its own burrow or in glass observation tubes, by narrowing its body and then burrowing (with continual extrusions of the proboscis, and uprisings of the parapodial girdles) along its own ventral surface. In this way it can turn in a tube which, at other times, it seems comfortably to fill (Fig. 14C). The problem now arises, how does this performance start? Living worms, when watched,[1] can occasionally be seen to assume a remarkable

[1] To study the movements of the proboscis and head, it is convenient to tie the whole worm with fine string about at the level of chaetigerous annulus v, to cut away everything behind the ligature, and to put the isolated front end in sea water under a binocular microscope. The preparations stay active for hours, and frequently show the turning attitude described above.

attitude, in which the dorsal wall of the head and of the first two or three segments is greatly distended, while the ventral wall shows extreme longitudinal contraction (Fig. 14A). The prostomium and mouth are thereby come to be directed backwards: the attitude can be roughly imitated by 'burying one's chin in one's chest'. Now the assumption of this attitude always heralds an outburst of proboscis activity. The first extrusion begins while the worm is still in the attitude, and the proboscis therefore emerges in a tailward direction. As this extrusion completes itself, the whole anterior end assumes a more usual configuration. If the worm is lying in a dish of sea water, this results in a forward swing of the proboscis (Fig. 14B); but if the worm is in a tube, the forward swing cannot occur, and subsequent extrusions, made in the usual manner, will serve to pull the head farther and farther along the worm's ventral surface (Fig. 14C). The metastomial muscle runs like a sling over the mouth, and, if it contracts simultaneously with the more ventral longitudinal columns from which it arises, will play an important and perhaps essential role in the assumption of the attitude of Fig. 14A.

The *statocysts*,[1] whose form was beautifully described by Ehlers (1892), are a pair of blind in-pushings of the epidermal layer of the body wall, which pass through the circular muscle layer (Figs. 9, 10, 13, *stat.*). Their openings are slit-like and dorsi-ventrally elongated. Each leads into a tube with a lumen of the same form, and which opens forwards at its deep end into a spherical bulb. The whole organ is therefore rather retort-shaped. It contains various foreign objects, such as quartz grains, fragments of spicules and diatom shells, etc., covered with more or less well-marked layers of a 'chitinoid' secretion (Ashworth, 1904).

The statocyst is provided with a rather complicated musculature, whose functions are obscure. The muscles are: (i) the dorsal muscle of the statocyst (Fig. 10B, *dors.m.stat.*), which runs dorsally and medially; its more anterior fibres continue into the corresponding muscle of the opposite side, while its hinder ones are inserted into the posterior end of the nuchal pouch, just below its retractor; (ii) a number of slips of muscle running back to the longitudinal columns adjacent to the statocyst; (iii) the ventral muscle of the statocyst (Figs. 10, 13, *vent.m.stat.*), which crosses the metastomial muscle, as a thin sheet or as a series of fine strands, to the tissue round the connectives. On the whole, it seems likely that the dorsal muscle of the statocyst is derived, as the metastomial muscle is, from the longitudinal layer; the anatomical relations of the ventral muscle, on the other hand, are consistent with its being a member of the oblique muscle series.

[1] The statocysts lie at the level of the notopodia; as they are invaginations producing a chitinoid secretion, and as the notopodial chaetae have sensory nerve endings round their bases (Retzius, quoted by Ehlers, 1892), it is tempting to think of them as the peristomial notopodia. The idea was discussed at length by Ehlers (1892), who decided against it, on the ground that certain polychaetes of other families have statocysts, neuropodia and notopodia in the same segment.

According to von Buddenbrock (1912, 1913), the statocysts of *Arenicola* are used to guide the worm when burrowing down into the mud.

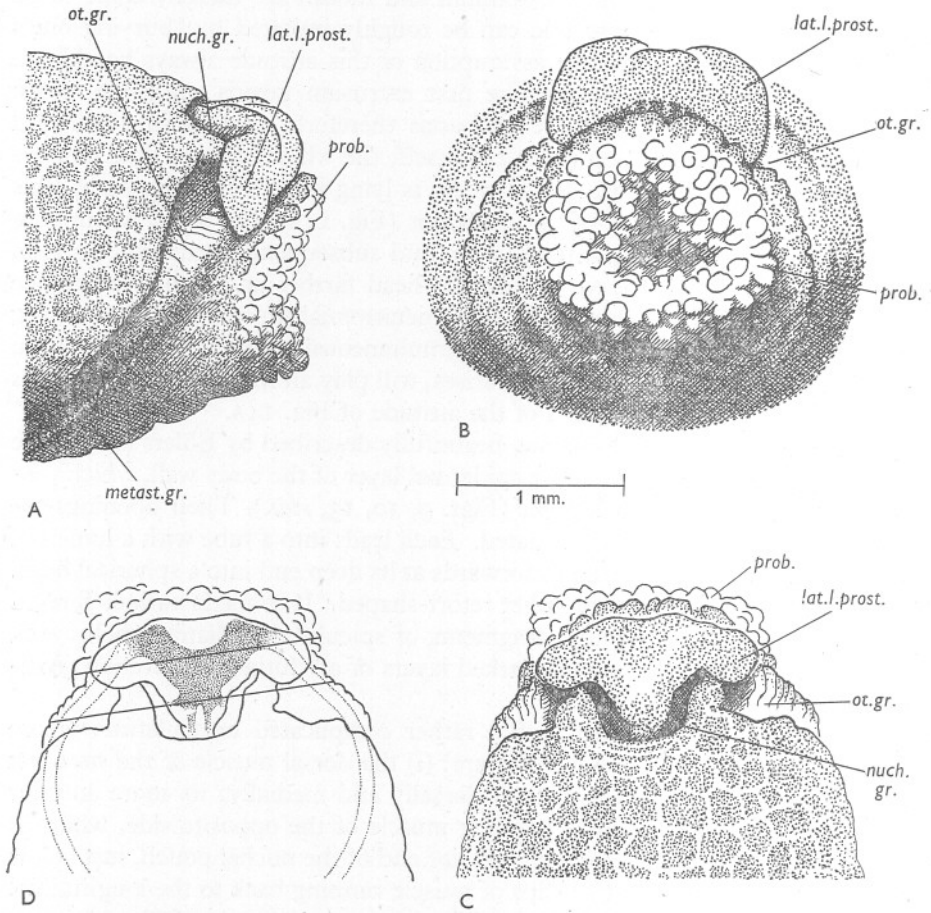


Fig. 15. *Arenicola claparedii*. Lateral view (A), anterior view (B) and dorsal view (C) of a Naples specimen killed by the Mg-formalin method. D, outline of the dorsal view with the brain and connectives given as in Fig. 9D; the ruled lines give the positions of the transverse sections in Fig. 17. Lettering as on p. 44.

*Arenicola claparedii*

The prostomium of *claparedii* differs in two important respects from that of *marina*. In the first place, it is prolonged laterally into two large, vertical flaps, the lateral lobes (Fig. 15, *lat.l.prost.*). In the second place, it is not retractile; nuchal pouch and retractor muscle are lacking (Fig. 16D). The nuchal groove lies, as in *marina*, round the sides and hind-end of the prostomium (Figs. 15, 17, *nuch.gr.*). It will be seen, on comparing Figs. 9 and 15, that the prostomium is relatively larger in the latter. This results, partly at

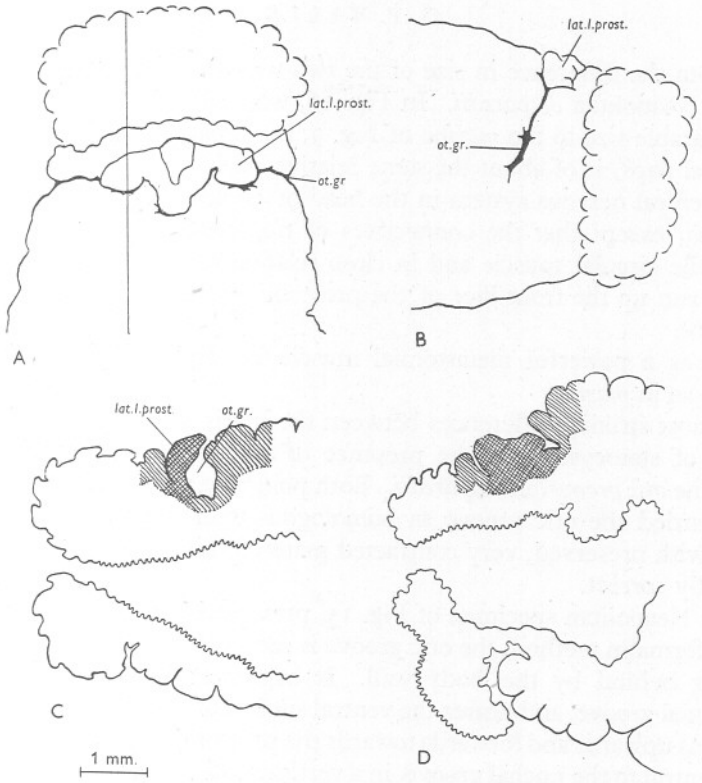


Fig. 16. *Arenicola claparedii*. American specimens, killed by means unknown to the writer. A, B, dorsal and lateral views of the same specimen. C, sagittal section of the same, cut along the ruled line in A, to show how the lateral wing of the prostomium (cross-hatched) overhangs the otic groove. D, median sagittal section of another specimen, for comparison with Fig. 11.

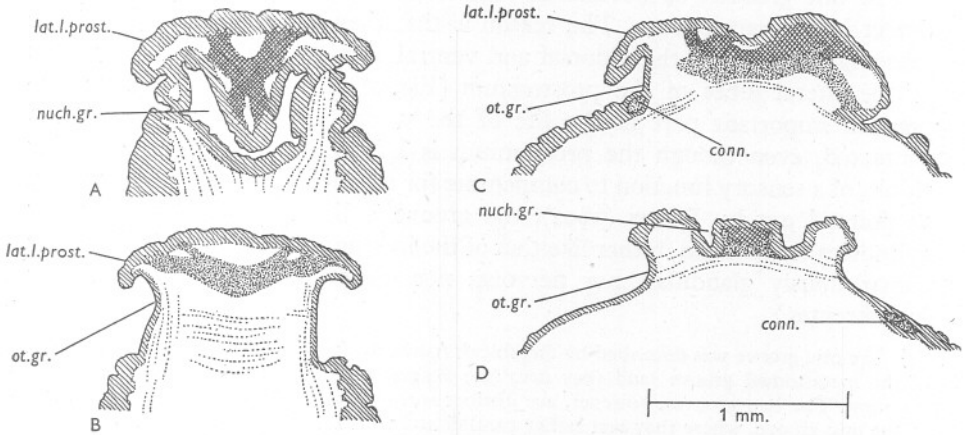


Fig. 17. *Arenicola claparedii*. Naples specimens, killed in Mg-formalin. A, horizontal section through the nuchal groove and the superficial part of the brain. B, horizontal section through the otic grooves and the deep part of the brain. C, D, transverse sections, corresponding approximately to the ruled lines in Fig. 15D. Conventions as in Fig. 12. Lettering as on p. 44.

least, from the difference in size of the two worms. Fig. 15 was drawn from a small, Neapolitan *claparedii*. In Fig. 16, which is from a Pacific specimen of comparable size to the *marina* of Fig. 9, the prostomium (after subtracting the lateral flaps) is of about the same relative size.

The central nervous system in the head of *claparedii* is very similar to that of *marina*, except that the connectives of *claparedii*, like its nerve cord, lie outside the circular muscle and in close relation to the epidermis. The connectives run up the front face of the prostomium, medial to the lateral lobes (Fig. 15D).

There is a powerful metastomial muscle in *claparedii*, having the same relations as in *marina*.

The most striking differences between the heads of the two species are the absence of statocysts, and the presence of a new structure, which will be termed the *otic groove*, in *claparedii*. Both points were noted by Ehlers (1892), who regarded the otic groove as homologous with the statocyst; but as he worked with preserved, very contracted material, his account of the groove is not wholly correct.

In the Neapolitan specimen of Fig. 15, preserved in the relaxed attitude by the Mg-formalin method, the otic groove is seen as a large, open shelf, slightly overhung behind by the body wall. It begins at a point just above the metastomial groove, and nearer the ventral surface of the worm than the dorsal, and it runs upwards and forwards towards the prostomium.[1] It ends, lateral and rather ventral to the nuchal groove, in a vertical wall (Figs. 15A, 17). Strands of muscle run across, below the brain, from the otic groove of one side to that of the other; these are indicated in Fig. 17D; if the otic groove indeed represents the statocyst, they might be its dorsal muscle.

The otic grooves, so obvious in relaxed animals, may be very difficult to detect in contracted ones. The reason is that they are closed, partly by the pressing together of their dorsal and ventral borders, and partly by means of the lateral lobes of the prostomium (Fig. 16C). The groove appears to play an important part in the life of the worm, since its surface is thus protected, even though the prostomium is left exposed, and one naturally thinks of a sensory function to compensate for the lack of statocysts. However, as pointed out by Ehlers (1892), the groove is lined by an unusually low cylindrical epithelium, rather like that of the interannular grooves; it is neither conspicuously glandular, nor nervous, nor ciliated; in a word, 'ein sehr indifferentes'.

[1] The otic groove was described by Gamble & Ashworth (1900, p. 501) as 'an enlargement of the metastomial groove' and they deny the suggestion of Ehlers that it represents the statocyst. The two grooves, however, are distinct and easy to distinguish at the ventral end of the otic groove, where they run rather parallel and with the otic groove slightly dorsal to the metastomial.

*Arenicola ecaudata*

The general appearance of the head in *ecaudata* is different in many ways from that of *marina*. The nuchal groove is very long, resembling in shape a U whose vertical limbs have been bent outwards, their tips reaching more than half way towards the ventral line. The area between this groove and the mouth is divided more or less obviously by a transverse fold, which separates the upper lip in front from the prostomium behind. The latter is a flat area,

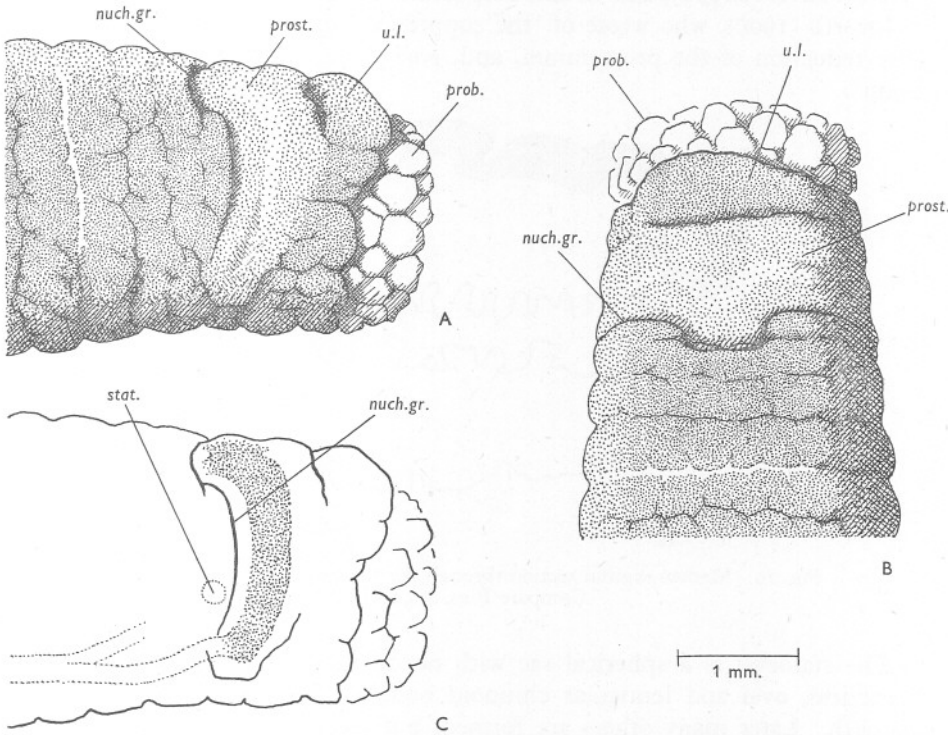


Fig. 18. *Arenicola ecaudata*. Lateral view (A) and dorsal view (B) of a specimen killed in Mg-formalin. C, outline of the lateral view, with the positions of the right statocyst and the central nervous system indicated; the part in relation with the epidermis is stippled. Lettering as on p. 44.

often hardly distinguishable from the general body wall; but in good specimens, a broad, rather smooth, very shallow depression, corresponding to the Y-groove on the prostomium of *marina* and indicating the position of the brain, can be seen; this depression is drawn pale in Fig. 18. The prostomium extends slightly farther ventrally than does the nuchal groove. There is no nuchal pouch, and the prostomium is obviously not retractile (Fig. 19).

The connectives resemble the nerve cord in lying deep to the circular muscle layer, from which they are separated by a coelomic space. On reaching the corners of the prostomium, they enter into close relation with the epidermis,

and proceed dorsalwards as the brain. This organ is dotted in Fig. 18C; its outlines are, however, rather ill-defined and it gives off numerous nerves to the nuchal groove and the anterior body wall.

The form of these structures in *ecaudata* can be derived from that in *marina* by supposing that the corners of the brain and prostomium are dragged for a great distance in a latero-ventral direction. It will be noted that the brain is relatively large. 'Le cerveau est relativement developpé pour une Arénicole' wrote Fauvel (1899*a*), and in this respect he was more exact than Gamble & Ashworth (1900), who wrote of 'the suppression of the prostomium' and of 'the reduction of the prostomium, and, *pari passu*, the simplification of the brain'.

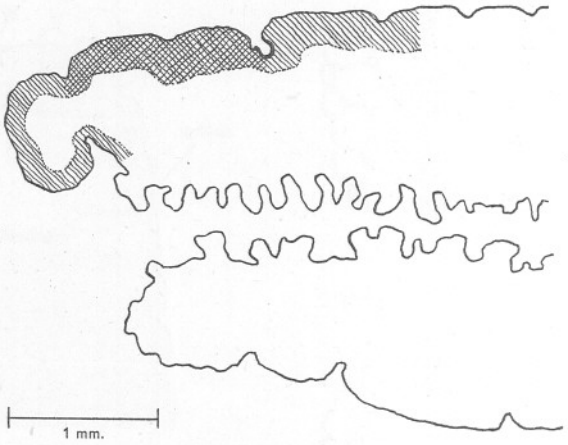


Fig. 19. Median sagittal section through the head of *Arenicola ecaudata*. Compare Figs. 11, 16D.

The statocyst is a spherical sac with no duct to the exterior; it contains 'spherical, oval and lenticular chitinoid bodies...there is at first only one statolith. Later many others are formed, but the original one remains conspicuous by reason of its larger size' (Ashworth, 1912). It corresponds in position with the statocyst of *marina*, and lies on the superficial face of, and partly embedded in, the longitudinal muscle layer. It receives a nerve from the connective, shortly before the latter enters the brain.

Owing to the smooth face which the longitudinal layer presents to the coelome in this species, the special muscles of the head are hard to make out in dissections. However, examination of the cleared and flattened body wall with polarized light shows that a metastomial muscle exists, having essentially the same relations as in *marina* or *claparedii*.

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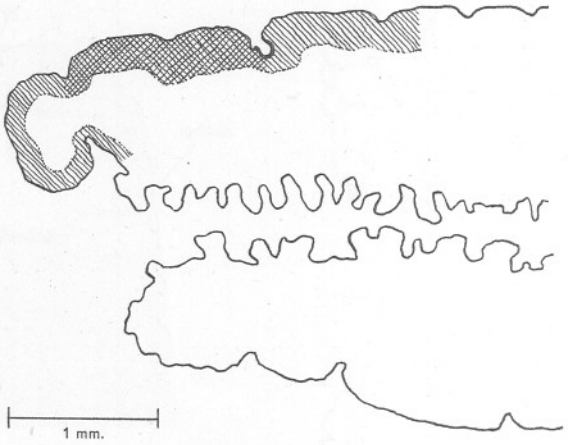


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Owing to the smooth face which the longitudinal layer presents to the coelome in this species, the special muscles of the head are hard to make out in dissections. However, examination of the cleared and flattened body wall with polarized light shows that a metastomial muscle exists, having essentially the same relations as in *marina* or *claparedii*.

## THE POSTERIOR REGION ('TAIL')

For many decades, the genus *Arenicola* has been divided into 'caudate' and 'ecaudate' sections. All the species have a head, whose characters have already been noted. This is followed, in the 'caudate' species, by a number of trunk segments with parapodia, and in which all the septa, except the first, third and fourth, have practically disappeared; and this again by the tail, in which appendages are lacking but the septa persist. The number of trunk segments varies, in different 'caudate' species, from 16 to 20. The 'ecaudate' division consists of two species, *ecaudata* and *grubii*. In *ecaudata*, the head is followed by a trunk region resembling in many points that of the 'caudate' species; for example, it lacks septa except for i, iii and iv; the vessels of septum vii are specialized to form the hearts; and so on. The first gill, however, is rather farther back; on chaetigerous annulus xv instead of vii. There follows a rather gradual transition (through segments xvii to xix) to a region in which the septa persist, and which is externally distinguishable from the trunk.[1] In the trunk segments, the four annuli that separate any two chaetigerous annuli are very equal in size and pigmentation; in the tail, on the other hand, the second (and sometimes the third) of the four is rather larger and more deeply coloured than the others; this gives the tail as a whole a banded appearance, except in the darkest specimens. It seems clear enough that a differentiation exists, corresponding to, though less profound than, that of the 'caudate' species. A similar differentiation, a couple of segments farther forwards, is traceable in *grubii*. However, it is with *marina* and *claparedii*, in which the tail is most distinctively specialized, that we shall now be concerned.

### *Arenicola marina*

The fact that the tail segments of *marina* are short at its base and lengthen towards the tip, is suggested by surface inspection and established by dividing the tail horizontally (Fig. 20). The fact is interpreted by Ashworth (1912) as follows: 'During development, new chaetiferous segments are formed immediately in front of the terminal segment or pygidium. In the ecaudate species all the segments are produced in this growing zone, the activity of which becomes exhausted at about the end of the post-larval stage. In the caudate species, after the full number of chaetiferous segments has been formed, new segments are evidently produced at the anterior end of the tail; for in this region each segment is short from before backwards, while in the middle and posterior regions of the tail the segments are longer, and, in adult or late post-larval specimens, are subdivided into annuli.... In *A. marina* there may be 60 to 70 tail segments, though usually there are fewer owing to losses posteriorly.'

Now horizontal sections, either of large or small *marina*, never show a new segment in the act of formation at the base of the tail. The animal of Fig. 20 is

[1] This distinction is clearer in preserved than in living worms.

typical; even the shortest tail segments have a definite and uniform length (in this case, of 3 annuli), and the foremost of all is rather longer than those which follow it. Having examined many specimens, I do not believe that there is any formation of new segments at the tail base.

Fig. 21 gives the number of annuli per segment in three worms of different size, and affords a representative picture of the mode of growth of the tail. The counting of the annuli was not always exact, because it is sometimes doubtful whether an incipient annulus, in process of formation, should be counted or not: the use of smoothed curves is therefore legitimate. As the worms grow, the segments evidently lengthen; segment xv, for instance, has 2, 6 and 12 annuli in the three worms; and this growth becomes more rapid tailwards.

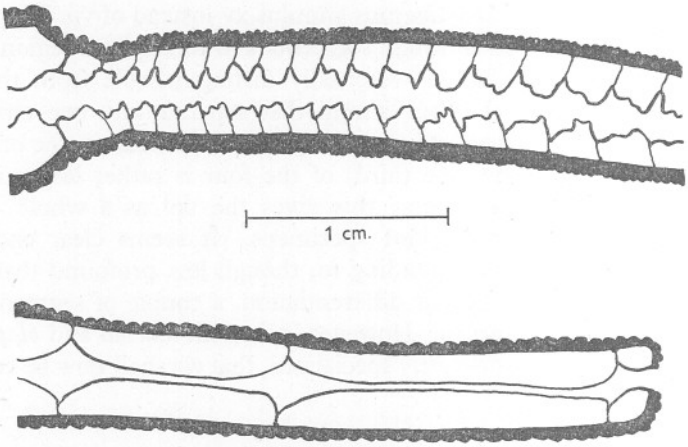


Fig. 20. Horizontal sections through the base and tip of the tail of an *Arenicola marina* of overall length 140 mm.

The following interpretation is suggested. The pygidial growth zone first lays down the trunk segments, then a great number of tail segments; these are at first very short and serve as a reserve stock; then they lengthen, the hinder ones more rapidly than the front. The graph clearly shows that losses from the hind-end must occur, not only as accidents but of necessity, as the hinder segments would otherwise become impossibly long. The worms in the graph had 44, 28 and 18 tail segments, in ascending order of size.

The reason for this fountain of tail production is not obvious at first sight. The hinder segments may be nearly 2 cm. in length; if the largest worm of Fig. 21 started with the '60 to 70 tail segments' which Ashworth gives as the maximum for this species, it has clearly lost about a metre of tail or potential tail; more than five times its overall length at death. The method adopted by *ecaudata*, of growing a tail of appropriate length and tolerating such losses as may occur, would seem more economical. 'Adult specimens of this species',

wrote Ashworth (1912) of *ecaudata*, 'seldom exhibit as many segments as they possessed at the end of the post-larval stage, but occasionally an unabbreviated example is met with, in which case the number of segments is about 60 to 64.

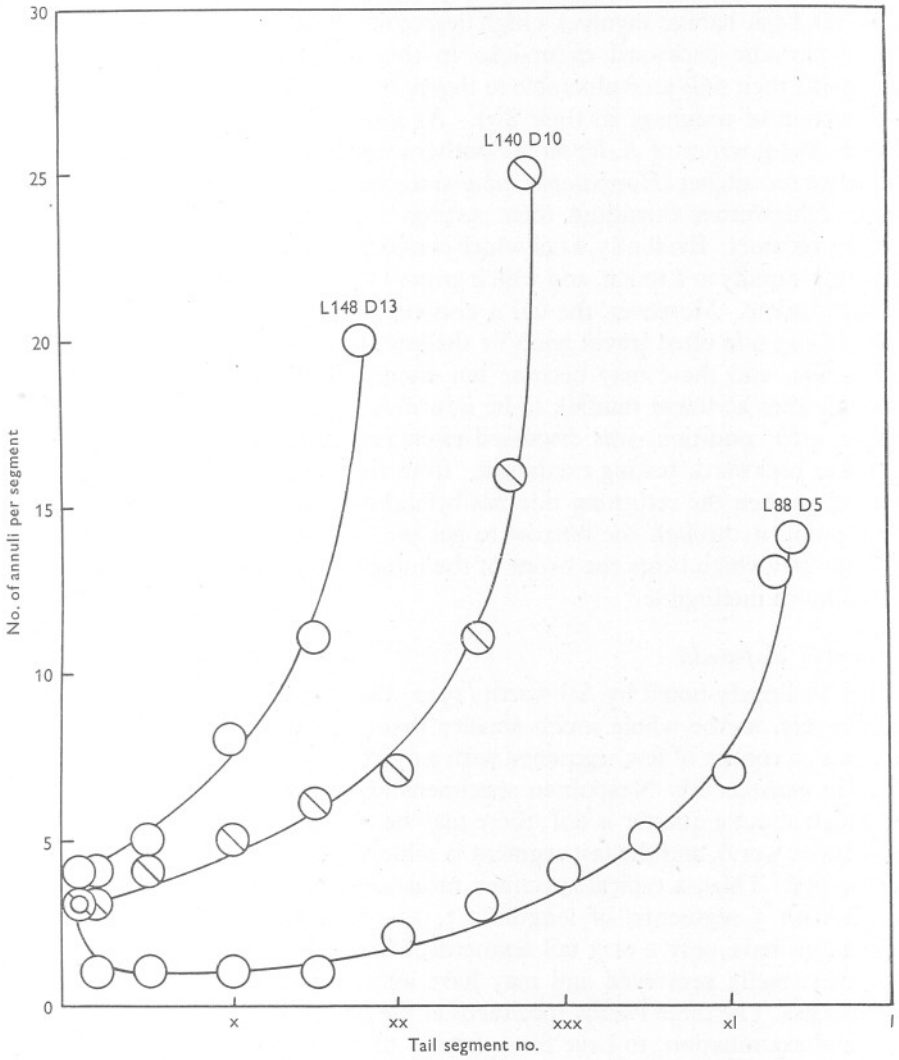


Fig. 21. The number of annuli per tail segment in three specimens of *Arenicola marina*. The total length, and trunk diameter, are given, in mm., by the graph of each specimen.

There are about 45 to 50 segments in average specimens.' These figures include trunk segments. An average *ecaudata*, then, starts with 60-odd segments, of which it loses 20 or 25%; a large *marina* has lost more than 50% of

its initial 80 or 90; and the lengthening of the segments in *marina* makes its losses the greater in proportion.

As already noted, *marina* generally lives on muddy sand flats, while *ecaudata* is found in sandy material among stones or the breakdown fragments of rocks. The sand-flat habitat involves a high degree of exposure of the tail. Lugworms make periodic backward excursions to the surface to defaecate, at which moments their tails are vulnerable to those predators which do not resent a high proportion of roughage in their diet. At low tide, sea birds may intervene. Stach (1944) writes of *A. loveni*, a Southern species very similar to *marina*, that 'The oyster catcher (*Haematopus fuliginosus*) was often observed to peck off the tails of lugworms extruding their castings'. High tide will doubtless bring other predators. Evidently, a tail which contains no very essential organs, which shortens rapidly at a touch, and which grows from reserve segments at the base, is appropriate. Moreover, the tail is also exposed to physico-chemical assault. The falling tide often leaves pools or shallow sheets of water over the burrows of *marina*, and these may become hot enough in bright sunshine, or dilute enough after a violent rainfall, to be injurious to the worms. Their behaviour under such conditions was discussed elsewhere (Wells, 1949*a*). They appear to make backward 'testing excursions' from time to time towards the surface, and only when the returning tide has brought cooler or more saline water do they pump it through the burrow to get the oxygen they need. Once again, it is the tail which bears the brunt of the injurious conditions, and its renewal is the more intelligible.[1]

*Arenicola claparedii*

It was already noted by Ashworth (1912) that Neapolitan specimens of this species are on the whole much smaller than Pacific ones. In both, the tail appears to consist of few segments, with a much less well-marked size gradient than in *marina*. My Neapolitan specimens are mostly 40–60 mm. in length, of which about a quarter is tail; there may be 12 tail segments, but usually the number is 5 or 6, and the last segment is seldom much more than twice as long as the first. Thus, a typical specimen measures overall 41 mm.; this includes a tail with 5 segments, of lengths 1·7, 2, 2·3, 3 and 3·6 mm. My Pacific specimens have only 2 or 3 tail segments, all of about equal length; they are, however, badly preserved and may have autotomized some tail segments in the process. The three Pacific specimens at the British Museum all appear (from external examination) to have few—from 5 to 7—tail segments.

All of these specimens are adult, and it is difficult to discuss the significance of their tail numbers without information about the post-larval stages, which

[1] The tail is also specialized with regard to its movements. The irrigation waves, by which water is driven through the tube, typically start at the junction of trunk and tail in *marina* and move forwards. If reversed (tailward) irrigation is in progress, they die out at the junction. In *ecaudata*, on the other hand, they run forwards from the hindmost end of the body. It appears likely that the tail of *marina* is responsible for the very rapid ejection of the faecal cylinders.

does not appear to be available. Similar tails occur in *A. cristata* Stimpson, at Wood's Hole, and for this species the development is known. Ashworth (1912) writes of adult American *cristata*, that the tail usually consists of 7–10 segments. By the kindness of Prof. Ritchie, of the University of Edinburgh, I have been allowed to dissect one of Ashworth's largest specimens; its overall length is 434 mm., and it has 7 tail segments, measuring, from base to tip, 12, 16, 17, 18, 19, 23 and 31 mm. Now the development of *cristata* was described by Lillie (1905), and the post-larva is figured by Ashworth (1912). The pygidial growth zone forms about 40 tail segments before its activity ceases, and, in the post-larva, these show a beautiful size gradient, as in adult *marina*. Apparently *cristata* resembles *marina* in the essential mechanism, but its reserve is smaller, and is often more completely spent. The same may be true of *claparedii*.

## Summary

Worms for dissection, or for museum preservation, should be prepared by the magnesium-formalin method, of which two modifications are given in the text.

The body of *Arenicola* is differentiated into: (*a*) an achaetous 'head', comprising the prostomium and a small number (probably two) of subsequent segments, (*b*) a 'trunk', composed of a number, varying somewhat with the species, of chaetigerous segments, and (*c*) a '*tail*', which may or may not be chaetigerous according to the species. The method of subdividing the body according to the distribution of the gills, so often met with in the literature, is misleading because it conceals the very fundamental differentiation between 'head' and 'trunk'.

The main layers of the body wall are described. There are grounds for supposing that the circular muscle layer plays a greater part than the longitudinal in the maintenance of a postural fluid pressure in active worms.

The parapodial derivatives are the neuropodia, the notopodia, and the parapodial girdles; details of all three, and especially of their musculatures and movements, are given in the text. The extent to which these structures are developed varies from species to species, as well as from segment to segment within a species; the latter differentiation (at least in *marina*) corresponds to functional differences in the attitudes and movements of the segments. *Claparedii* differs from *marina*, chiefly in the great development of the parapodial girdles of the more anterior trunk segments, with concomitant reduction of the intervening ordinary annuli, and in the comparative shortness of the hinder neuropodia. *Ecaudata* is especially distinguished by the slight development of the parapodial girdles and the length of the neuropodia, especially in the more anterior segments.

The head is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus. All species have a metastomial

muscle, derived from the longitudinal layer, and playing an important part in the process of turning in the tube. The chief special sense organ appears to be the nuchal groove. The main differences between the three species are as follows: *marina* has a nuchal pouch into which the prostomium can be retracted; *claparedii* lacks statocysts and has, instead, a large and rather complex otic groove of unknown function; *ecaudata* has a nuchal groove and brain which extend for a great distance towards the ventral line.

The tail of *ecaudata* bears parapodia and gills; it differs from the trunk in having well-developed septa and in respect of the external annulation. The tail of *marina* is achaetous and grows backwards from reserve segments, laid down early in life, at its base. The rate of tail production in this species is great, and probably related to the hazards which the sand-flat habitat involves for the tail. The tail in adult *claparedii* has few segments. It is compared in the text with that of *A. cristata* Stimpson; and the conclusion is drawn that in both species the facts are essentially as in *marina*, but the reserve is smaller and soon exhausted.

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## Appendix

### *Reference letters used in the text-figures*

| | |
|---|---|
| *circ.m.* | circular muscle |
| *conn.* | connective nerve |
| *dest.* | destruction zone |
| *dors.l.* | dorsal line |
| *dors.m.stat.* | dorsal muscle of the statocyst |
| *dors.v.* | dorsal vessel |
| *ep. & c.t.* | epithelium and connective tissue |
| *form.* | formative zone |
| *g.* | gill |
| *h.l.* | hinge line |
| *interann.n.* | interannular nerve |
| *lat.l.prost.* | lateral lobe of the prostomium |
| *lat.neur.v.* | lateral neural vessel |
| *long.m.* | longitudinal muscle |
| *metast.gr.* | metastomial groove |
| *metast.m.* | metastomial muscle |
| *m.h.* | muscles of the hinge |
| *m.parap.c.* | muscles of the parapodial canal |
| *n.c.* | nerve cord |
| *neph.* | nephridium |
| *neph.l.* | nephridial line |
| *neph.long.v.* | nephridial longitudinal vessel |
| *neph.p.* | nephridiopore |
| *neurop.* | neuropodium |
| *notop.* | notopodium |
| *notop.b.* | notopodial base |
| *notop.l.* | notopodial line |
| *notop.long.v.* | notopodial longitudinal vessel |
| *notop.t.* | notopodial tip |
| *nuch.gr.* | nuchal groove |
| *nuch.p.* | nuchal pouch |
| *obl.m.* | oblique muscle |
| *obl.m.notop.* | oblique muscle of the notopodium |
| *ot.gr.* | otic groove |
| *parap.c.* | parapodial canal |
| *prob.* | proboscis |
| *prost.* | prostomium |
| *prot.m.neurop.* | protractor muscle of the neuropodium |
| *prot.m.notop.* | protractor muscle of the notopodium |
| *ret.m.neurop.* | retractor muscle of the neuropodium |
| *ret.m.notop.* | retractor muscle of the notopodium |
| *ret.m.nuch.p.* | retractor muscle of the nuchal pouch |
| *stat.* | statocyst |
| *stom.* | stomach |
| *u.l.* | upper lip |
| *vent.m.stat.* | ventral muscle of the statocyst |
| *vent.v.* | ventral vessel |

# THE SEASONAL VARIATION IN WEIGHT AND CHEMICAL COMPOSITION OF THE COMMON BRITISH LAMINARIACEAE

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(Text-figs. 1–20)

CONTENTS



## Introduction

In previous publications the author (Black, 1948) has reported the seasonal variation in the total ash, iodine, crude protein, mannitol, laminarin and alginic acid contents of the Laminariaceae, *Laminaria cloustoni*, *L. digitata* and *L. saccharina*, for the 2-year period from November 1944 to October 1946.

The work has been continued for a further 2 years and this paper summarizes the seasonal variation in the above constituents, with the exception of iodine, for the period November 1946 to October 1948 inclusive. In addition, the seasonal variation in the fresh weight and dry weight contents has also been recorded.

The algae, in general, undergo such marked variations in chemical composition depending on the season of the year, the habitat, and the depth at which they grow, that any analysis of a sample for which the complete history is not given is of little value.

Cast weed, which usually has all the water-soluble constituents leached out either by the buffeting action of the waves before it is finally deposited on the beach, or by rain while exposed on the shore, may also have undergone appreciable bacterial decomposition, giving a false picture of the composition of the living plant. It is quite possible, too, that the time which elapses between the collection and drying may influence the composition, so that this time, together with the conditions of drying, should also be recorded.

The present investigation has shown that the method of sampling adopted is relatively sound, and that at any one time surprisingly small differences occur in the composition of individual plants taken from the same habitat, at the same depth, and dried under identical conditions.

The investigation is unique in that the method of sampling prevented the weed from coming into contact with rain, etc., which would affect its composition, and the plants were immediately dried under controlled conditions to reduce any chemical and biological changes to a minimum. Previous workers, on the other hand, do not state how their samples were collected, whether the weed was cut, or whether the samples were those of drift weed, and in what manner their samples were dried.

Although Stanford (1883, 1884*a*, *b*, 1886) in the second half of the nineteenth century carried out the pioneer work and laid the foundations for an industry based on the organic constituents of seaweed, it was not until 1919 that Lapicque carried out the first systematic investigation into the seasonal variation in the chemical composition of the marine algae. During the first world war, however, the demand for potash led to an intensive investigation being carried out by Hendrick (1916), but he was chiefly concerned with the analysis of the mineral matter of the algae.

From 1927 to 1929, Colin & Ricard (1929, 1930) collected monthly samples of *L. flexicaulis* and *L. saccharina* and examined them for dry weight, ash, mannitol, laminarin, algin and cellulose. Lunde (1937), investigating the possibilities of the seaweed off the coast of Norway as a source of raw material, collected monthly samples of *L. digitata* from 1935 to 1937 and analysed them for ash, mannitol, alginic acid, laminarin, fucoidin and nitrogen.

Similar investigations have been carried out in Japan by Atsuki & Tomoda (1926*a*, *b*), in Russia by Kizevetter (1938) and Vedrinskii (1938), and in Eire by Dillon (1943). Our knowledge, however, of the organic constituents of the marine algae is still incomplete. Accurate methods of analysis have been devised for the estimation of mannitol, laminarin, alginic acid and cellulose, while work is continuing on a method for the estimation of fucoidin. The fats and pigments require further investigation. Their nature and relative proportions in the algae are in many cases indeterminate.

No work appears to have been carried out on the algal proteins.

Minor constituents such as fucosterol and the neutral oils are at present being investigated, and it may well be that other valuable constituents have yet to be identified.

The work described in this paper forms part of the programme of research and development on seaweed undertaken by the Scottish Seaweed Research Association.

The author wishes to thank Miss B. Graham and Mr W. Cornhill for assistance with the analytical work and the Association for permission to publish.

## Investigations on separate constituents

In a brief review it is impossible to summarize all the work which has been carried out on the known constituents of the brown algae. The inorganic and several of the organic constituents have attracted the attention of numerous investigators, but it is unfortunate that often the results are somewhat conflicting.

### *Total ash*

The total ash consists of inorganic salts, presumably in solution in the cell sap, and the cations combined with the organic constituents such as alginic acid and fucoidin. In addition, the ash figure contains salts from the sea water retained on the surface of the plant. The plants were only allowed to drip before drying, since it was not considered advisable to wash off this surface water with distilled water which might affect the composition. Until about 1850 the ash of seaweeds, chiefly of the fucoid types, was the sole source of alkali for the soap and glass industries. This kelp industry was then threatened by the Le Blanc process, but as the use of iodine in medicine developed, a new kelp industry arose based on the ash of the laminarias; but this industry is also obsolete. Any future industry, however, based on seaweed will most likely depend on its organic constituents, which are mainly polysaccharide in character.

### *Trace elements*

The accumulation of trace elements in marine algae, which can be explained by considering alginic acid as an ion-exchange material, has been studied by Cornec (1919), Vernadskii (1930), Jones (1922), Öy (1940), and Wilson & Fieldes (1941).

A study of the trace elements present in the Laminariaceae and Fucaceae common to Scotland is at present being carried out and the results will be published in a future communication.

### *Mannitol*

Mannitol, a hexahydric alcohol common to all brown seaweeds, was first detected in *L. saccharina* by Stenhouse (1844). It appears to be the primary product of photosynthesis, previous workers having found only traces, or the complete absence, of free-reducing sugars. Like the mineral matter, the mannitol is probably all in solution in the cell sap, for if the living plant is put into distilled water the salts and mannitol rapidly diffuse through the cell wall into the surrounding water.

Although there is a recent patent by Berk (1940) on the extraction of mannitol from seaweed, the mannitol of commerce is obtained from manna, or is prepared synthetically by the catalytic reduction of fructose.

*Laminarin*

Laminarin has been the subject of investigation by various workers. It was first described by Schmiedeberg (1885), who isolated it from the Laminariaceae. It has since been studied by Krefting & Torup (1909), Kylin (1913), Gruzewska (1923), Colin & Ricard (1929), Lunde (1937), Nisizawa (1940), Le Gloahec & Herter (1940), and Barry (1938, 1939, 1941, 1942), and their work has been reviewed by Hassid (1944). Barry (*loc. cit.*) showed that laminarin consisted exclusively of glucose units, and that after methylation and hydrolysis it gave 2, 4, 6-trimethyl glucopyranose. He concluded that laminarin consisted of a chain of $\beta$-glucopyranose units bent into a spiral form.

Laminarin, therefore, differs fundamentally from starch and cellulose in that the glucose residues are combined by 1, 3-glycosidic linkages and not through carbon atoms 1 and 4.

The extent of oxidation of laminarin with periodic acid was used by Barry (1942) as an end group assay for this polysaccharide, and the results indicated a chain of sixteen glucose units. This chain length was not in agreement, however, with that obtained by the Haworth-Hirst method which indicated a chain length of about seventy-four glucose units.

The present investigation has shown that laminarin, present only in the frond, can be isolated in two forms, an almost water-insoluble form from *L. cloustoni*, which separates from cold water, and a more soluble form from *L. digitata*, which can only be obtained from aqueous solution on the addition of alcohol. The two forms are at present being studied.

It is not yet known what part laminarin plays in the metabolism of the algae.

*Alginic acid*

Alginic acid, found in all brown seaweeds, where it is believed to play an important part in the cell wall, was first isolated by Stanford (1883, 1884*a*, *b*, 1886) and has since been studied by the following workers: Hoagland & Lieb (1915), Nelson & Cretcher (1929), Bird & Haas (1931), Dillon & McGuinness (1931), Gomez (1933), Barry & Dillon (1935, 1936), Hirst, Jones & Jones (1939), Stewart & Lucas (1940), Speakman & Chamberlain (1944), Astbury (1945), and Wasserman (1949). It has been shown to be a polyuronide composed entirely of D-mannuronic acid.

Dillon & McGuinness (1931) believed that the alginic acid in the growing plant was combined with calcium and iron, and that desiccation destroyed the colloidal character of these compounds and rendered them insoluble. Bird & Haas (1931), on the other hand, believed that the alginic acid in the cell wall was in two forms: (*a*) a water soluble form, and (*b*) the acid in the free state. Recent adsorption experiments carried out by Wasserman (1949), however, have shown that the alginic acid occurs in the cell tissue of brown algae in the form of various metal salts, and is not present as the free acid.

*Crude proteins*

Except for the work of Haas and co-workers (1929, 1931, 1933, 1938), who succeeded in isolating an octapeptide of glutamic acid, no other work has been carried out on the nitrogen metabolism of the brown algae.

*Cellulose*

Although Kylin (1913, 1915, 1918, 1944) had shown that the cell-wall constituents of various seaweeds gave, with iodine and sulphuric acid, the characteristic blue colour of cellulose, considerable doubt existed for some time as to the occurrence of normal cellulose in marine algae. Thus Atsuki & Tomoda (1926*a*, *b*) stated that the greater part of the crude fibre of the laminarias consisted of the hemicelluloses, and that there was no evidence of the normal cellulose, while Ricard (1931), in the algae examined by him, did not obtain the characteristic reaction of cellulose, as found by Kylin. On the other hand, Naylor & Russel-Wells (1934) and Dillon & O'Tuama (1935) demonstrated the existence of normal cellulose in marine algae. Viel's (1939) survey of the literature reveals numerous contradictions, but recent work by Percival & Ross (1948*a*) has shown conclusively that the brown algae do contain cellulose which is fundamentally similar to the cellulose of the land plants.

*Fats*

Except for the work of Russel-Wells (1932) and Takahashi and his co-workers (1933, 1935, 1939), no other work appears to have been carried out on the fats of the Laminariaceae, and there is no information on the seasonal variation. Russel-Wells (1932) showed that a correlation existed between the fatty constituents and the depth of immersion of the algae. Takahashi *et al.* have, over a number of years, studied the fats of the indigenous algae of Japan and identified the various fatty acids.

*Pigments*

Although an appreciable amount of work has been carried out on the pigments of the Fucaceae, those of the Laminariaceae have received very little attention, the only recent work of a systematic nature being that of Manning & Hardin (1944).

## Preparation and Analysis of Samples

Each month, the samples of *L. cloustoni* were collected on the reef off Cullipool, Luing Island, in approximately 4 m. of water (D.L.W.O.S.T.), every effort being made to take them from the same spot and at the same depth. The open sea samples of *L. saccharina* were taken at Rudh-an-Aoil, Shuna Island and the sea-loch samples at Eilean Coltair, Loch Melfort, where the plants were growing in 3–4 m. of water (L.W.). As with *L. cloustoni*, the samples were obtained by trawling a multi-pronged grapnel for 2 min., hoisting the grapnel and lifting the weed into the boat.

The open-sea samples of *L. digitata* were taken at Atlantic Bridge and the

sea-loch samples at Eilean Coltair, Loch Melfort, where the plants were growing in 1 m. of water (L.W.). The samples were taken by hand at low water, when the plants were partially exposed. With each species, twenty plants were taken, measured and weighed. Two plants were selected for dry-weight determinations, and two were chosen at random for chemical analysis. The plants, separated into stipes and fronds, were draped over racks in a heated shed and dried at a temperature of 25–35° C. for approximately 48 hr., after which they were ground in a Christy and Norris No. 8 Laboratory Mill, fitted with a $\frac{1}{64}$ in. perforated plate screen, giving a powder which practically all passed through a sieve of 90 meshes to the inch. As the analytical methods were evolved it was found that this fine state of division was essential, especially for the method of estimating alginic acid.

The methods of analysis used were those previously employed by the writer (1948).

In the preparation of the samples for analysis, changes in composition due to respiration, etc., were negligible provided drying was carried out immediately after sampling; samples dried rapidly at 80–90° C. confirmed the results obtained at the temperatures employed in this investigation. On the other hand, plants killed in boiling absolute alcohol before drying, as is the normal procedure in plant analysis, showed considerable loss of mannitol and mineral matter, but it was found possible to kill sections of the laminarias in boiling chloroform without materially affecting the chemical composition.

## Results

The results, calculated on the anhydrous basis for the frond, stipe and whole plant, are given in Figs. 1–19 (pp. 53–67).

Before drying, the plants were divided into stipes and fronds which were weighed separately. From these results each constituent determined in stipe and frond was calculated for the whole plant.

Figs. 2, 8 and 12, giving the seasonal variation in the dry-matter contents of the fronds, the stipes and the whole plants, can be used to recalculate any of the results (expressed on the dry basis) on the fresh-weight basis.

In Fig. 20 (p. 68) the seasonal variation in the fresh weight of *L. saccharina* from Loch Melfort and Shuna Island is given, while the average figures for the three species are given in Table I.

## Discussion

### *General*

In general, the results agree reasonably well with those of the first 2 years investigated (Black, 1948), despite the fact that the summer of 1947 was exceptionally good with considerable sunshine, while 1948 was a very poor summer with considerable cloud and rain. Slight differences are occasionally found,

however, in the spring (March–April). At this period of the year, when a marked increase in the rate of photosynthesis occurs, the plant is actively producing a new frond, while the old frond is wearing away. The composition of the old frond (as shown in Table II) differs somewhat from that of the new frond, to which it is still attached, so that conditions such as rough weather, which influence the shedding of the old frond, will have an effect on the composition of the whole plant.

It would appear, therefore, that when the older part of the frond detaches itself it still contains mannitol and laminarin while the new growth contains no laminarin. This, no doubt, accounts for the sudden drop in laminarin in the spring. The new frond then undergoes a period of rapid growth and laminarin

TABLE I. MAXIMUM, MINIMUM AND AVERAGE WEIGHT OF PLANTS IN GRAMS

| | | Maximum | Minimum | Average of 450 plants |
|---|---|---|---|---|
| *L. cloustoni* | Frond | 936 | 510 | 681 |
| | Stipe | 1787 | 681 | 1192 |
| *L. saccharina* (open sea) | Frond | 1022 | 198 | 595 |
| | Stipe | 227 | 85 | 198 |
| *L. saccharina* (loch) | Frond | 936 | 198 | 595 |
| | Stipe | 227 | 85 | 170 |
| *L. digitata* (open sea) | Frond | 1901 | 340 | 965 |
| | Stipe | 426 | 142 | 255 |
| *L. digitata* (loch) | Frond | 823 | 198 | 426 |
| | Stipe | 227 | 85 | 142 |

TABLE II. COMPOSITION OF THE OLD AND NEW FROND OF *LAMINARIA CLOUSTONI* COLLECTED AT CULLIPOOL ON 14 APRIL 1947 (DRY BASIS)

| | Total ash | Mannitol | Laminarin |
|---|---|---|---|
| Old frond | 38·8 | 4·0 | 2·7 |
| New frond | 36·7 | 8·0 | Trace |

is absent. In general, this polysaccharide is almost completely absent when there is rapid growth, i.e. in all the laminarias in the spring, in *L. digitata* at Atlantic Bridge for the greater part of the year, in the annual *Saccorhiza bulbosa* already reported, and in all the samples of *Macrocystis pyrifera*, *Nereocystis luetkeana* and *Lessonia flavicans* so far examined.

While the percentage of laminarin in *Laminaria cloustoni* fronds is over 30 from August to December (dry basis), in *L. saccharina* and *L. digitata* it falls rapidly in September, reaching 4·7% in *L. saccharina* (open sea), 5·9% in *L. saccharina* (loch) and 7·5% in *L. digitata* (open sea). Parke (1948, and private communication) has found that growth in *L. saccharina* and *L. digitata* continues at a greater rate during summer and autumn than in *L. cloustoni*. With *L. cloustoni* fronds there was practically no growth from July to December in the sublittoral fringe zone, which confirms the author's suggestion that laminarin is generally found when there is 'restricted growth'.

In March, therefore, we find the algae high in proteins and alginic acid with

the cell sap high in mineral matter and low in carbohydrates, which have been used up during the winter in respiration and probably in the synthesis of amino-acids. In the spring a rapid increase in the rate of photosynthesis occurs accompanied by an increase in the mannitol content and a decrease in the ash content, while rapid growth of the plant results in a decrease in the crude protein content. A decrease in alginic acid occurs as a result of this increase in mannitol. As summarized in Fig. 19, when the results are calculated on the anhydrous basis, ash, proteins and alginic acid are at a maximum and mannitol and laminarin at a minimum at the beginning of the spring, while in the autumn the reverse is true.

In the first 2 years investigated, with the exception of *L. digitata* in 1948, a break or flattening out of the mannitol graph for the fronds occurs in July–August of each year. This coincides with (*a*) a slowing up in the rate of growth, (*b*) the absence of nutrients in the waters, and (*c*) the probable period of sporogenesis in the case of *L. digitata* and *L. saccharina*, so that these factors together with light which is at its maximum intensity at this time are all contributory factors influencing the chemical composition of the algae.

*Fronds* *Laminaria cloustoni*

In May 1947 the dry-weight content is at a minimum of 13·3% (Fig. 2), laminarin is at a minimum of 1·0% (Fig. 1), while the total ash is at a maximum 37·6% (Fig. 1). At this period the new frond has probably taken over photosynthesis and the old frond has been cast. The new frond contains 14·2% mannitol (Fig. 3) and 11·8% crude proteins (Fig. 4), the mannitol having been at a minimum in March (6·4%) and the proteins at a maximum (15%), while the alginic acid was also at a maximum (19·3%).

As the ash falls to a minimum of 13% in September-October the dry-weight content reaches a maximum of 32% in September, the alginic acid a minimum of 8%, and the laminarin a maximum of 32·4%, the ash graph (Fig. 1) being the inverse of the laminarin graph.

In 1948, maxima and minima of the same order of magnitude occur at approximately the same periods, with the exception of mannitol which is 25% from June to August compared with a maximum of 22·9% in August 1947. In general, the laminarin, dry weight and mannitol are parallel, showing minima in the spring and maxima in the autumn, while the ash, crude proteins and alginic acid are the reverse, showing maxima in the spring and minima in the autumn.

In Fig. 6 the ash graphs for the 4 years investigated are given and show that the results are reproducible within a month, e.g. an ash content of 30% occurs in June–July in 1945, 1947 and 1948, and in July–August in 1946.

The only striking difference in the composition of the fronds during the 4 years now investigated is in the laminarin content which progressively increases each year from 29% in 1945 to 34% in 1948, while later work to be

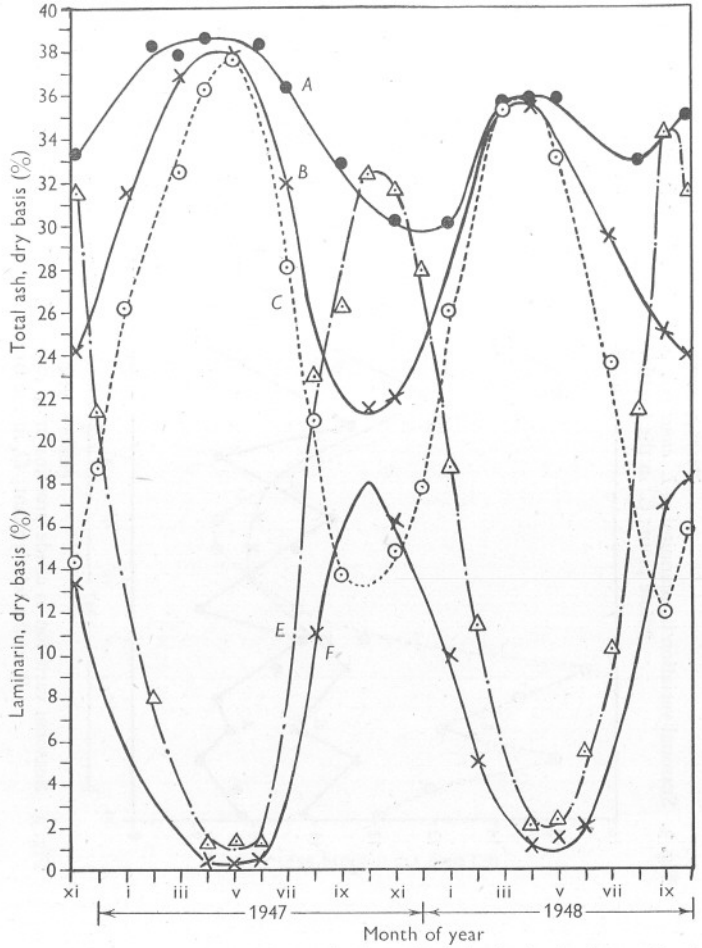


Fig. 1. Seasonal variation in total ash and laminarin in *L. cloustoni*. *A*, total ash in the stipes; *B*, total ash in whole plant; *C*, total ash in the fronds; *E*, laminarin in the fronds; *F*, laminarin in the whole plant.

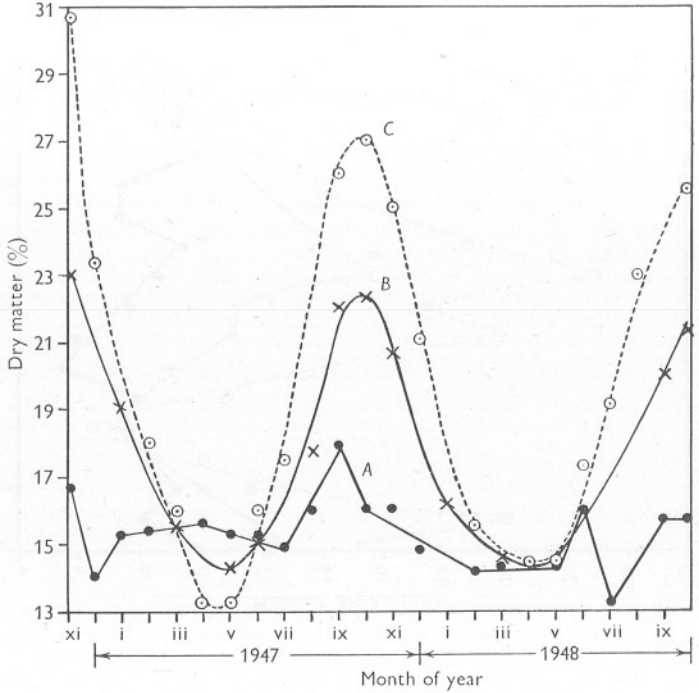


Fig. 2. Seasonal variation in dry matter in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plants; *C*, in the fronds.

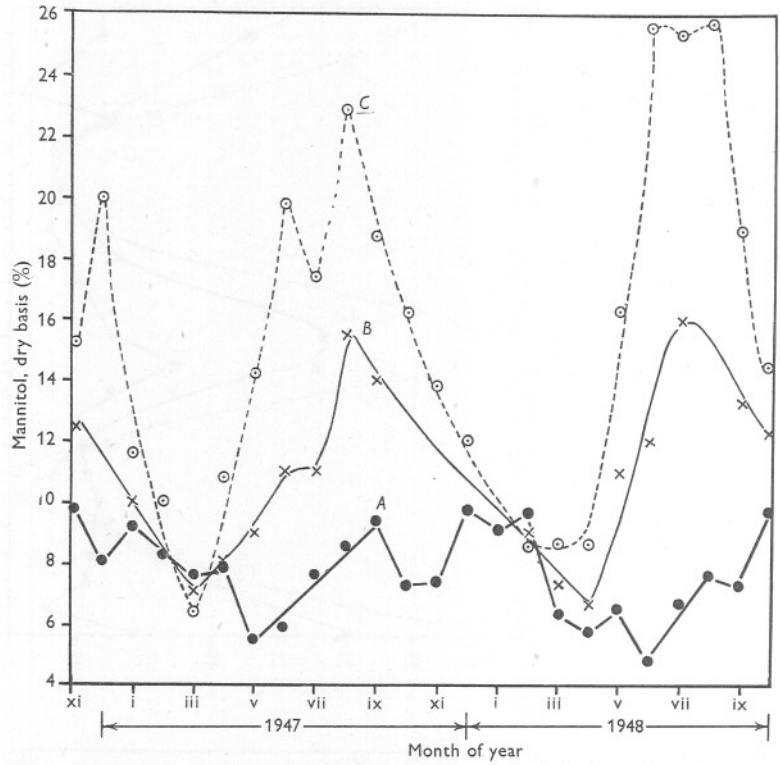


Fig. 3. Seasonal variation in mannitol in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plant; *C*, in the fronds.

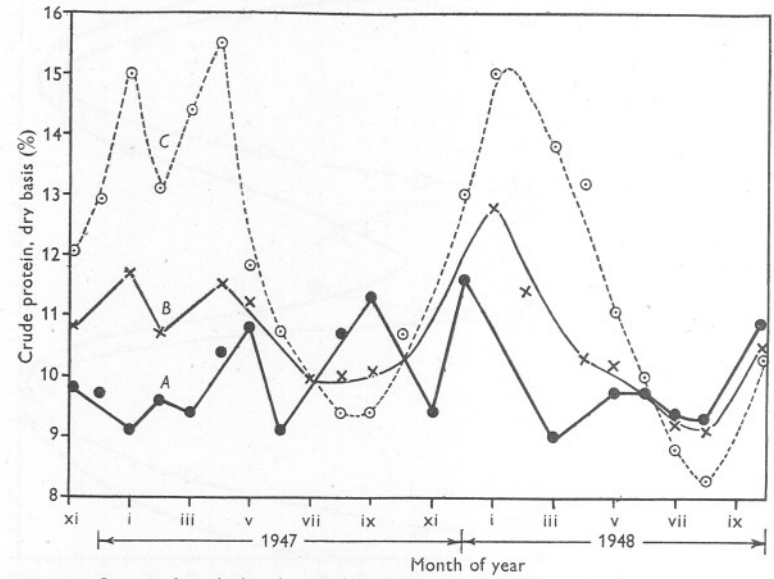


Fig. 4. Seasonal variation in crude proteins in *L. cloustoni*. A, in the stipes; *B*, in the whole plant; *C*, in the fronds.

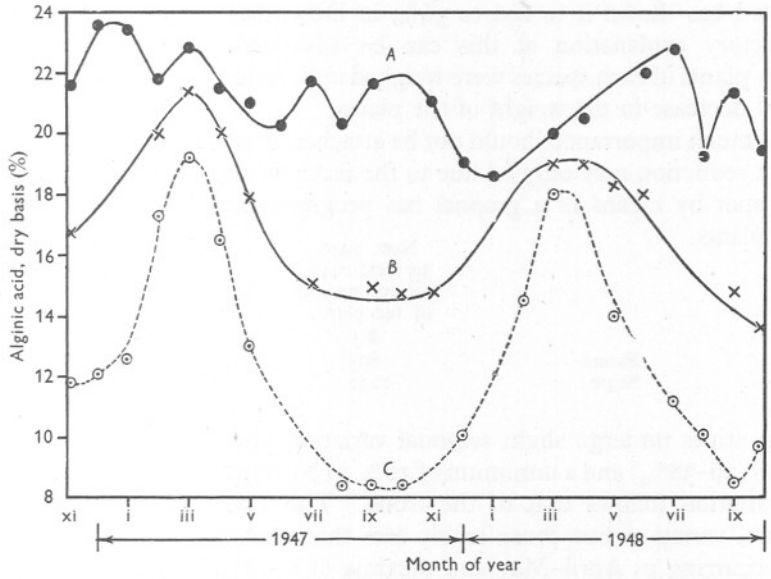


Fig. 5. Seasonal variation in alginic acid in *L. cloustoni*. *A*, in the stipes; *B*, in the whole plant; *C*, in the fronds.

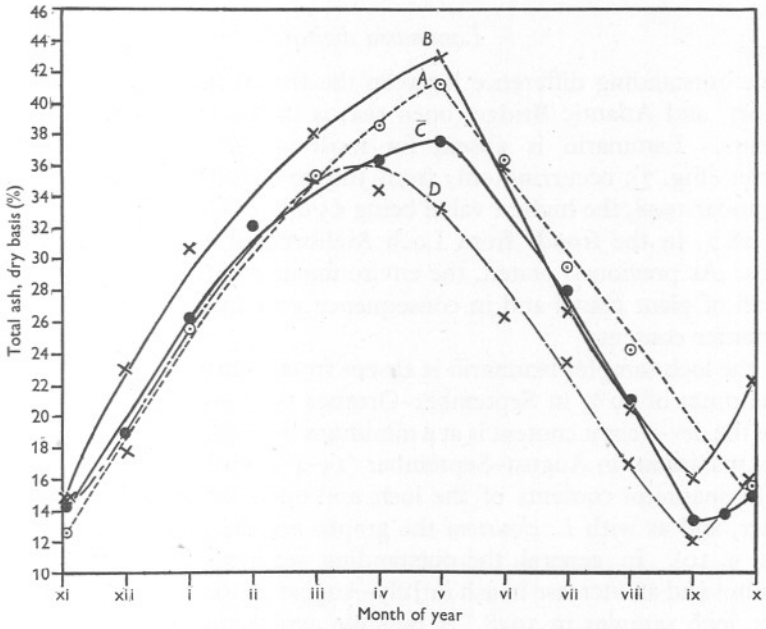


Fig. 6. Seasonal variation in total ash in *L. cloustoni* fronds. *A*, 1944–1945; *B*, 1945–1946; *C*, 1946–1947; *D*, 1947–1948.

reported has shown it to rise to 36% in December 1948–January 1949. No satisfactory explanation of this can be advanced. However, each month twenty plants of each species were weighed and the results indicate a progressive annual decrease in the weight of the plants.

Too much importance should not be attached to such figures, as the apparent weight reduction may only be due to the fact that repeated sampling from the same spot by means of a grapnel has progressively removed the larger and older plants.

| | Nov. 1946 to Oct. 1947 Average weight of 240 plants (g.) | Nov. 1947 to Oct. 1948 Average weight of 240 plants (g.) |
|---|---|---|
| Frond | 693 | 656 |
| Stipe | 1231 | 1141 |

*Stipes*

The stipes undergo slight seasonal variation, the ash being at a maximum in May (36–38%) and a minimum of 30% in November–December; in general, the variation follows that of the frond. The mannitol graph also shows seasonal variation but considerably less than that in the fronds, minima of 5% occurring in April–May and maxima of 9–10% in September–October. The dry weight content, however, shows very little variation (13–18%; Fig. 2).

The alginic acid shows no regular variation and fluctuates between 19 and 24%.

## *Laminaria digitata*

*Fronds*

The outstanding difference between the fronds from Eilean Coltair (Loch Melfort) and Atlantic Bridge (open sea) is in the laminarin and dry-weight contents. Laminarin is absent for most of the year from the open-sea samples (Fig. 7), occurring only from July to October 1947 and from August to October 1948, the highest value being 15·6% in October 1948, as compared with 28% in the fronds from Loch Melfort and over 30% in *L. cloustoni* fronds. As previously stated, the environment at Atlantic Bridge favours the growth of giant plants and in consequence very little variation occurs in the dry matter content.

In the loch samples laminarin is absent from February to April, and reaches a maximum of 20% in September–October 1947 and 28% in October 1948, while the dry-weight content is at a minimum from January to March (11–12%) and a maximum in August–September (23–4%) in both 1947 and 1948.

The mannitol contents of the loch and open-sea samples are remarkably similar, and as with *L. cloustoni* the graphs are the inverse of the ash graphs (Figs. 9, 10). In general, the outstanding features are a temporary drop in mannitol and an increase in ash in July–August of 1947, and at the same period in the loch samples in 1948. A possible explanation of this is advanced in a recent publication (Black & Dewar, 1949).

The crude-protein graphs (Fig. 15) are very similar for loch and open-sea samples, exhibiting maxima of 12–14% between February and April and

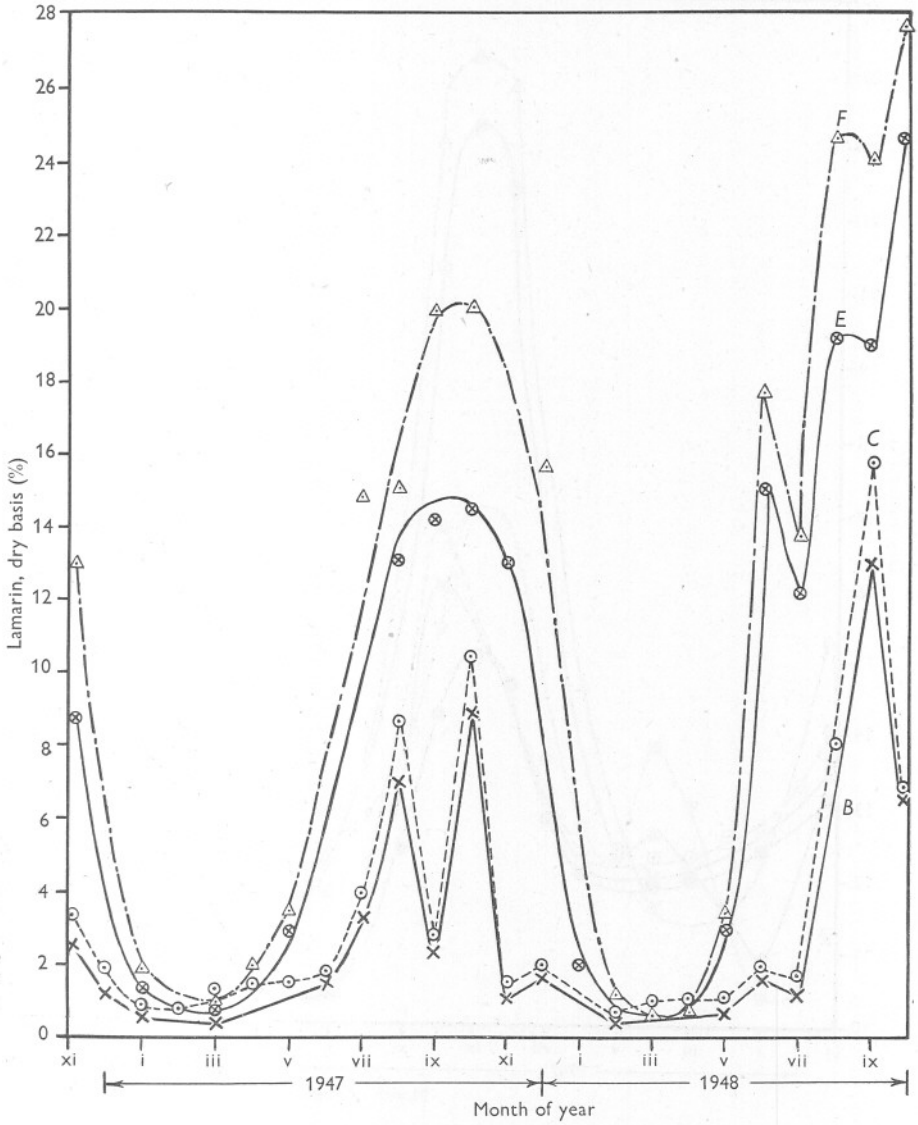


Fig. 7. Seasonal variation in laminarin in *L. digitata*. *B*, open-sea whole plant; *C*, open-sea fronds; *E*, loch whole plant; *F*, loch fronds.

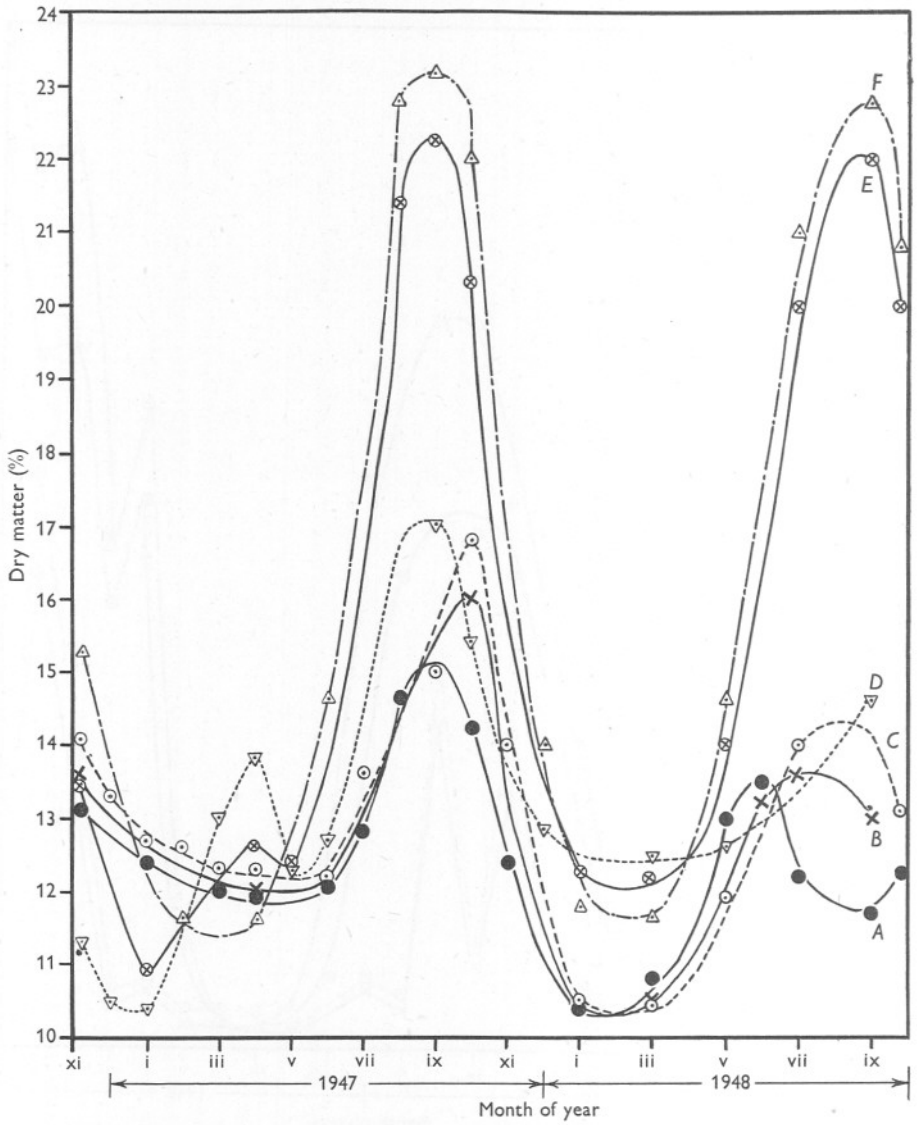


Fig. 8. Seasonal variation in dry-matter content in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch stipes; *E*, loch whole plant; *F*, loch fronds.

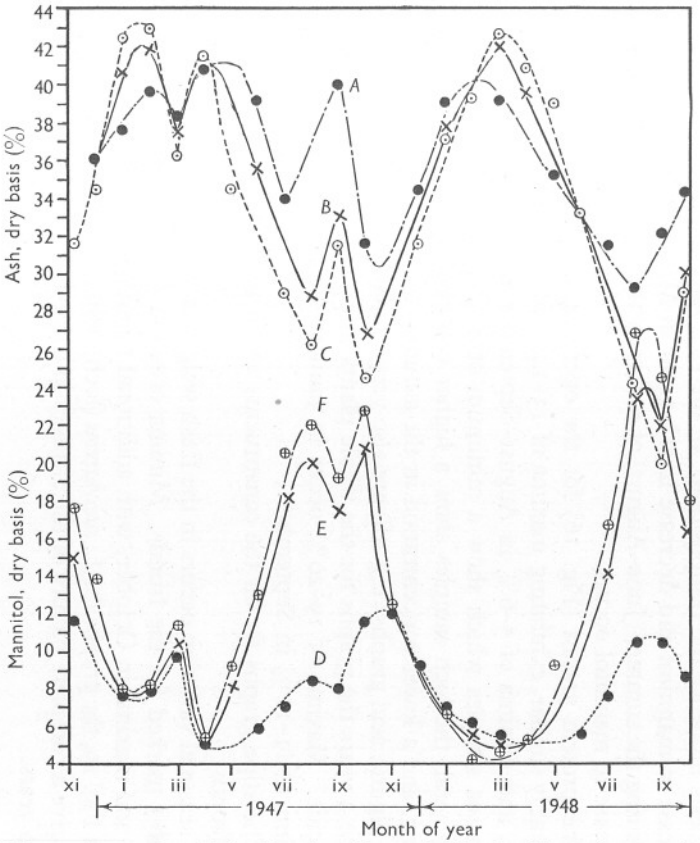


Fig. 9. Seasonal variation in ash and mannitol in *L. digitata* (open sea). *A*, ash in the stipes; *B*, ash in the whole plant; *C*, ash in the fronds; *D*, mannitol in the stipes; *E*, mannitol in whole plant; *F*, mannitol in the fronds.

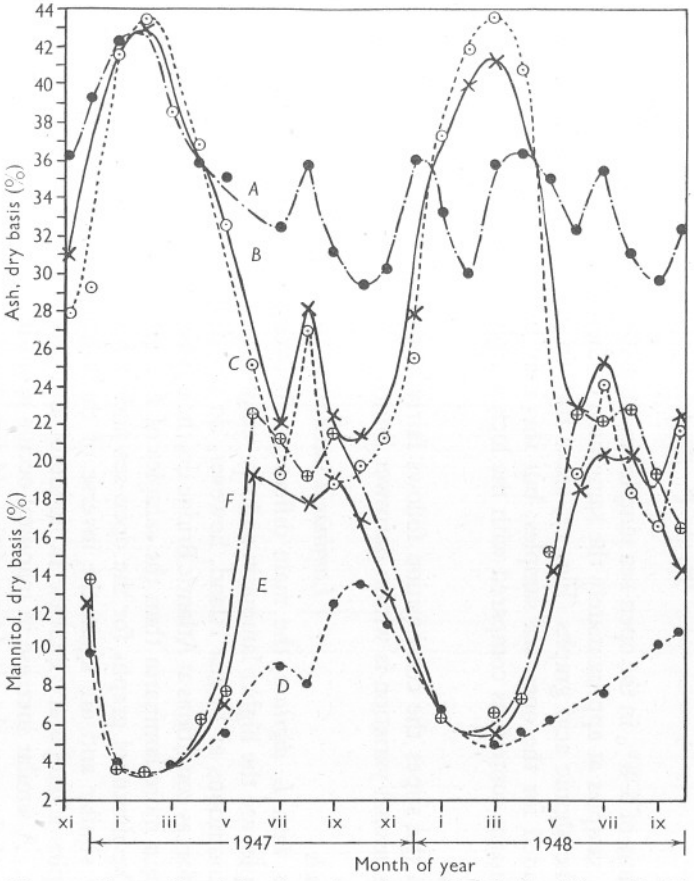


Fig. 10. Seasonal variation in ash and mannitol in *L. digitata* (loch). *A*, ash in the stipes; *B*, ash in whole plant; *C*, ash in the fronds; *D*, mannitol in the stipes; *E*, mannitol in the whole plant; *F*, mannitol in the fronds.

minima of 6–8% in the open-sea samples in August–October, and 4–6% in the loch samples at approximately the same time of the year.

The alginic acid graphs (Fig. 17) show that, in general, higher values are obtained for the open-sea samples, but this may be the result of the lower laminarin content as compared with the loch samples.

*Stipes*

In the stipes the composition follows fairly closely that of the fronds but the seasonal variation is within narrower limits.

*Laminaria saccharina*

*Fronds*

As with *L. digitata*, the main differences between the open-sea and loch samples are the higher laminarin and dry-weight contents of the loch samples. As conditions at Shuna Island, however, do not differ so much from Loch Melfort as conditions at Atlantic Bridge do, the open-sea samples of *L. saccharina* contain more laminarin than the samples of *L. digitata* from Atlantic Bridge.

The mannitol graphs for the open-sea and loch samples (Figs. 13, 14) are very similar and are again the inverse of the ash graphs. In the open-sea samples a temporary increase in mannitol and drop in ash occur in March 1947. A similar increase in mannitol occurs again in March 1948, but at this time of the year the shedding of the old frond and a rapid increase in photosynthesis influence the composition. In the loch samples a similar temporary increase in mannitol and decrease in ash occur in March 1947.

During the summer (June–August) of each year the characteristic temporary decrease in mannitol occurs.

The protein graphs (Fig. 16) for the open-sea and loch samples are remarkably similar, exhibiting maxima of 13–14% in February–March of each year, and minima of 5–6% in August–September with the exception of the open-sea samples which show a minimum of 8% in July–September 1947. In general, the loch samples show a higher concentration of proteins in the spring, and a lower concentration in the autumn, than the open-sea samples. The alginic acid graphs (Fig. 18) are also very similar, and for the greater part of the 2 years the graphs for the whole plants from the two localities actually coincide. Maxima of 19–20% occur in January–February of each year and minima of 11–12% in September.

The stipe graphs for all the constituents are in general parallel to those of the fronds.

A seasonal variation occurs in the fresh weight of the plants (Fig. 20) which is most marked for the fronds. Minima occur in January–February of each year and maxima in October, with additional maxima in July 1948.

In Fig. 19, the graphs for *L. saccharina* (loch), whole plant, are superimposed and give a complete picture of the changes in composition which occur during the 2 years.

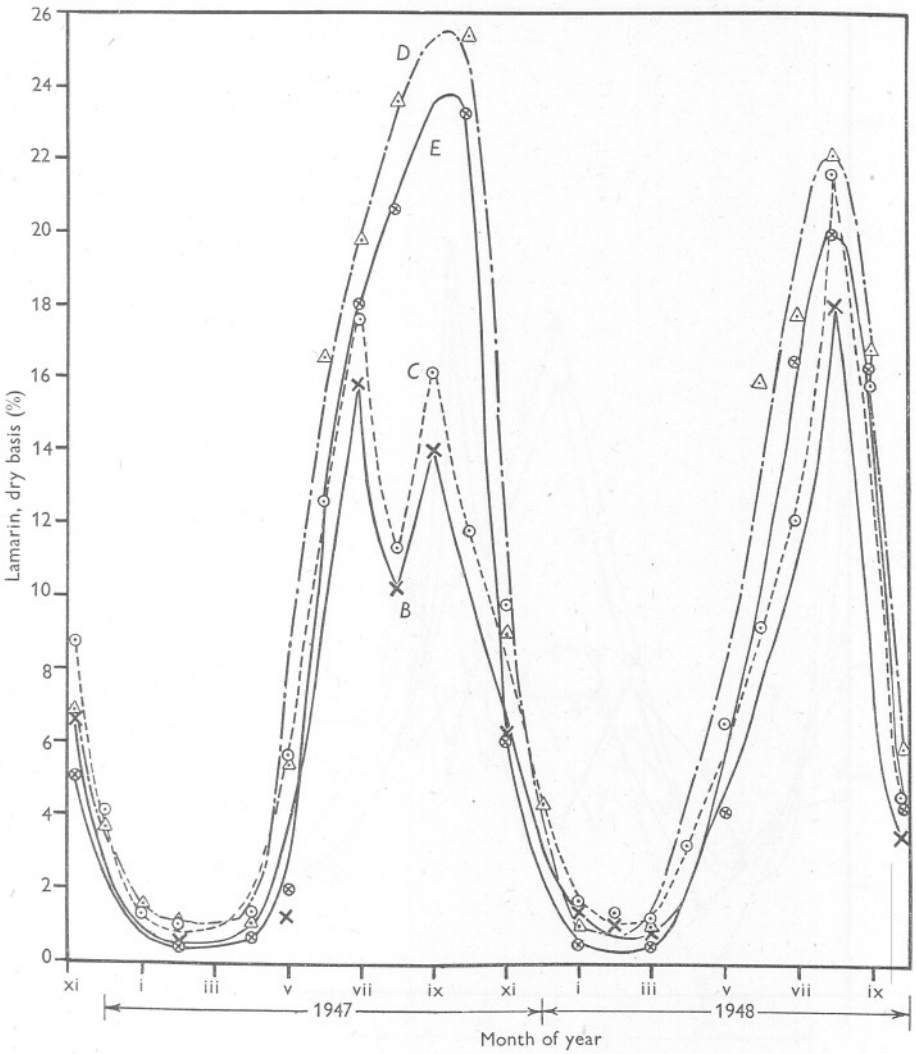


Fig. 11. Seasonal variation in laminarin in *L. saccharina*. *B*, in the open-sea whole plants; *C*, in the open-sea fronds; *E*, in the loch whole plants; *D*, in the loch fronds.

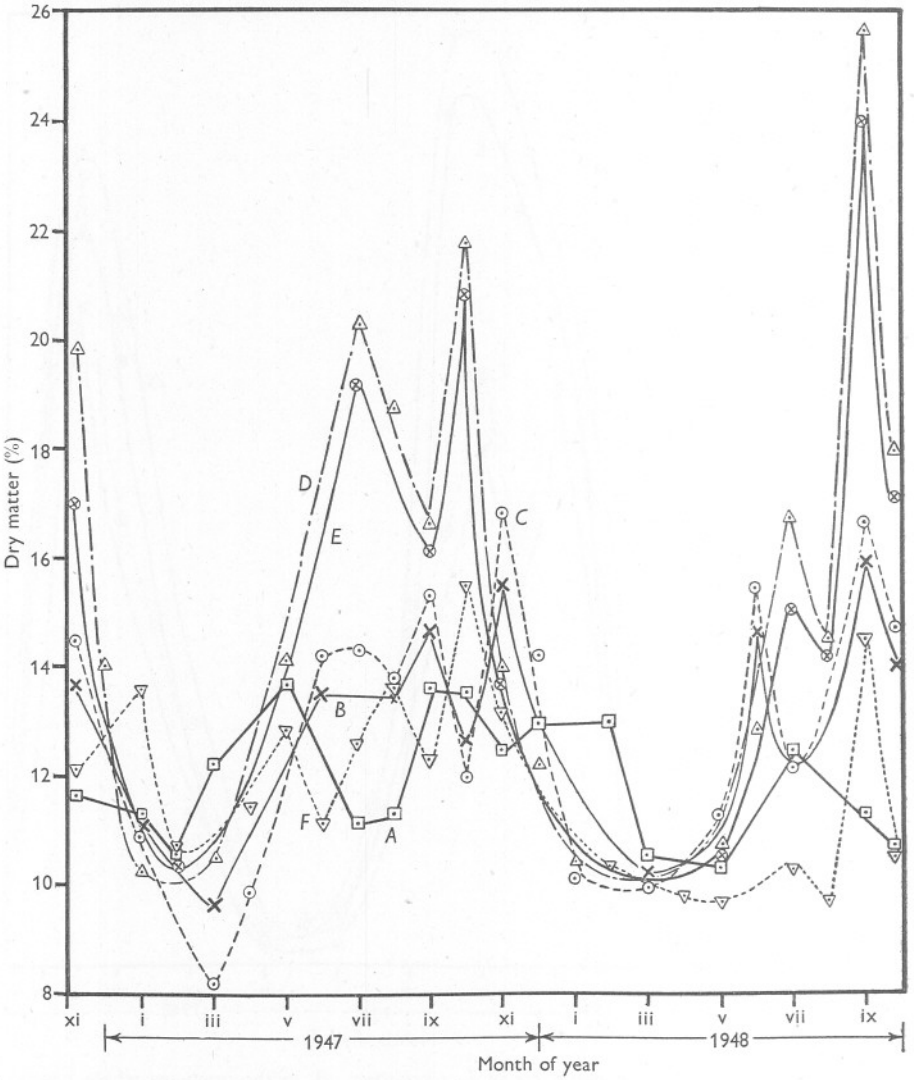


Fig. 12. Seasonal variation in dry matter in *L. saccharina*. *A*, in the open-sea stipes; *B*, in the open-sea whole plants; *C*, in the open-sea fronds; *D*, in the loch fronds; *E*, in the loch whole plants; *F*, in the loch stipes.

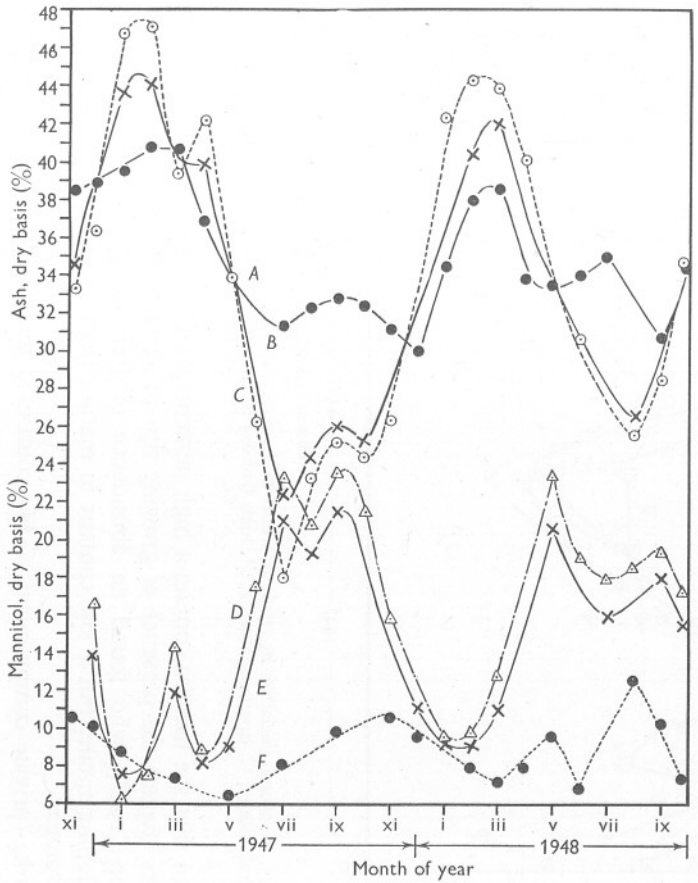


Fig. 13. Seasonal variation in ash and mannitol in *L. saccharina* (open sea). *A*, ash in the stipes; *B*, ash in the whole plant; *C*, ash in the fronds; *D*, mannitol in the fronds; *E*, mannitol in the whole plant; *F*, mannitol in the stipes.

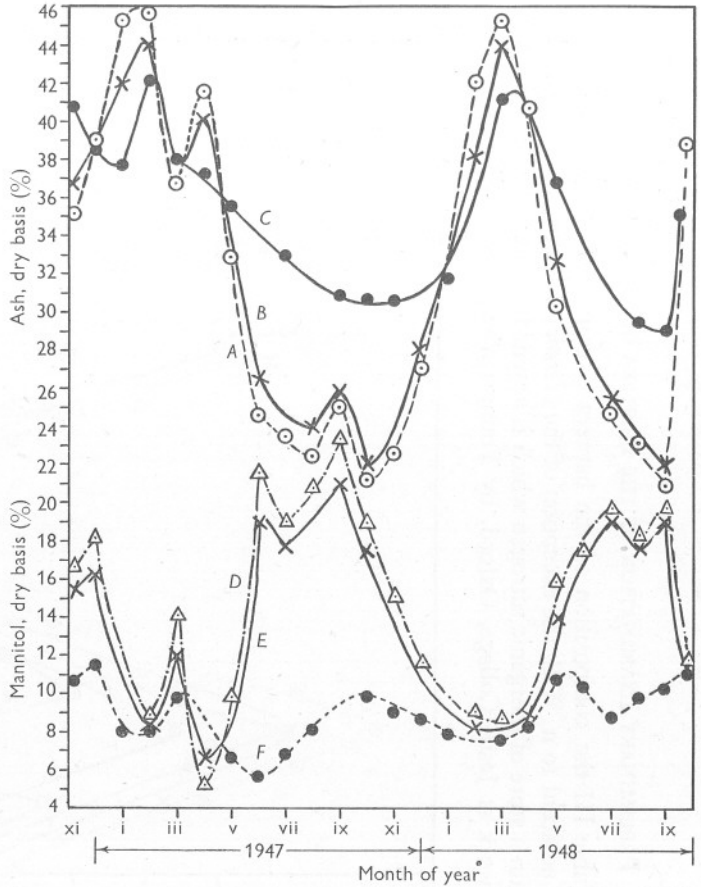


Fig. 14. Seasonal variation in ash and mannitol in *L. saccharina* (loch). *A*, ash in the fronds; *B*, ash in the whole plant; *C*, ash in the stipes; *D*, mannitol in the fronds; *E*, mannitol in the whole plant; *F*, mannitol in the stipes.

## Preliminary Examination of the Haptera of the Laminarias

In Table III the composition of the haptera is compared with that of the stipe adjacent to it. With the exception of the *Nereocystis* stipe the haptera all contain a store of inorganic nitrogen which is absent from the adjacent stipes, and work at Jesus College, Oxford, by Young (private communication) has

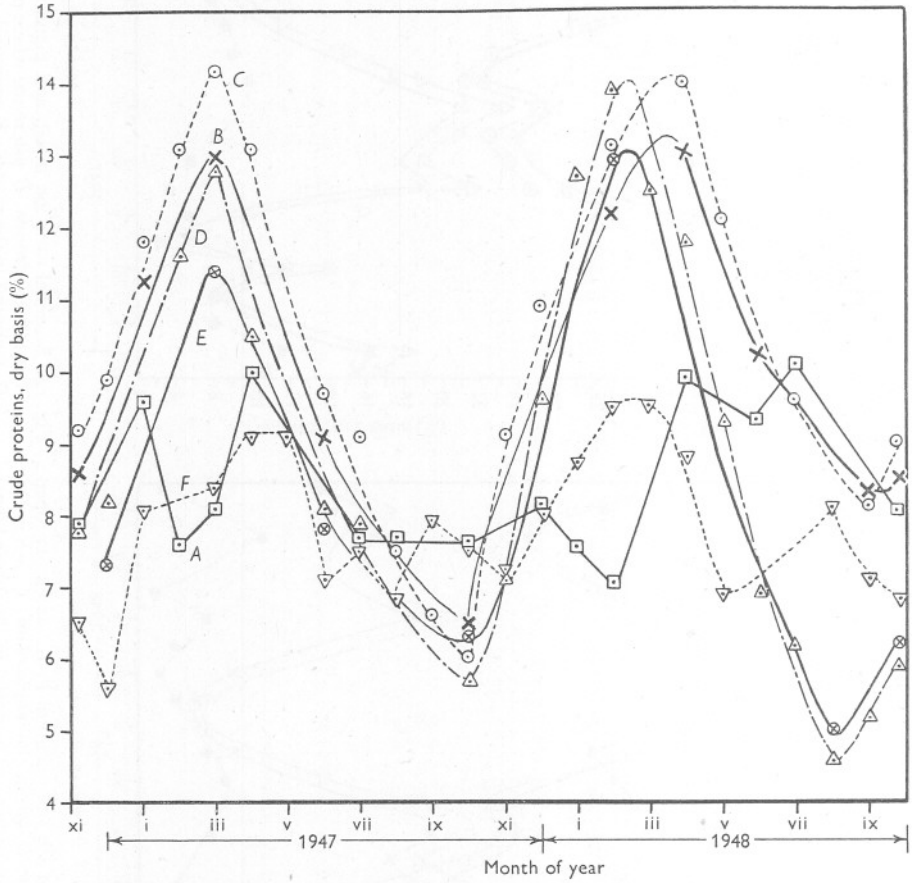


Fig. 15. Seasonal variation in crude proteins in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

shown that the haptera contain a high percentage of free amino-acids. These results suggest the presence of growing tips in agreement with the result of Allsop (1948), who found an abundance of free amino-acids in actively developing tissue, but a low content in mature tissues not specially adapted for storage.

Parke (private communication) has confirmed that the haptera develop as

TABLE III. COMPOSITION OF THE HAPTERA OF THE LAMINARIACEAE *LAMINARIA CLOUSTONI*, *L. DIGITATA* AND *L. SACCHARINA*, AND *NEREOCYSTIS LUETKEANA* (DRY BASIS).

| Sample | Date and place of collection | Total ash | Mannitol | Laminarin | Alginic acid | Crude proteins | In-organic nitrogen |
|---|---|---|---|---|---|---|---|
| *L. cloustoni*, holdfast | July 1948, Cullipool | 34·1 | 6·0 | < 1·0 | 6·6 | 14·0 | 0·17 |
| *L. cloustoni*, stipe adjacent | July 1948, Cullipool | 35·9 | 6·7 | < 1·0 | 22·9 | 9·4 | Nil |
| *L. digitata*, holdfast | Oct. 1948, Atlantic Bridge | 32·4 | 8·4 | < 1·0 | 18·8 | 15·3 | 0·20 |
| *L. digitata*, stipe adjacent | Oct. 1948, Atlantic Bridge | 34·2 | 8·6 | < 1·0 | 30·6 | 8·1 | Nil |
| *L. saccharina*, holdfast | Oct. 1948, Shuna Island | 37·3 | 7·4 | < 1·0 | 7·5 | 15·9 | 0·18 |
| *L. saccharina*, stipe adjacent | Oct. 1948 Shuna Island | 34·6 | 7·3 | < 1·0 | 24·9 | 9·1 | Nil |
| *N. luetkeana*, holdfast | Oct. 1948, San Juan, Wash., U.S.A. | 39·0 | 1·2 | < 1·0 | 6·9 | 16·3 | 0·41 |
| *N. luetkeana*, stipe adjacent | Oct. 1948, San Juan, Wash., U.S.A. | 40·8 | 1·2 | < 1·0 | 13·8 | 5·8 | 0·29 |

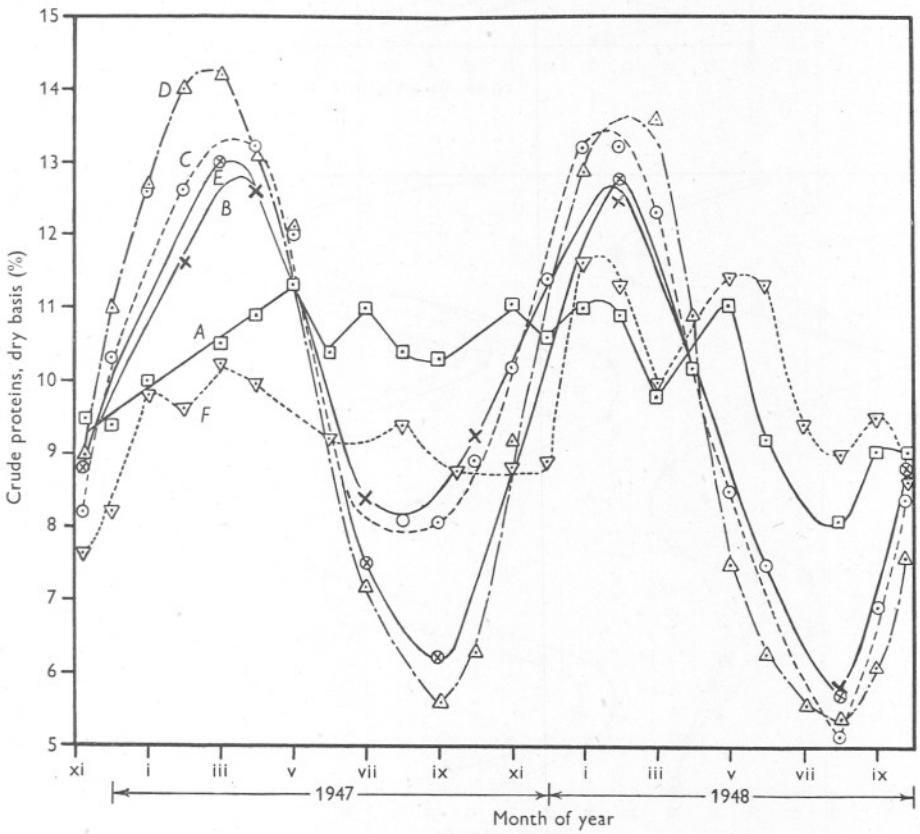


Fig. 16. Seasonal variation in crude proteins in *L. saccharina*. *A*, open-sea stipes; *B*, open-sea whole plants; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

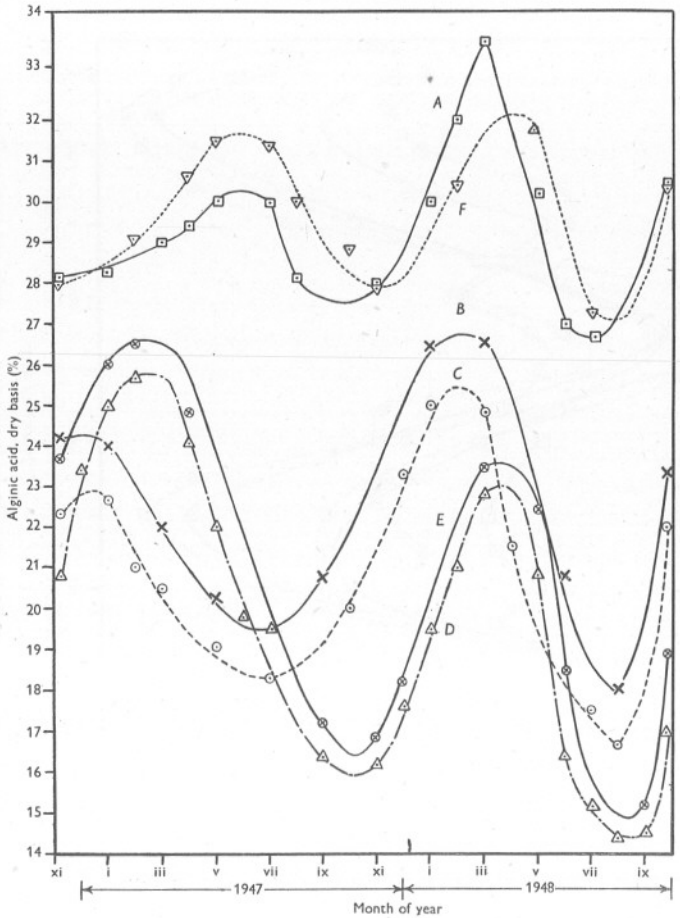


Fig. 17. Seasonal variation in alginic acid in *L. digitata*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

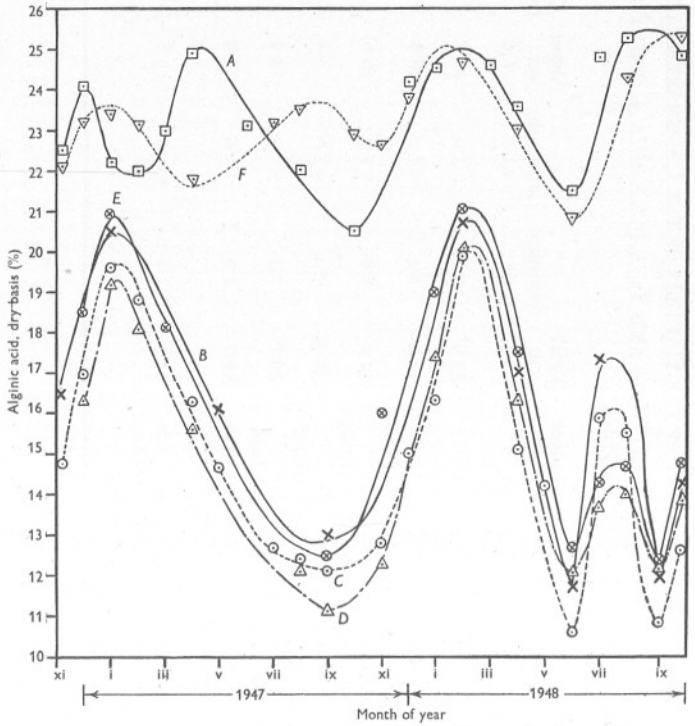


Fig. 18. Seasonal variation in alginic acid in *L. saccharina*. *A*, open-sea stipes; *B*, open-sea whole plant; *C*, open-sea fronds; *D*, loch fronds; *E*, loch whole plants; *F*, loch stipes.

outgrowths from a meristematic layer on the outside of the stipe, and once they start to form the tips can be regarded as growing tips.

It is interesting to note the low percentage of alginic acid, when determined by the standard method (Black, 1948). When the method was modified so that after soaking in acid the sodium carbonate was added without filtering off the

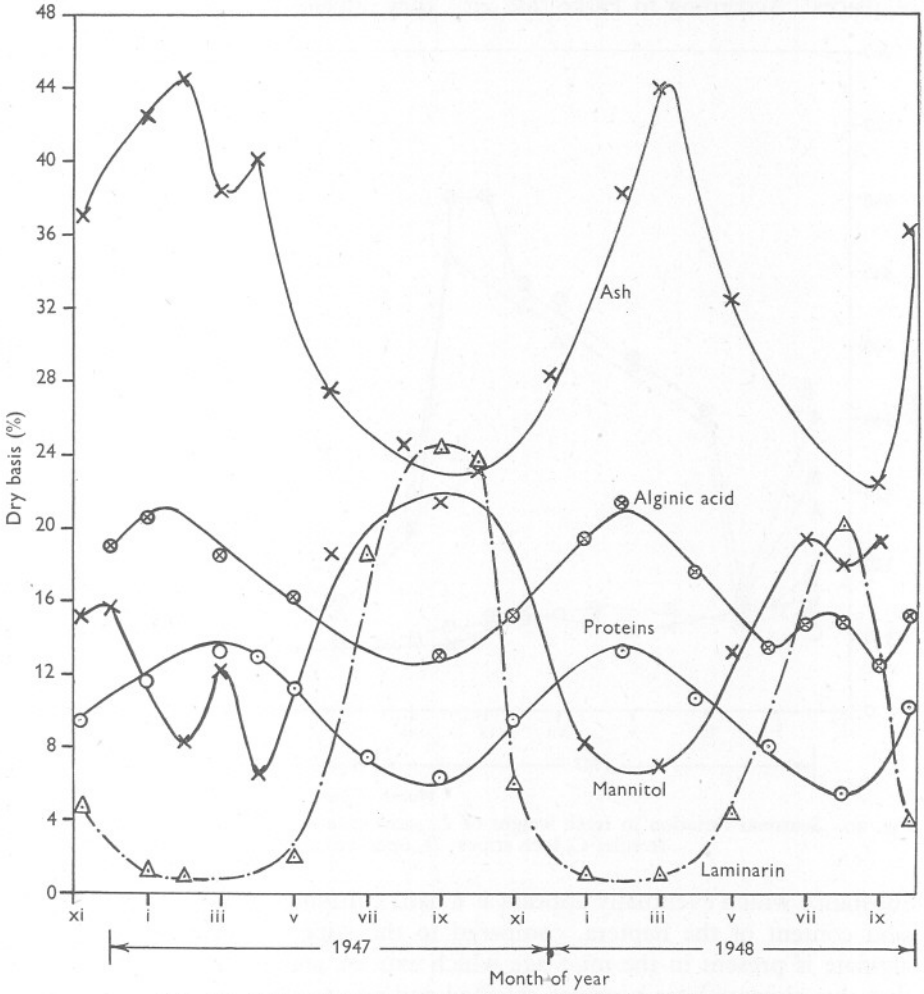


Fig. 19. Seasonal variation in *L. saccharina* (loch) whole plant.

weak acid solution, a result of 14·8% was obtained for the haptera of *Laminaria cloustoni*. When the alginic acid was determined by the carbazole method of Percival & Ross (1948*b*) a figure of 20·4% was obtained. The results indicate that in the haptera there is present either a water-soluble or a very low-grade alginate which requires further investigation.

The results show, however, that the haptera of *L. digitata* are considerably higher in alginic acid than those of *L. cloustoni* and *L. saccharina*, which may account for the very firm attachment which the holdfast of *L. digitata* has for the substratum.

The haptera as they touch the substratum become attached in a number of places. According to Parke (*loc. cit.*) they appear to secrete some sticky

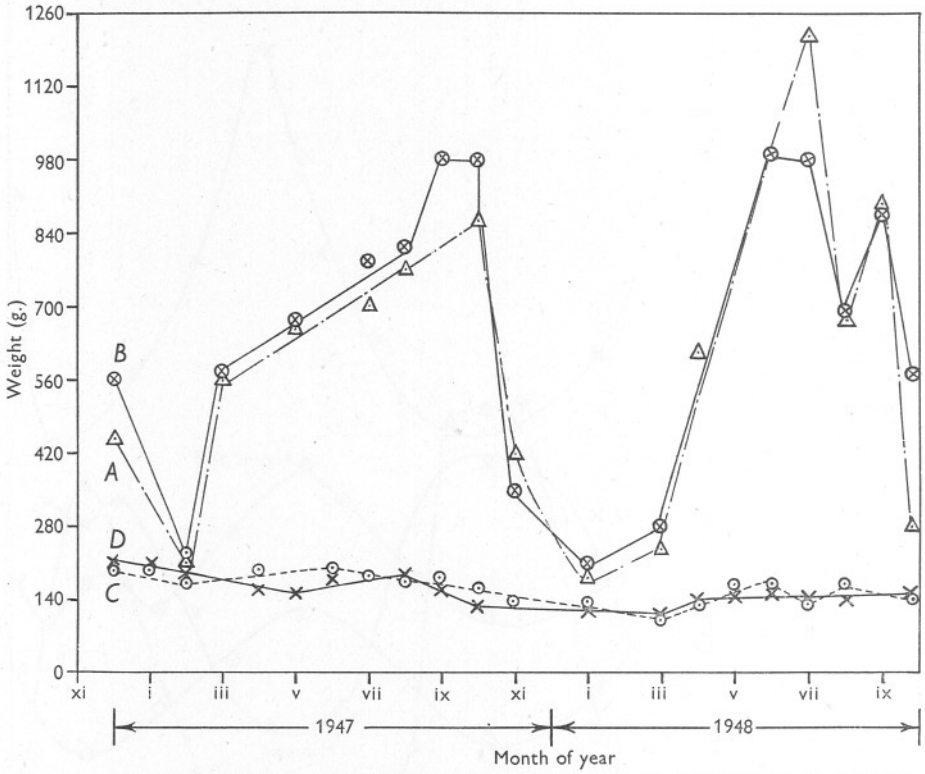


Fig. 20. Seasonal variation in fresh weight of *L. saccharina* in *A*, loch fronds; *B*, open-sea fronds; *C*, loch stipes; *D*, open-sea stipes.

substance which eventually appears as a hard chitinous layer. The low alginic acid content of the haptera, compared to the stipe, might indicate that an alginate is present in the mucilage which exudes, and there is the possibility that this alginate later becomes calcified and assists in cementing the haptera to the substratum.

## Summary

The seasonal variations in the total ash, crude proteins, mannitol, laminarin and alginic acid contents are given for monthly samples of the Laminariaceae, *L. cloustoni*, *L. digitata* and *L. saccharina* from November 1946 to October

1948, samples of *L. digitata* and *L. saccharina* having been taken at different localities to determine the effect, if any, of the degree of exposure on the chemical composition.

The results agree favourably with those of the first 2 years examined and indicate that, with only a few exceptions, results might be reproducible in the corresponding season of any year, and it should be possible, therefore, to predict the approximate composition in subsequent years.

As before, the marked seasonal variations in chemical constitution occur in the fronds, where the bulk, if not all, of the photosynthesis occurs. The stipes undergo some variation parallel to that in the fronds, but within narrower limits, while laminarin is absent throughout the year.

In the fronds in the spring, mannitol is at a minimum and laminarin is absent, while the crude proteins, ash and alginic acid are at a maximum. In the autumn the reverse is true. The dry-matter content shows a corresponding variation, being at a minimum in the spring and a maximum in the autumn, but the variation is greatest in the loch samples and in *L. cloustoni* at Cullipool.

In the case of *L. digitata* and *L. saccharina*, the main effect of different degrees of exposure is that in the plants from the more sheltered localities (lochs) the laminarin and consequently the dry-weight contents are higher than in the more exposed samples, which might indicate 'restricted' growth in the lochs.

The fresh weight of the plants undergoes a similar seasonal variation, being at a minimum in the spring and a maximum in late summer.

A preliminary examination of the haptera has been carried out, and indicates a high inorganic nitrogen and free amino-acid content, while there is evidence of the presence of a lower grade alginate than is present in the adjacent stipe.

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# A NOTE ON THE BARNACLE LARVAE OF THE CLYDE SEA AREA AS SAMPLED BY THE HARDY CONTINUOUS PLANKTON RECORDER

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In the course of an extensive series of tests on the Hardy Continuous Plankton Recorder (Hardy, 1939) carried out in the Clyde Sea Area during March and April 1949, a number of runs were made both during the time of the spring diatom outburst and over the period when barnacle larvae were a dominant feature of the zooplankton. It should be emphasized that the work was originally planned not as a plankton study but only as an investigation of the comparative performance of a number of recorders. Nevertheless, the limited data on cirripede larvae do give some quantitative information regarding the distribution and the total population of barnacle larvae over a moderately large area, and the quantitative relations of the stages, as well as providing some evidence bearing upon the hypothesis that the diatom outburst is a controlling factor in the development of the later stage larvae.

Since the results of these tests have not yet been published the following points regarding the performance of these recorders may be mentioned:

(1) The excellent depth-keeping properties of the machines have been fully confirmed; a constant depth of $10 \pm 0{\cdot}5$ m. was maintained over long distances by both machines under test.

(2) The amount of water filtered is probably the theoretical volume, since great increase in filtering surface (obtained by fitting large nets inside the machines) gave no significant increase in catch. This was true even with clogging which became apparent during the diatom outburst. It should, however, be remembered that the diatom was largely *Skeletonema costatum*; quantities of larger phytoplankton species could lead to incomplete filtration.

Thanks are due to Mr W. W. Brown who took part in the recorder investigations, to Mr M. W. H. Bishop for confirming the identity of the larval stages counted, and to Captain Stewart and the crew of the *Calanus* for their willing help in all the boat work.

## The Collection and Counting of the Material

The plankton recorders were towed together in pairs under varying experimental conditions, and a statistical examination of the results has shown that in none of the tows here quoted was there any significant difference in the performance of the two machines. In Table I, therefore, only the mean catch

TABLE I. CIRRIPEDE LARVAE FROM THE CLYDE SEA AREA POPULATION, EARLY SPRING 1949; TOTAL CATCHES AND THEIR COMPOSITION

| | | Total catch cirripede larvae | | The percentages stages, (i) *B. balanoides*, (ii) *B. crenatus* from subsample counts | | | | | | | Estimated numbers in original sample | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Run | Nauplii | Cyprids | | Cyprids | VI | V | IV | III | II+I | Cyprids | VI | V | IV | III | II+I |
| 21. iii. 49 | 2 | 1839 | 6 | (i) | 0·2 | 3·4 | 7·3 | 9·6 | 36·3 | 14·4 | 4 | 62 | 132 | 174 | 657 | 261 |
| | 3 | 1776 | 0 | (ii) | 0·6 | 1·1 | 7·3 | 5·2 | 7·8 | 1·6 | 11 | 20 | 132 | 94 | 141 | 29 |
| | 4 | 1418 | 5 | (i) | 0·9 | 4·6 | 16·4 | 14·5 | 34·6 | 17·3 | 13 | 66 | 233 | 206 | 492 | 246 |
| | | | | (ii) | 0·0 | 3·3 | 2·3 | 1·4 | 1·9 | 1·9 | 0 | 47 | 33 | 20 | 27 | 27 |
| | 5 | 2230 | 14 | (i) | 0·2 | 5·1 | 16·4 | 19·3 | 29·9 | 9·2 | 5 | 114 | 368 | 433 | 671 | 207 |
| | | | | (ii) | 0·1 | 4·6 | 5·3 | 3·4 | 2·1 | 0·7 | 2 | 103 | 119 | 76 | 47 | 16 |
| 22. iii. 49 | 6 | 1504 | 2 | (i) | 0·4 | 3·2 | 13·8 | 11·5 | 39·6 | 14·3 | 6 | 48 | 208 | 173 | 596 | 215 |
| | | | | (ii) | 0·0 | 5·1 | 1·9 | 6·5 | 1·4 | 0·1 | 0 | 77 | 29 | 98 | 21 | 2 |
| | 7 | 1337 | 3 | (i) | 0·4 | 1·9 | 13·0 | 12·2 | 30·5 | 17·1 | 5 | 26 | 174 | 164 | 409 | 229 |
| | | | | (ii) | 0·0 | 7·4 | 5·2 | 6·3 | 3·5 | 0·7 | 0 | 99 | 70 | 84 | 47 | 9 |
| 23. iii. 49 | 8 | 1848 | 10 | (i) | 0·7 | 3·3 | 12·8 | 24·1 | 34·8 | 11·1 | 13 | 61 | 238 | 448 | 647 | 206 |
| | | | | (ii) | 0·0 | 1·9 | 1·9 | 2·2 | 1·4 | 0·1 | 0 | 35 | 35 | 41 | 26 | 2 |
| | 9 | 2886 | 27 | (i) | 0·2 | 2·8 | 12·7 | 27·8 | 28·7 | 5·7 | 6 | 82 | 370 | 810 | 836 | 166 |
| | | | | (ii) | 0·0 | 6·4 | 5·3 | 5·3 | 1·7 | 0·2 | 0 | 186 | 154 | 154 | 50 | 6 |
| | 10 | 2959 | 27 | (i) | 0·2 | 2·6 | 7·5 | 27·5 | 24·2 | 10·1 | 6 | 78 | 224 | 821 | 723 | 302 |
| | | | | (ii) | 0·4 | 5·2 | 4·2 | 5·4 | 6·3 | 2·1 | 12 | 155 | 125 | 161 | 188 | 63 |
| | 11 | 3633 | 46 | (i) | 0·3 | 3·0 | 8·6 | 24·1 | 24·1 | 9·6 | 11 | 110 | 316 | 887 | 887 | 353 |
| | | | | (ii) | 0·8 | 7·5 | 5·3 | 8·4 | 5·1 | 1·1 | 29 | 276 | 195 | 309 | 188 | 40 |
| 4. iv. 49 | 12 | 2717 | 1888 | | | | | | | | | | | | | |
| | 13 | 2064 | 1472 | (i) | 26·9 | 19·5 | 8·7 | 4·5 | 1·4 | 0·7 | 895 | 649 | 289 | 150 | 47 | 23 |
| | 14 | 1650 | 1019 | (ii) | 10·0 | 5·3 | 5·6 | 1·9 | 0·6 | 0·3 | 338 | 176 | 186 | 63 | 20 | 10 |
| | 15 | 1326 | 1169 | | | | | | | | | | | | | |
| 5. iv. 49 | 16 | 1674 | 1475 | (i) | 42·8 | 10·9 | 4·8 | 1·6 | 0·6 | 0·1 | 1563 | 398 | 175 | 58 | 22 | 4 |
| | 17 | 2117 | 2036 | (ii) | 16·8 | 4·5 | 4·6 | 0·6 | 0·3 | 0·0 | 613 | 164 | 168 | 22 | 11 | 0 |

for the two machines on any given run is shown (columns 3 and 4). The recorders were run at their 'standard' depth of 10 m. The duration of each tow was half an hour at a speed of 8 knots (nominal), so that, neglecting the effect of tidal currents and wind, 4 nautical miles of water were filtered through the standard $\frac{1}{2} \times \frac{1}{2}$ in. nozzle, a total of 1·2 cu.m. of water per haul.

The area sampled extended from the north end of the Largs Channel to a point some 8 miles farther south, off the Little Cumbrae Island, the channel between the islands and the mainland being approximately 1 mile wide throughout this distance. The particular position of any run was not noted, the choice being dictated by considerations of convenience as regards the major project, namely the testing of the plankton recorders. The samples, therefore, although not random in the statistical sense, are probably representative of the conditions over this particular area.

For the purpose of all these tests the propellers of the machines were removed; in some the gauze remained stationary across the tunnel, whilst in others the inside mechanism was removed and a small net attached at the inner end of the fore part of the water tunnel. At the termination of each run the gauze both over the tunnel and for some distance on either side was cut out and, together with the catch, transferred to a breffit containing formalin; if a net had been used inside the recorder, it was carefully removed and the contents washed by means of a wash-bottle into a breffit.

The whole catch was first counted without sub-sampling, the barnacle larvae being recorded as nauplii and cyprids irrespective of stages or species; the mean catches per run for the two machines are shown in columns 3 and 4 of Table 1. The catches were then subsampled (some after pooling several samples) by Russell & Colman's technique (1931), and the number of the various stages of *Balanus balanoides* (Linn.) and *B. crenatus* Brug. counted in each subsample (one-tenth of the total catch). The percentages of these stages as determined from the counts of such subsamples are shown in columns 5–10. An estimate of the actual numbers of the various stages present in the original sample (single or pooled) was then calculated from these percentages and the mean value of the total number in the original sample or samples, and these estimates are given in columns 11–16.

The 'standard' gauze (60 mesh) was used in the recorders, and a microscopic examination of such gauze showed the holes to be approximately square and between 0·2 and 0·25 mm. in cross-section. Pyefinch (1948*a*) gives the full length of Nauplius I as 0·34 mm. in *B. balanoides* and 0·28 mm. in *B. crenatus*, while from his diagrams the carapace width of this stage in its widest part is slightly less than 0·25 mm. for the former, but only 0·15 mm. for the latter. Stage II of *B. balanoides* is given as 0·54 mm. full length and from the diagram 0·35 mm. carapace width, whilst Stage II of *B. crenatus*, which is rather more slender, is 0·44 mm. long and about 0·25 mm. greatest width. It would appear, therefore, that with the gauze used in these experi-

ments there is some chance that Nauplius I of both *B. balanoides* and *B. crenatus* and possibly Nauplius II of the latter were not caught quantitatively. It must, however, be remembered that the effective width of the animal is increased by the presence of appendages. Further, during many of these runs diatoms were very abundant, and considerable clogging of the gauze resulted; in these circumstances the effective opening of the gauze would be reduced and any loss of the earlier naupliar stages to some extent prevented.

## The Weather and Hydrographic Conditions

During the course of all these collections and throughout the whole of the period covering the spring diatom outburst the weather was good. Winds, in general from the south-west, were moderate, the mean speed from 16th to 31st March being 10 m.p.h. The wind freshened during the first few days of April (19 m.p.h.). The daily surface sea temperatures (mean 7·53° C.) were rather higher than the average and varied only from 7·2 to 7·8° C. during this period, whilst the salinity, 31·5 °/₀₀, was normal for this period. The upper layers of the water at this time are homothermal, with consequent considerable

Table II

| | 1948–49 (° C.) | 10-year mean (° C.) |
|---|---|---|
| November | 10·6 | 10·1 |
| December | 9·4 | 8·4 |
| January | 7·9 | 7·3 |
| February | 7·4 | 6·6 |
| March | 7·2 | 6·9 |
| April | 8·2 | 7·2 |

vertical mixing, so that hauls at 10 m. may reasonably be considered as representative.

In view of the extraordinary barnacle settlement, one of the heaviest for many years, it is of interest to record that throughout the winter and during the spring the sea temperatures (surface values) had been considerably higher than normal (Table II).

## The Distribution of Larvae in Space and Time

The results set out in Table I indicate that over the whole area and over a considerable period of time the population of barnacle larvae showed no enormous fluctuations. Considering the catches of total larvae as separate samples of the larval population of the whole area sampled there is no significant difference between the means of the catches on the first 2 days (analysis performed on logarithmic values of catches), $t = 1{\cdot}568$, $n = 4$, $P = 0{\cdot}2$; there is a significant difference between the first two and the third day, $t = 3{\cdot}505$, $n = 8$, $P = 0{\cdot}02$–$0{\cdot}01$; but no significant difference between the third day and the last

2 days, $t = 1{\cdot}103$, $n = 8$, $P = 0{\cdot}3$. The mean for the first 2 days was 1689 larvae and the mean for the rest of the period was 3204 larvae.

The population and its composition over the area was remarkably constant on some of the days. Since each traverse extended 4 miles, the off-shore population even if made up of small swarms would be adequately sampled.

An analysis of variance for the first day, neglecting the cyprids since they were present in very small numbers, is given in Table III.

TABLE III

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Main effects: | | | |
| Hauls (H) | 2 | 0·2731 | 0·1366 |
| Species (Sp) | 1 | 3·4476 | 3·4476 |
| Stages (St) | 4 | 0·9311 | 0·2328 |
| First-order interactions: | | | |
| H × Sp | 2 | 0·1748 | 0·0874 |
| H × St | 8 | 0·5384 | 0·0673 |
| Sp × St | 4 | 0·7334 | 0·1834 |
| Second-order interaction: | | | |
| H × Sp × St | 8 | 0·3120 | 0·0390 |
| Total | 29 | — | — |

The mean square for H × Sp and H × St are not significant when tested against H × Sp × St. The values may be pooled giving a new residual of 0·0570 (18 degrees of freedom); and the value for hauls is not significant. There is therefore no significant difference between the hauls, and no significant difference between the proportion of species and stages in the hauls.

For the second day the analysis of variance is given in Table IV.

TABLE IV

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Main effects: | | | |
| Hauls (H) | 1 | 0·0433 | 0·0433 |
| Species (Sp) | 1 | 2·3318 | 2·3318 |
| Stages (St) | 4 | 1·0856 | 0·2714 |
| First-order interactions: | | | |
| H × Sp | 1 | 0·1868 | 0·1868 |
| H × St | 4 | 0·1126 | 0·0282 |
| Sp × St | 4 | 2·6738 | 0·6685 |
| Second-order interaction: | | | |
| H × Sp × St | 4 | 0·0659 | 0·0165 |
| Total | 19 | — | — |

Again H × St mean square is not significant, but at the 5% level the H × Sp mean square is significant. The value for the hauls is not significant. The proportion of the species therefore varied during the hauls, although the

proportion of the stages remained unchanged. However, on the third day, although H × St is not significant the value for H × Sp is high, indicating considerable variation in the proportions of the species in the hauls. The analysis of variance is given in Table V.

TABLE V

| Source of variation | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Main effects: | | | |
| Hauls (H) | 3 | 1·8688 | 0·6229 |
| Species (Sp) | 1 | 4·0622 | 4·0622 |
| Stages (St) | 4 | 2·8604 | 0·7151 |
| First-order interactions: | | | |
| H × Sp | 3 | 0·8770 | 0·2923 |
| H × St | 12 | 0·4702 | 0·0392 |
| Sp × St | 4 | 2·5485 | 0·6371 |
| Second-order interaction: | | | |
| H × Sp × St | 12 | 0·2214 | 0·0185 |
| Total | 39 | — | — |

The wide day-to-day fluctuations often reported may be due to sampling techniques and also, particularly in respect of Stages I and II nauplii, to the effect of the abundant supply of parent stock when sampling is effected by nets attached to fixed inshore structures.

## The Barnacle Larvae Population

It was found as a result of the present tests that in spite of such diatom clogging as was apparent at the time, the plankton recorders filtered the theoretical quantity of water. It is, therefore, possible to obtain an accurate estimate of the barnacle population, although such an estimate suffers from the disadvantage that nothing is known of the vertical distribution of the population.

The mean number of larvae per haul over the whole period is 2636 and this is taken in 1·2 cu.m. which gives 2197 larvae per cu.m. Pyefinch (1948*b*) gives 13,644 as the highest average daily haul for a single month. Now this figure was obtained with a 50 cm. net fished for 1 hr. under conditions which do not permit quantitative deductions. However, at a tidal speed of 1 knot the theoretical volume filtered is approximately 350 cu.m. of water per hour. Such a comparison suggests either that nets fished on the tide in this manner are not fishing effectively, or that the larval populations here recorded were very much higher than those previously recorded.

It is of some interest to calculate an approximate estimate of the total barnacle larvae population for the whole of this body of water. If it is assumed that the larvae were uniformly distributed down to a depth of 10 m., a reasonable assumption in view of the vertical mixing at this time of the year, and taking the area to be approximately 8 square miles and using the above value for the mean population density, the number of larvae is of the order of $6 \times 10^{11}$.

### The Relation of the Stages

Pyefinch (1948*b*), Johnstone, Scott & Chadwick (1924), and Fish (1925) consider that between the Stages I and II Nauplii and the cyprid stage there is a considerable depletion of the population, although no cause is suggested. According to Pyefinch the interval between Nauplius III and the cyprid stage is of the order of 15–21 days. In the present instance such a developmental period would mean that all the barnacle larvae from Stage III to cyprids present in the first runs (21 March) should have appeared as cyprids by the time the run was taken on 5 April. Taking the *higher* population of the 23rd to represent this earlier stage of the population, the mean number of III to cyprid stages was 1894 and 580 for *B. balanoides* and *B. crenatus*, respectively. On 5 April the corresponding catches were 1563 and 614. This does not indicate any depletion of stock between Stage III and cyprid. It is possible that the depletion takes place between Stages I + II and III (on this point the data give no information), but it is suggested that the apparent depletion may be due to the fact that in taking samples off in-shore structures, as was done by Pyefinch and Fish, the numbers of Stages I and II are not representative of the planktonic content of the whole body of water. The catches of these two stages will be grossly influenced by the close proximity of the parent stock. It is also perhaps significant in this connexion, that Pyefinch found this discrepancy less for *B. crenatus*, a sublittoral species, and that his figures also show a much less discrepancy when the Stage III and cyprid populations are compared for *B. balanoides*. Johnstone *et al.* took their samples in the in-shore waters across Port Erin Bay and the proximity of parent stock may be partially responsible for the apparent discrepancy. Also it is to be noted that, according to the catches of these workers, there is a great increase in the diatom population at the time the cyprids were being caught; clogging of their nets may have resulted in the filtration of less water than was filtered when nauplii were the main larval stage present, under which circumstances more water would be filtered when the earlier stages were being sampled. Development takes place over a period of approximately 1 month, during which considerable dispersion of the larvae takes place (as indicated by the above results) so that the whole body of water should be sampled for the stages in order to compare any changes within the population. Further, the above results suggest that there is no reason to assume, as does Pyefinch, either that the cyprids tend to occur in greater numbers in-shore, or that they would become more abundant in in-shore waters later in the tide.

### The Effect of Diatoms on the Larval Development

It has been maintained by Pyefinch (1948*b*) that the development of the later stages of the nauplii and the production of cyprids is considerably interfered with by a heavy diatom population. This does not seem to be true in the present series. On 16 March few diatoms were present, but the spring outburst of

*Skeletonema costatum* began between the 16th and 21st of that month, reached its maximum between the 22nd and 25th and was virtually over by the 31st. A lack of records does not allow speculation before the diatom outburst took place, but it is clear that development from Stage III to cyprids was never interfered with by the diatom outburst, since this is the period over which it has been shown that the earlier nauplii stages completed their development with the production of the 'corresponding' number of cyprids. That cyprid development took place is substantiated by the fact that settlement on the shore was first observed on 3 April (35–40 newly settled cyprids per sq.in.) and that there subsequently developed one of the heaviest settlements which has been seen in this area for a number of years. A non-toxic panel exposed on a raft in-shore during this period (in connexion with another investigation) and withdrawn on 15 April had 231 (mean of four separate counts) barnacles of less than 1 mm. in size per sq.in.

## Summary

A series of results is presented on the barnacle larvae population of an area of the Firth of Clyde, over a 15-day period in the spring taken by means of a modified Hardy Plankton Recorder.

The records and observations on barnacle settlement indicate that the larval population was considerably greater than usual.

The total larval population showed no great fluctuations from day to day, and on a given day the composition of the population over a wide area was often reasonably constant.

Evidence is presented that there is no great depletion of the population between Nauplius III and cyprid stages. It is suggested that the depletion previously reported may be due in part to the method of sampling or to the conditions at the time of sampling.

During the time when the evidence indicates no depletion of population there was a heavy diatom outburst, which in this instance did not appear to interfere with the larval development.

Data are given on the density of settlement.

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# *OPHIOPSILA ANNULOSA* (M. SARS) IN THE PLYMOUTH AREA

By H. G. Vevers, M.A., D.Phil.

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Norman (1905) gave a short account of the distribution of the ophiuroid, *Ophiopsila annulosa*, having dredged it himself from Birterbuy Bay, Ireland, in 1874, and from outside Dartmouth Harbour in 1904. He also obtained specimens in 1903 from the Plymouth Laboratory; these had been dredged in 12–25 fathoms on Mewstone Ledge and Stoke Point Grounds, near Plymouth, and were recorded as not uncommon in the red sandstone, especially in old *Pholadidea* crypts. Mortensen (1927) expressed some doubt as to Norman's identification of the Irish specimens; he noted that the Plymouth specimens had been found in exactly the same locality and habitat as the smaller and commoner species, *Ophiopsila aranea*, and considered that the presence of the larger species in British waters could not be definitely settled until new records were to hand. *O. annulosa* was not recorded in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931) and no specimens have been found in the reference museum at the Laboratory.

On 8 July 1948 a single perfect specimen of *O. annulosa* was dredged by R.V. *Sabella* on the Mewstone Grounds in 20 fathoms. This specimen was not found in the crevices of the sandstone boulders, but came up loose in the dredge bag. A second specimen, for which I am indebted to Mr P. G. Corbin, was dredged on the Mewstone Grounds ($\frac{3}{4}$ mile south of the Mewstone, 18–20 fathoms) on 5 April 1949.

Furthermore, it has now been possible, through the courtesy of Dr H. W. Parker, to examine the specimens of *O. annulosa* in the Department of Zoology at the British Museum (Natural History). Three of the four specimens are from Norman's collections (viz. Birterbuy Bay 1874, Kenmare Bay 1877, and Zoological Station Naples 1887), while the remaining specimen was collected at Naples in 1948. These specimens undoubtedly belong to the same species as the specimens taken at Plymouth in 1948 and 1949. They were easily distinguishable from *O. aranea* Forbes, the marked brown and white banding of the robust arms and the large number of arm spines in *O. annulosa* being quite characteristic.

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# THE OCCURRENCE OF THE SMOOTH SAND-EEL, *GYMNAMMODYTES SEMISQUAMATUS* (JOURDAIN), IN THE PLYMOUTH AREA, WITH NOTES ON *G. CICERELUS* (RAFINESQUE), AND *G. CAPENSIS* (BARNARD)

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## Distribution and Plymouth Records of *Gymnammodytes semisquamatus*

*Gymnammodytes semisquamatus* (Jourdain), the smooth sand-eel occurring along the Atlantic seaboard of north-western Europe, has been separated by Duncker & Mohr (1939) as a distinct species from the Mediterranean smooth sand-eel, *G. cicerelus*[1] (Rafinesque). Until Raitt's discovery (1934, 1935) of the abundance of *G. semisquamatus*[2] in Scottish waters, only six specimens had been recorded farther north than the English Channel:

> Shetlands, one specimen as *Ammodytes siculus*, Günther (1867). Southern Norway, five specimens as *A. cicerellus*, Collett (1904), Grieg (1912). It has recently been identified by Poll (1947) from the West Hinder Bank in the southern North Sea (seventeen specimens, 15 May 1907). It does not occur in Swedish waters as stated in Corbin & Vati (1949, pp. 289–90) on Lönnberg's (1915) authority. When this was written it had unfortunately not been possible to consult Lönnberg (1915), and the error is a repetition of one occurring in Raitt's papers (1934, 1935).

The species has, however, long been known from the southern half of the mouth of the English Channel in the St Malo area, and along the Atlantic coast-line of France, Spain and Portugal, although not validly distinguished from *Gymnammodytes cicerelus* until the publication of Duncker & Mohr's study:

> St Malo area, as *Ammodytes semisquamatus*, Jourdain (1879), Moreau (1891). Atlantic coast, as *A. cicerellus*, France, Acloque (1900), Spain and Portugal, de Buen (1935), Gonçalves (1942).

*Gymnammodytes semisquamatus* was first identified in the Plymouth area in July 1947, and has since been taken during all months of the year.

It also occurs in the Irish Sea off the Isle of Man, a single specimen having been identified among a small part of the collection of the Marine Biological

[1] Dr E. Trewavas, British Museum (Natural History), has kindly pointed out that *cicerelus* is the original spelling of Rafinesque.

[2] Recorded as *Ammodytes cicerellus*, before Duncker & Mohr's separation of the two species.

Station, Port Erin, Isle of Man.[1] It was taken locally, although the date and precise place of capture were not recorded.

Raitt's records from Scottish waters, this single specimen from the Irish Sea, and the occurrence of the species in the Plymouth area indicate a continuous distribution from the Faroes, southwards along the west coast of Scotland, through the Irish Sea to the Western Channel mouth, joining thence with the previously known distribution along the Atlantic coast-line of France, Spain and Portugal.

The use of a trawl with a covered cod-end will, no doubt, reveal the species to be fairly widely distributed in the Irish Sea and Celtic Sea. It will be of interest to know whether it also occurs along the Atlantic coast of Ireland.

The following are the records from the Plymouth area:[2]

> Twelve specimens were caught in the trawl on eight occasions (Mar. 1949, May 1949, June 1948 and 1949, July 1947, Aug. 1949, Sept. 1949). Forty-three specimens were taken by the dredge in shell gravel on seventeen occasions, once in Bigbury Bay and sixteen times from the Eddystone shell gravel (Jan. 1949, Feb. 1949, March 1948 and 1949, July 1949, Sept. 1948, Oct. 1947, Nov. 1947–9, Dec. 1948). Not infrequently, however, none has been caught during a day's dredging for *Amphioxus* on this ground. Ninety-six specimens were taken in six Agassiz trawl hauls on the Eddystone shell gravel (Feb. and Apr. 1949). This number is noteworthy since the Agassiz trawl can be towed for very little longer than 5 min. on this ground owing to its small area between the submerged long sharp reefs standing out from the main Eddystone Rock. Eight specimens were caught in a short trawl haul to the east of the Eddystone lighthouse, with the cod-end of the trawl covered with small mesh netting ($\frac{3}{8}$ in. bar), as used in the shell-gravel dredge and the Agassiz trawl (May 1949). One specimen was found in a whiting's stomach (Apr. 1949) and seven specimens in perfect condition were taken from the stomach of a turbot trawled to the south-west of Looe (May 1949).

Several observations may be made from these records. Before the present interest developed, the Agassiz trawl was seldom used on the Eddystone shell-gravel patch. Moreover, in the past, while sorting dredge hauls of shell gravel at sea, all attention was concentrated on securing *Amphioxus*; sand-eels, for which there was no special demand, are unlikely to have received the same attention. They are frequently damaged when caught in the dredge and may have been discarded for this reason, or, if brought in to the laboratory, were probably not closely examined. It seems reasonable then to infer that the species has previously been overlooked in the Plymouth area, and is not a recent arrival.

The infrequent captures in the trawl of very few specimens of *Gymnammodytes semisquamatus* reveal that the normal mesh size of the cod-end does not effectively retain sand-eels. This is amply borne out by the fact that the great

[1] The writer is indebted to Mr J. R. Bruce for kindly providing this material for examination.

[2] The writer's sincere thanks are due to Lieut.-Commander C. A. Hoodless, D.S.C., R.N.R., and Mr W. J. Creese, and to the members of the crews of R.V. *Sabella* and M.F.V. *Sula* for their constant watch for, and help in securing, specimens.

majority of Raitt's very large collection of Ammodytidae were caught while trawling with a small-mesh cover to the cod-end.[1]

The body form of a sand-eel and its ability to burrow in the dense medium of sand or shell gravel conceivably give it a greater chance than other 'trawl fish' of successfully escaping from the violent hurly-burly occurring in the cod-end of a trawl when fishing.

From the records of the area, it also appears that *G. semisquamatus* is an off-shore species with a preference for shell gravel grounds. Shore seining for sand-eels is commonly practised in many districts, but no specimens of *G. semisquamatus* have been seen during examination of a number of seine catches from Salcombe and the Exe estuary; in them *Ammodytes tobianus* was abundant, together with comparatively few *A. lanceolatus*. Nor has the species been taken by digging or hooking on the shore at several localities in South Devon and North Cornwall where both *A. tobianus* and *A. lanceolatus* were found.[2]

Although the actual numbers of *G. semisquamatus* caught in the dredge are low, they represent a considerable density of the species in the shell gravel in relation to the small volume of soil obtained by a dredge haul. The larger numbers caught by the Agassiz trawl on the shell gravel support this indication of a concentration, and it is further emphasized by the absence of *G. semisquamatus* from numerous Agassiz hauls made on other grounds in the Plymouth area including a number of 'control' hauls made close in to the Eddystone, but not actually on the shell gravel. The records of trawl-caught specimens show, however, that the species is not confined to the area of shell gravel. In relation to the above observations, the selectivity of the small mesh of the Agassiz trawl and the dredge must obviously be borne in mind. It is to be expected that more extensive use of a covered cod-end on the trawl will give fuller information on the distribution of the species.

A further point of interest is a seasonal alternation of the occurrence of trawled specimens (including those from the turbot and whiting stomachs) and dredged specimens. The occurrences are shown by months in Table I. Specimens caught by the Agassiz trawl and the small-mesh cod-end are not included since so few hauls were made with these nets.

It may be argued from the small number of records that this difference is fortuitous. On the other hand, the laboratory's two ships trawl throughout the year, and although not as frequent as trawling, dredging is necessitated by the constant demand for *Amphioxus*, whenever weather conditions are calm enough to work close to the Eddystone on the shell gravel. The seasonal difference

[1] Ascertained, by courtesy of Dr C. E. Lucas, from records at the Marine Laboratory, Scottish Home Department, Aberdeen.

[2] In the course of collecting, *Gymnammodytes semisquamatus* and *Ammodytes lanceolatus* have been taken together in the same haul. The characteristic lateral line of *semisquamatus* immediately distinguishes it. Although it has not been caught with *A. tobianus*, the same feature would also certainly distinguish it in this combination of species.

evident in Table I derives then from all-the-year-round sampling and in this event would appear to be a real one.

TABLE I. MONTHS IN WHICH *GYMNAMMODYTES SEMISQUAMATUS* HAS BEEN TAKEN IN THE PLYMOUTH AREA BY TRAWL AND DREDGE, JULY 1947 TO NOVEMBER 1949

| Dredge | Trawl |
|---|---|
| Jan. | — |
| Feb. | — |
| Mar. | Mar. |
| — | Apr. |
| — | May |
| — | June |
| July | July |
| — | Aug. |
| Sept. | Sept. |
| Oct. | Oct. |
| Nov. | — |
| Dec. | — |

There is thus a tentative indication of a winter concentration of the species in the shell gravel and a summer dispersal away from it. From examination of the gonad condition of the material, it would appear that the winter concentration in the shell gravel is associated with spawning. Very much fuller data are obviously necessary for confirming any of these indications; it is felt, however, that they are of some value in view of the lack of any knowledge about the life history of the North Atlantic smooth sand-eel.

## THE NUMBER OF VERTEBRAE IN THE THREE SPECIES OF *GYMNAMMODYTES*

The number of vertebrae in *G. semisquamatus* from this area[1] is given in Table II for comparison with counts of specimens from Scottish waters (Corbin & Vati, 1949). There is very close agreement between the means of these two samples. Table II also contains vertebral counts of *G. cicerelus*, the Mediterranean smooth sand-eel. Previous vertebral-count data of the species (Fage, 1918; Duncker & Mohr, 1939) relate to a small number of specimens. The present sample of thirty-nine specimens (6·8–10·0 cm.) from the Naples area[2] is large enough to give a mean value, and it can be seen that this is not far removed from that of *G. semisquamatus*. It would be of interest to obtain further vertebral counts of *G. cicerelus* from other Mediterranean localities to examine whether there is extensive variation between different populations, as, for example, in *Ammodytes marinus* (see references in Corbin & Vati, 1949, Table II, p. 302), and in particular whether the vertebral number of the Black Sea population differs greatly from that of the Mediterranean population.

[1] The writer's sincere thanks are due to Surgeon-Commander D. R. F. Bertram, O.B.E., R.N., Royal Naval Hospital, Stonehouse, for the provision of beautifully clear X-ray plates of these specimens from which the counts were made.

[2] The writer is much indebted to Dr R. Dohrn, Director of the Stazione Zoologica, for this material.

Vertebral counts of fifty-nine specimens of the South African smooth sand-eel, *Gymnammodytes capensis* (Barnard, 1927), of 6·9–9·5 cm. length, are also included in Table II.[1] They were collected by R.R.S. *Discovery* in Elephant Bay, Angola, South Africa (Station 271, 29 July 1927, seine net, 5–0 m. depth). The wide difference between the vertebral counts of *G. semisquamatus* and *G. capensis* is remarkable in view of the extremely close similarity of external features in the two species. The specimens of *G. capensis* were very carefully compared with *G. semisquamatus* from this area and from Scottish waters, and it was found

TABLE II. THE NUMBER OF VERTEBRAE IN *GYMNAMMODYTES SEMISQUAMATUS*, *G. CICERELUS* AND *G. CAPENSIS*

| No. of vertebrae (including urostyle) | *G. semisquamatus* | | *G. cicerelus* | *G. capensis* |
|---|---|---|---|---|
| | Plymouth | Scotland | | |
| 57 | .. | .. | .. | 5 |
| 58 | .. | .. | .. | 23 |
| 59 | .. | .. | .. | 22 |
| 60 | .. | .. | .. | 9 |
| 61 | .. | .. | .. | .. |
| 62 | .. | .. | .. | .. |
| 63 | .. | .. | .. | .. |
| 64 | .. | .. | .. | .. |
| 65 | .. | 1 | 7 | .. |
| 66 | 2 | 1 | 17 | .. |
| 67 | 15 | 10 | 13 | .. |
| 68 | 43 | 20 | 2 | .. |
| 69 | 33 | 15 | .. | .. |
| 70 | 13 | 4 | .. | .. |
| 71 | 1 | .. | .. | .. |
| 72 | 1 | .. | .. | .. |
| Total no. of specimens | 108 | 51 | 39 | 59 |
| Mean vertebral no. | 68·44 | 68·16 | 66·26 | 58·59 |
| $\sigma_{mean}$ | ±0·098 | ±0·144[2] | ±0·131 | ±0·113 |
| $\sigma$ | 1·017 | 1·027[2] | 0·819 | 0·857 |

that the two species could not be reliably distinguished by external features other than the numerical differences, noted by Duncker & Mohr (1939), of the number of fin-rays and the number of ventral pores in the lateral line. No differences of pigmentation were observed. Duncker & Mohr (1939) also distinguish *G. semisquamatus* and *G. capensis* by differences of the position of the tip of the pectoral fin and the end of the ventro-lateral skin-fold in relation to the line of insertion of the first ray of the dorsal fin. These differences could not, however, be confirmed in the above material. In the great majority of the *G. semisquamatus* and *G. capensis* examined, both the tip of the pectoral

[1] The writer is much indebted to Dr E. Trewavas, British Museum (Natural History), for the loan of the specimens for examination and of excellent X-ray plates from which the counts were made.

[2] Under *G. semisquamatus*, in Corbin & Vati, 1949, Table II, p. 302, the values of ±0·127 and 0·901 should be amended to read ±0·144 and 1·027 respectively.

and the end of the ventro-lateral skin-fold were in line with the insertion of the first ray of the dorsal fin; in some few specimens they extended very slightly beyond this line or were just short of it, by an interval of less than 1·0 mm. The interval in Duncker & Mohr's figs. 4*a* and 4*c* is considerably larger than this.[1] It is possible that there is some variation of these relative lengths with size, although no evidence of this was seen in the material examined. Nor, as these authors state, was the ventro-lateral skin fold of *G. capensis* observed to be less well developed than in *G. semisquamatus*. The external non-metameric differences between these two species appear therefore to be of little or no value for specific identification.

It may be added that, in the Mediterranean and Black Sea specimens of *G. cicerelus*, the tip of the pectoral extended slightly beyond (not more than 1·0 mm.) the line of the first ray of the dorsal. This is in agreement with Duncker & Mohr's description, although the pectoral is well short of this line in their fig. 4*b*[1].

## Summary

*Gymnammodytes semisquamatus*, the North Atlantic smooth sand-eel, has a continuous distribution from southern Norway to the southern Atlantic coast-line of Spain. Its occurrence in the Irish Sea and in the Plymouth area are new records. In the latter area it is an off-shore species, apparently concentrating in shell gravel in winter for spawning. It has a mean vertebral number of slightly over 68 (Plymouth and Scottish specimens). A small sample of the Mediterranean species, *G. cicerelus*, gives a mean of just over 66, while the South African species, *G. capensis*, which is indistinguishable from *G. semisquamatus* by external non-metameric characters, has a much lower mean of 58·5.

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[1] Duncker & Mohr's (1939) fig. 4 is approximately natural size for adults of the three *Gymnammodytes* species.

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# RECORDS OF PILCHARD SPAWNING IN THE ENGLISH CHANNEL

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(Text-fig. 1)

The pilchard, *Clupea pilchardus* Walbaum, is known to spawn in summer in the southern North Sea in the neighbourhood of the Sandettié Bank (Buchanan-Wollaston, 1911; Furnestin, 1939*a*, 1945) and in the eastern English Channel off Beachy Head (Furnestin, 1939*a*, 1945). Furnestin (1939*b*, 1945) concludes from these records that spawning is in all probability continuous throughout the Channel from the southern North Sea to the Celtic Sea. There appear, however, to be no previous references to pilchard spawning in the central part of the English Channel. The following records from the area are of interest therefore, and provide confirmation of Furnestin's conclusion.

The station positions and numbers per haul are shown in Fig. 1 and Table I. The plankton samples were collected in 1947 and 1948 by ½ hr. oblique hauls of the 1 m. stramin ring-net during cruises of the motor yacht *Manihine*, which was placed at the disposal of the British Museum (Natural History) through the generosity of Major H. W. Hall, M.C. In 1948, a number of surface hauls with a medium silk townet were also taken by Mr M. H. W. Gall from his yacht *Colleen*. The writer is much indebted to the Trustees and Director of the British Museum for the opportunity of examining the *Manihine* collections, and to Mr Gall for the *Colleen* material.

A number of the *Colleen* stations (*C*1–12) were worked in the southern North Sea (see Gall, 1949, fig. 13, p. 772). Pilchard eggs were taken at four of these stations; at the northern entrance to the Straits of Dover (*C*9, Sandettié Bank; *C*10, south-east of Goodwin Lightship) and to the north-east off the Belgian coast (*C*7, north-east of Bligh Bank; *C*8, East Hinder Bank). None occurred at stations off the Norfolk coast (*C*1, *C*3 and *C*4) or close in to the Belgian coast (*C*5, *C*6 and *C*12). The presence of pilchard eggs in the area of the East Hinder and Bligh Banks slightly extends to the north-east the known spawning area of the species in the southern North Sea.

The *Manihine* stations, all of which were worked in the English Channel, fall into two groups; one to the west, the other to the east of the Isle of Wight. The monthly means of the numbers of pilchard eggs from all stations (positive and negative) of the two groups are given on p. 94.

## TABLE I. NUMBERS OF PILCHARD EGGS, ETC. PER ½ HR. OBLIQUE HAUL OF THE 1 M. STRAMIN NET

* denotes figure obtained by subsampling.

| Station number (date in parentheses) | Station position | Pilchard eggs (Mackerel eggs) | *Sagitta setosa* (*Sagitta elegans*) | *Muggiaea atlantica* (*Muggiaea kochi*) |
|---|---|---|---|---|
| | M.Y. *Manihine* | | | |
| 23–25 July 1947 | | | | |
| 1 (23) | 50° 29′ N., 1° 41′ W. | 200* | 28 (22) | .. |
| 2 | 50° 20′ N., 1° 43′ W. | 1 | 1 (2) | .. |
| 3( 24) | 50° 39′ N., 0° 10′ W. | .. | 14 (3) | .. |
| 5 | 50° 19′ N., 0° 00′ | 123 | .. | .. |
| 6 | 50° 09′ N., 0° 05′ E. | 147 | .. | .. |
| 7 | 49° 57′ N., 0° 07′ E. | 4 | .. | .. |
| 8 (25) | 49° 55′ N., 1° 54′ W. | .. | .. | .. |
| 9 | 50° 03′ N., 1° 51′ W. | 68 (28) | .. | .. |
| 10 | 50° 11′ N., 1° 47′ W. | 38 (28) | .. | .. |
| 27–28 August 1947 | | | | |
| 11 (27) | 50° 26′ N., 0° 25′ E. | 97 | 8 | .. |
| 12 | 50° 27′ N., 0° 29′ E. | 3 | 5 | .. |
| 13 | 50° 20′ N., 0° 37′ E. | .. | .. | .. |
| 14 | 50° 13′ N., 0° 46′ E. | .. | .. | .. |
| 16 (28) | 50° 47′ N., 1° 10′ E. | .. | 1 | .. |
| 17 | 50° 35′ N., 1° 20′ E. | 1 | 3 | .. |
| 18 | 50° 03′ N., 1° 37′ E. | .. | 1 | .. |
| 6–7 May 1948 | | | | |
| †19 (6) | 50° 39′ N., 0° 39′ E. | 4980* | | |
| †20 | 50° 53′ N., 0° 53′ E. | 2468* | | |
| 21 | 50° 47′ N., 1° 10′ E. | 1980* | .. | .. |
| 22 | 50° 38′ N., 1° 24′ E. | 9 | .. | .. |
| 24 | 50° 13′ N., 0° 46′ E. | 3 | 1 | .. |
| 25 (7) | 50° 36′ N., 0° 26′ E. | 8680* | 1 | .. |
| 26 | 50° 27′ N., 0° 29′ E. | 480* | .. | .. |
| 27 | 50° 20′ N., 0° 39′ E. | 440* | .. | .. |
| 15 June 1948 | | | | |
| 33 | 50° 40′ N., 0° 11′ W. | 800* | 2 | .. |
| 34 | 50° 27′ N., 0° 18′ W. | 600* | .. | .. |
| 35 | 50° 18′ N., 0° 02′ W. | 260* | 13 | .. |
| 36 | 50° 09′ N., 0° 05′ W. | 820* | 2 | .. |
| 37 | 50° 00′ N., 0° 00′ | 660* | .. | .. |
| 3–4 July 1948 | | | | |
| 40 (3) | 50° 29′ N., 1° 42′ W. | 800* | .. | .. |
| 41 | 50° 20′ N., 1° 39′ W. | 62 | .. | .. |
| 42 | 50° 11′ N., 1° 45′ W. | 479 (21) | .. | .. |
| 43 (4) | 49° 54′ N., 2° 10′ W. | 29 (54) | 4 | .. |
| 44 | 49° 51′ N., 2° 18′ W. | .. (10) | 8 | .. |
| 45 | 49° 54′ N., 1° 55′ W. | 44 (12) | .. | .. |
| 31 August 1948 | | | | |
| 47 | 49° 55′ N., 2° 08′ W. | .. | 128 | .. (2) |
| 48 | 49° 52′ N., 2° 10′ W. | .. | 168 | .. (2) |
| 49 | 49° 50′ N., 2° 08′ W. | .. | 72 | .. |
| 50 | 49° 49′ N., 2° 28′ W. | .. | 23 | 1 (8) |
| 51 | 49° 50′ N., 2° 21′ W. | .. | 2 | 3 (7) |
| 15, 26 September 1948 | | | | |
| 52 (15) | 50° 06′ N., 3° 27′ W. | .. | 207 (1) | 96 (21) |
| 53 | 50° 00′ N., 3° 16′ W. | .. | 1000* | 61 (11) |
| 54 | 49° 51′ N., 3° 07′ W. | .. | 500* | 93 (37) |
| 57 (26) | 50° 31′ N., 1° 25′ E. | 2 | 10 | .. |
| 58 | 50° 38′ N., 1° 26′ E. | 20 | 13 | .. |
| 59 | 50° 47′ N., 1° 07′ E. | 8 | 1 | .. |
| | Yacht *Colleen*‡ | | | |
| *C*1 (15. vii. 48) | 52° 28′ N., 1° 47′ E. | .. | | .. |
| *C*3 (16) | 52° 43′ N., 2° 18′ E. | .. | | .. |
| *C*4 (19) | 52° 26′ N., 2° 24′ E. | .. | | .. |
| *C*5 (23) | 51° 51′ N., 3° 38′ E. | .. | | .. |
| *C*6 | 51° 55′ N., 3° 29′ E. | .. | | .. |
| *C*7 (24) | 51° 48′ N., 2° 58′ E. | 76 | | .. |
| *C*8 | 51° 36′ N., 2° 41′ E. | 33 | | .. |
| *C*9 (25) | 51° 12′ N., 1° 54′ E. | 8 | | .. |
| *C*10 (29) | 51° 11′ N., 1° 39′ E. | 11 | | .. |
| *C*12 (30) | 51° 11′ N., 2° 41′ E. | .. | | .. |
| *C*13 (5. viii. 48) | 50° 46′ N., 1° 34′ E. | .. | | .. |
| *C*16 (14) | 50° 36′ N., 0° 03′ W. | 4 | | .. |
| *C*17 (15) | 50° 21′ N., 0° 34′ W. | .. | | .. |
| *C*19 (16) | 49° 45′ N., 1° 00′ W. | .. | | .. |
| *C*20 (20) | 2 mls. N. of Alderney Lt. House | 1 | | .. |
| *C*21 (21) | 50° 23′ N., 1° 51′ W. | .. | | .. |
| *C*22 (24) | 50° 16′ N., 1° 33′ W. | .. | | .. |
| *C*23 | 50° 07′ N., 2° 21′ W. | .. | | .. |
| *C*24 (6. ix. 48) | 50° 04′ N., 4° 22′ W. | .. | | .. |
| *C*25 | 49° 56′ N., 3° 47′ W. | .. | | 1 numerous eudoxids |
| *C*26 (9) | 49° 47′ N., 2° 01′ W. | .. | | .. |
| *C*27 (10) | 49° 56′ N., 1° 47′ W. | .. | | .. |
| *C*28 (11) | 50° 11′ N., 1° 33′ W. | .. | | .. (1) numerous eudoxids |

† The writer is indebted to Mr A. C. Simpson, Fisheries Laboratory, Lowestoft, for the counts of pilchard eggs from these two stations.

‡ Catches not examined for mackerel eggs and *Sagitta* spp.

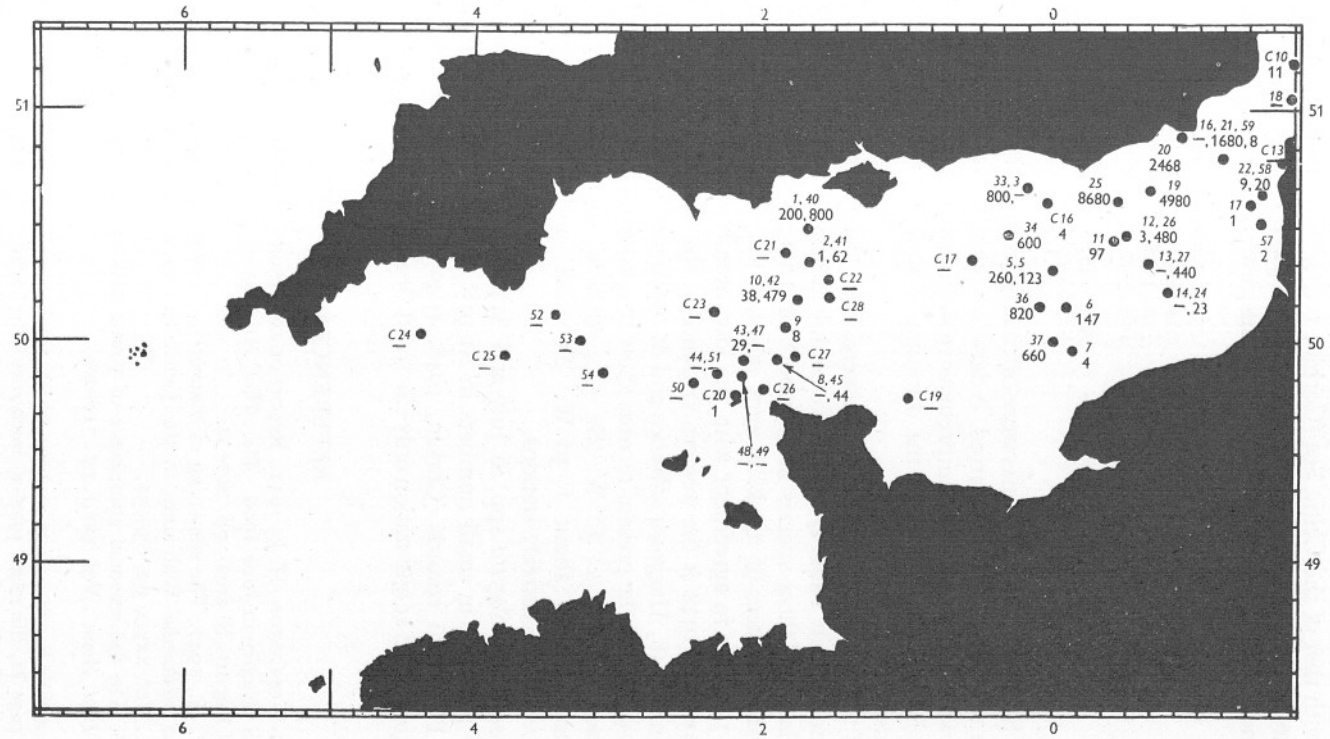


Fig. 1. Records of pilchard spawning in the English Channel in 1947 and 1948. Station numbers are shown in italics. The lower figures are the numbers of pilchard eggs per haul. Stations worked by the *Colleen* have the prefix *C*; those worked by the *Manihine* have no prefix. Several of the stations which were close together have for convenience been indicated by a single point on this chart.

In order roughly to compare the intensity of spawning in the central English Channel with that of the Celtic Sea (Corbin, 1947),[1] the means of the present records have been multiplied by four (figures in parentheses) to approximate the 1 m. net catches to those of the 2 m. ring-trawl. It should be noted that

| Western stations | | | Eastern stations | | |
|---|---|---|---|---|---|
| | | | May 1948 | 2379 | (9516) |
| | | | June 1948 | 628 | (2512) |
| July 1947 | 61 | (244) | July 1947 | 68 | (272) |
| July 1948 | 236 | (944) | | | |
| Aug. 1948 | Nil | | Aug. 1947 | 14 | (56) |
| Sept. 1948 | Nil | | Sept. 1948 | 10 | (40) |

the Celtic Sea spawning intensities were calculated from positive stations where more than 100 eggs per haul occurred. A detailed quantitative comparison of the two areas would require more comprehensive sampling in the English Channel. It should be further noted that the duration of some of the *Manihine* hauls varied considerably.

Data of the numbers per haul of mackerel eggs, *Sagitta* spp. and *Muggiaea* spp. are included in Table I, as they are complementary to the observations on the abundance of these species in Plymouth off-shore waters.

The small numbers of mackerel eggs taken in the central Channel in July 1947 and 1948 are in agreement with the low intensity of spawning observed in July 1937 and 1938 at the western entrance of the Channel (Corbin, 1947).

In autumn 1948, *Muggiaea atlantica* and *M. kochi* were plentiful off Plymouth (Corbin, 1949), and the present records show that both species were distributed up Channel to about 2° 30′ W. (St. 51), with *M. kochi* extending slightly farther eastwards to about 1° 30′ W. (St. *C*28) and also out-numbering *M. atlantica* at the easterly stations.

The absence of *Sagitta* spp. in July and August, 1947, in May–July 1948, and their presence in small numbers in August and September 1948, agrees with the Plymouth records (Corbin, 1948, 1949). In the eastern Channel, *S. elegans* occurred at one station only (St. 3, off Beachy Head, three specimens).

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[1] The writer wishes to correct an error which occurred in this paper. In the last line of Table III, page 81, the mean 1937–39 intensities of pilchard spawning should be amended to read: April 6680, May–June 14,843, July 4701.

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# ON THE PRODUCTION OF LIVING MATTER IN THE SEA OFF PLYMOUTH

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(Text-figs. 1–10)

CONTENTS



A study, now in progress, of the phosphorus cycle in the sea off Plymouth required some knowledge of the amount of plants and of several ecological groups of animals. There were no existing data except for zooplankton and the larger net-caught phytoplankton.

From information supplied by friends and colleagues, it was possible to make tentative estimates of the average biomass of other groups of animals occurring below unit area of the sea.

Although some of these estimates are derived indirectly and are indeed tentative, together they provide a framework on which to compute the food supply and food requirements of the animal population. There results a picture, crude and in part indefinite, of the quantitative relations between the different ecological groups and of how change of circumstance may affect the populations. It is the aim of this essay to present this picture.

The help of many friends and colleagues is gratefully acknowledged, both in supplying information and in amending drafts of this essay. To Mr P. G. Corbin and Mr P. S. B. Digby, who collected, sorted and weighed hauls of plankton in June 1947, and to Dr L. H. N. Cooper, who collected many samples for me, I am further indebted.

## The Phytoplankton

The great difference in size of the various species which make up the community in these seas is perhaps more striking than the diverse shape of the different species.

| | Contents, sap and tissue (cubic microns) |
|---|---|
| Diatoms | 20–20,000,000 |
| Dinoflagellates | 500–100,000 |
| Flagellates | 14–500 |
| Coccolithophores | 14–500 |

Even among individuals of the same species, notably in species of diatoms, there are very considerable differences in size. Thus a large individual of *Ditylum Brightwellii* may have a volume of one to two million cubic microns and a small individual of fifty thousand—a thirty-fold difference in size within the same species.

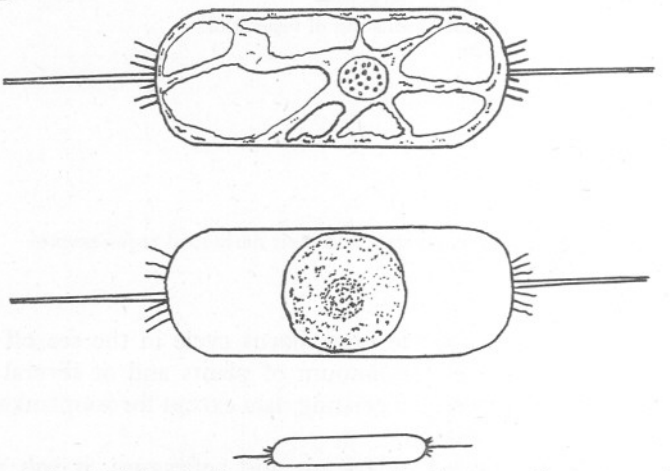

Fig. 1. Cells of *Ditylum Brightwellii*. Large cells about 90 $\mu$ diameter, small cell 15–20 $\mu$ diameter. (After Gross, 1937.)

Normally these plants are considered in terms of their linear dimensions; but the cubic dimensions of their cell contents will give a better measure of each individual's value as food for other organisms.

In some species the cells appear well filled with living tissue; in other species there is more sap than tissue. Thus, in *Ditylum*, the protoplasm normally lines the inside of the cell and projects as a network through the watery sap. It readily responds to stimulus, such as a fall in temperature, by rounding into a ball. It is then seen to occupy only a quarter of the cell content.

Given a suitable intensity of light, and a sufficient supply of dissolved nitrogen and phosphorus compounds in forms which they can absorb, these plants are capable of very rapid growth. Thus, Braarud (1945) has observed that some of the smallest plants double in numbers every 5 hr., while larger

species required 10–75 hr. The optimum light intensity and temperature also differ for different species.

One of the earliest and most illuminating experiments on the rate of growth was made by Gaarder & Gran (1927) in the following manner. Water was collected on 22 March from Oslo Fiord, the population density of the dominant species determined, and the water then put into flasks which were hung at different depths in the fiord. The temperature was 1·8° C. After 3 days, on the 25th, the population density was again determined.

| | Percentage increase in 24 hr. | | |
|---|---|---|---|
| Depth (m.) | *Lauderia glacialis* | *Thalassiosira gravida* | *Thalassiosira Nordenskioldii* |
| 0 | 77 | 59 | 10 |
| 2 | 79 | 58 | 73 |
| 5 | 70 | 55 | 67 |
| 10 | 28 | 34 | 23 |
| 20 | 0 | 0 | 0 |

Compared with conditions in the English Channel at the end of March, this fiord water is 6–7° C. colder, less transparent, but richer in nutrient salts. It is notable that optimum growth took place in the upper 5 m., whereas off Plymouth and the Firth of Clyde in summer the optimum probably lies at about 10 m. depth, due to greater transparency of the water.

Several experiments have shown that if water is collected off Plymouth at about this season of the year, and kept at room temperature in a flask in a north window, where the intensity of light is similar to that at some 10 m. depth in the sea, the plant cells proliferate and use up the available nutrient salts within a few days. If the nutrient salts are increased ten-fold and the water is kept aerated, within about 14 days they are all utilized by the plants and a crop is produced having the same species constitution, but very many times denser, than that which appears in the sea at the time of the phyto-plankton maximum. In some experiments it was found necessary also to add iron in an available form in order to ensure complete utilization of the nutrients.

Another characteristic of these unicellular plants is their high proportion of protein and fat when their organic content is compared with that of land plants. Various analyses of marine diatoms collected from the sea show 30–40% of protein and 7–10% of lipoids in their tissue. Recent analyses by Ketchum & Redfield (1949) of a number of unicellular algae, mostly fresh water, grown in artificial light, showed that composition of their organic matter was surprisingly similar: protein, 41–54%; carbohydrates, 20–38%; lipoids, 20–27%.

These algae were grown in water containing a plentiful supply of available nitrogen and phosphorus, and of carbon dioxide. Under conditions where either available nitrogen was deficient or both nutrients were deficient, the plants contained a smaller proportion of protein.

These various analyses show that marine phytoplankton has a remarkably high food value for animals. The protein content of the plants and the rapidity with which they can grow are outstanding features.

*Methods of estimation*

Owing to the great difference in size of the individual organisms comprising the plant community, it is a matter of practical difficulty to determine the population density or standing crop of plants per unit area of the sea. Catches made by net, either hauled vertically through the whole column of water or towed horizontally at various depths, collect a proportion of the organisms—a proportion which varies greatly with time and position. Concentration of the plants in a sample of water, by sedimentation, centrifuging, or by filtration through a membrane, and counting the individuals has been extensively employed. In order to arrive at the quantity or volume of plant tissue in the organisms, measurements of individuals, often of complicated shape, are needed, and small errors in linear measurements cause large errors in the estimate of volume. Moreover, the proportion of plant tissue in cells containing vacuolar sap is difficult (or even impossible) to gauge. Counting and measurement require much time. Unless the results can be expressed in terms of quantity of plant tissue they do not give a direct measure of the food value of the standing crop to the animal dependent on it for food.

In order to obtain the numerous observations necessary to assess the ever-changing crop, an indirect method has been rather extensively employed. The approximate quantity of chlorophyll in the plants can be quickly determined; it does not provide a direct linear measure of the organic matter in the plants, but it is perhaps as good an overall measure as could be obtained by any other method and allows numerous observations. In addition to providing a rough measure of the vegetable organic matter, experiments by Gessner indicate that it provides a direct measure of the capability of the plants to produce organic matter. He kept waters from a number of Bavarian lakes, having different phytoplankton floras, in the same light intensity at the same temperature. The quantity of chlorophyll in the phytoplankton showed a near relation to the assimilation which took place in unit time in the water from eleven lakes out of thirteen (Fig. 2). Hence the quantity of chlorophyll in the water gives a measure of the capacity or potentiality of the plants contained in it to produce vegetable food for the animal population.

In using chlorophyll determinations to compute the quantity of vegetable organic matter in the sea, two operations are involved which need consideration—there is the technique of estimating the chlorophyll in the plants filtered from a sample of sea water, and, having determined the quantity of chlorophyll in the plants below a unit area of the sea, there remains how best to gauge from it the quantity of vegetable tissue in which it had existed.

Chlorophyll occurs in algae as a mixture of chlorophyll *a* and chlorophyll *c*

(chlorofucin), always in conjunction with carotinoid pigments, largely fucoxanthin. The yellow carotinoids and the green chlorophylls leach out from the plants into 80% acetone, or into alcohol. Whichever solvent is used, substantially the same depth of green colour results, and this green colour has the same tint or hue whether it is extracted from diatoms, fucoid sea weeds or a common golden brown flagellate. Hence the proportion of chlorophylls to carotinoids is similar.

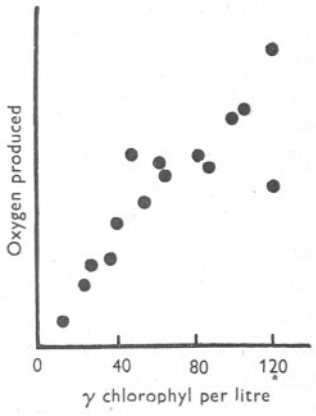


Fig. 2.

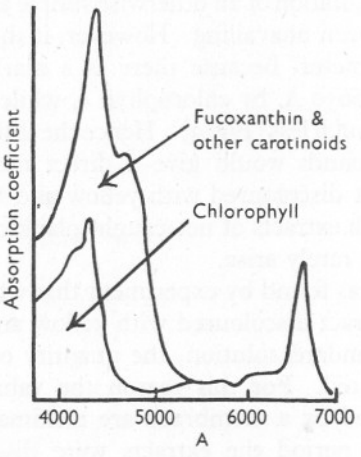


Fig. 3.

Fig. 2. Relation between assimilation and chlorophyll content of waters from thirteen Bavarian lakes. (After Gessner, 1943.)

Fig. 3. Absorption spectra in acetone of the pigments in the diatom *Nitzschia closterium*. (After Dutton & Manning, 1941.)

In consequence, these extracts can be matched visually against a stable and reproducible green standard solution. This is more yellowish green than a solution of pure chlorophyll; it can be evaluated against chlorophyll solution to which a yellow has been added to assist colour matching. To do this exactly would entail a pure preparation of chlorophylls *a* and *c* in the proportion in which they occur in algae. It is not necessary for our purpose to express the colour in terms of chlorophyll concentration because the depth of yellow-green colour in the extract is directly proportional to the green chlorophyll in it, provided it matches in tint or hue the permanent standard. Then the colour of the extract can be expressed in *arbitrary units*, proportional to its chlorophyll content and proportional to the concentration of the permanent standard.[1]

[1] A permanent standard which is in use consists of a mixture of nickel sulphate and potassium chromate in dilute acid, the quantity containing $4{\cdot}6 \times 10^{-6}$ g. $NiSO_4 6H_2O$ and $25 \times 10^{-6}$ g. $K_2CrO_4$ being taken as containing one arbitrary unit of yellowish green pigment (one *U.P.P.*). A green permanent standard has been matched with a mixture of pure chlorophyll *a* and *b* by Guthrie; when more yellow is added to this green standard, the quantity matching one *U.P.P.* is that which, without added yellow, matches a solution containing *c.* 0·003 mg. of chlorophylls *a* and *b*.

When the plankton is filtered from sea water and extracted with solvent, the solution is often an exact match in tint or hue as well as in depth of colour with a suitable dilution of the permanent yellow-green standard. At other times the residue after filtration contains detritus and pigmented animals from which yellow or brown pigments dissolve. Then all that can be done is to guess the dilution of the permanent standard which contains about the same degree of *green* colour. Such a guessed estimate may be very inexact. Attempts to overcome this limitation of an otherwise simple and rapid technique with simple apparatus have been unavailing. However, it should be possible with a sensitive spectrophotometer, because there is a marked absorption of light of wave-length 6550–6650 A. by chlorophyll *a*, while between 6200 and 6300 A. absorption is very much less (Fig. 3). Hence the difference in absorption by light of these two wave bands would give a direct measure of the chlorophyll content of an extract discoloured with yellow and brown pigments.

With extracts of net-caught plankton these difficulties of assessing the green colour rarely arise.

It was found by experiment that when trying to evaluate the green colour in an extract discoloured with yellow and brown pigments, by comparison with the standard solution, the quantity of green in the extract was usually overestimated. For this reason the values shown in Fig. 4 for phytoplankton retained by a membrane are maximal between June and September, during which period the extracts were discoloured. The probability of an overestimate during this period is indicated in Fig. 4 by a series of dots below the value actually estimated.

The *ratio of chlorophyll to organic matter* doubtless varies between algae of different species, and varies in any one species with the quantity of reserve material which has been laid down—diatoms are known to form droplets of free fatty acids in their cytoplasm, usually when growing slowly. Furthermore, when diatoms are grown in a dim light they appear browner and may contain a greater proportion of chlorophyll than when grown in a brighter light. However, if representative samples of phytoplankton are taken from whole water columns, and consist of many species, these differences in the ratio will tend to even out.

Data concerning this ratio of chlorophyll to organic matter, both direct and indirect, are sparse, but suffice to give a rough value of its magnitude.

On several occasions net hauls from bottom to surface in the sea off Plymouth have yielded catches consisting of diatoms with few zooplankton organisms, most of which could be separated from the catch. Analyses of these showed that diatoms containing one *U.P.P.* contained 0·00013 and 0·00010 mg. of phosphorus. Diatoms collected in the Gulf of Maine have been analysed by both Redfield and by Waksman; the mean value of their analyses show a ratio of C : N : P equal to 100 : 16 : 1·67. This indicates that their organic matter consisted of some 47 % protein and 53 % carbohydrates and lipoids, and con-

tained 0·75 % of phosphorus. Combining this value with that relating green colour to phosphorus content, the result indicated that diatoms containing one *U.P.P.* of green colour contained 0·0135–0·0175 mg. of dry organic matter. These deduced quantities of organic matter may be low, because the diatoms analysed for their C : N : P ratio were collected in the Gulf of Maine where the water is richer in phosphate than in the English Channel. Experiment has shown that diatoms grown in low concentrations of phosphate tend to contain less in proportion to their organic content.[1]

A culture of a brown chrysomonad flagellate was analysed by the writer. The quantity of this which contained one *U.P.P.* of green pigment was found to contain 0·0094 mg. of organic matter by loss on ignition. This value is probably too low, since the rather violent centrifuging necessary to concentrate the flagellates caused some to disrupt, discharging soluble organic matter into the water.

These estimates point to a mixed community, growing at all depths in the nutrient poor waters of the English Channel, containing about 0·016 mg. dry ash-free organic matter per unit of green colour or one *U.P.P.* This estimated ratio is no more than a rough approximation. It is unlikely to be less than half or more than double the true mean ratio. Rather many practical difficulties need to be overcome in order to improve this rough approximation.

A number of net catches consisting of diatoms, often with other plankton organisms, from the surface water of the Gulf of Maine have been examined by Riley (1941). From a regression equation it was found that diatoms containing one *U.P.P.* of green colour contained, on the average, 0·035 mg. of dry organic matter. This value may be higher than for a representative sample from all depths since the diatoms were collected from the surface layer. Various observations in the past, and a rough experiment by the writer, suggest that diatoms contain less pigment when grown in strong light than when grown in dim light, but further experiment is necessary to determine whether the light intensity affects the ratio of chlorophyll to organic matter in the diatoms.

[1] In addition to the classic observations by Ketchum on the marine diatom *Nitzschia closterium*, Redfield & Ketchum (1949) found that the fresh-water alga, *Chlorella pyrenoidosa*, grown in artificial light, accumulated much less phosphorus when grown in a phosphate-poor medium.

In culture rich in phosphate and nitrate, algae contained 2·69 % of their dry weight as phosphorus.

In culture deficient in phosphate and nitrate, algae contained 1 % of their dry weight as phosphorus.

In culture rich in nitrate, deficient in phosphate, algae contained 0·59 % of their dry weight as phosphorus.

In culture rich in phosphate, deficient in nitrate, algae contained 1·8 % of their dry weight as phosphorus.

It is of interest that the protein-carbohydrate-lipoid ratios in the organic matter of several fresh-water unicellular algae were very similar to that of a marine diatom grown under similar cultural conditions.

*The Standing Crop of Phytoplankton*

During 1949 a position 5 miles seaward from Plymouth, having 50 m. depth of water, was sampled at intervals. Hauls with a net of fine bolting silk, having, when wet, meshes with pores of $41 \times 52\,\mu$, were made through the whole water column from surface to bottom; the quantity of water filtered being registered by a meter in the mouth of the net. The catches were extracted with solvent and the green colour estimated. The result is shown in Fig. 4. It shows similar seasonal variations but lesser quantities than found in a series of observations made in exactly the same manner throughout 1933 and 1934.

At the same time, equal quantities of water, collected from 5, 15, 25, 35 and 45 m. depth, were mixed to give a *composite sample* representative of the whole water column. Two-litre portions of the composite samples were filtered through a small disk of Whatman no. 2 filter-paper under a head of 2–3 cm. of water. The residue was extracted with solvent and the depth of green colour determined. From observations in Long Island Sound, Riley had concluded that this filter-paper held back 90% or more of the phytoplankton organisms, little more being held back by a membrane filter. On and after 26 April filtration through a Gradocol membrane, average pore diameter $0{\cdot}9\,\mu$, was adopted. Extracts of the phytoplankton collected on filter-paper contained less green than extracts collected on the membrane.

| Composite sample collected | Green colour, expressed in *U.P.P.* per cubic metre of water | |
|---|---|---|
| | By filtration through paper | By filtration through membrane |
| 26 April | 7,500 | 12,000 |
| 7 May | 6,000 | 11,000 |

On both occasions the water contained many small flagellates. The tint or hue of the extract was similar to that of the nickel standard.

At the end of May a notable quantity of organic detritus had accumulated in the water; and from then until August the extracts were seriously discoloured with yellow-brown pigments.

Provided the depth of water exceeds the depth of the photosynthetic zone, it is of interest to compare the standing crop of phytoplankton below unit area of the sea at different positions. The mean value of a number of observations made in the Gulf of Maine on seven occasions are plotted in Fig. 5. Water samples had been filtered through Whatman no. 2 filter-paper and the green pigment extracted from the residues was estimated. It is seen that in that sea-area, where the nutrient-salt content is over three times greater than during recent years in the English Channel, the chlorophyll in the plants below a square metre is considerably greater than in the water off Plymouth.

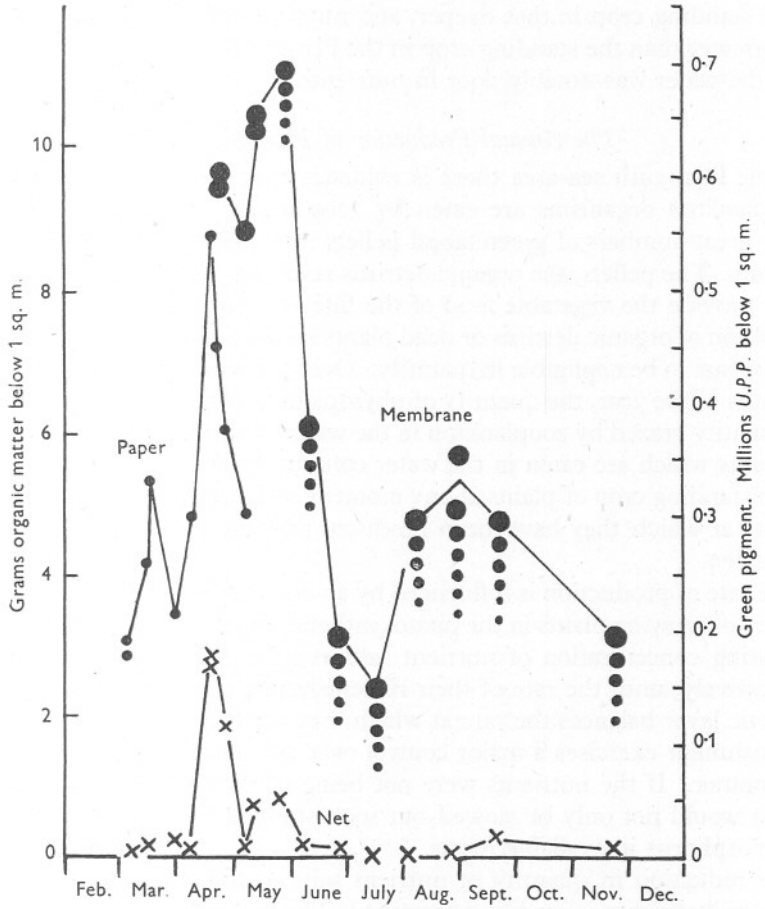


Fig. 4. The quantity of green pigment and the (calculated) quantity of organic matter in the phytoplankton at a position 5 miles seaward from Plymouth during 1949.

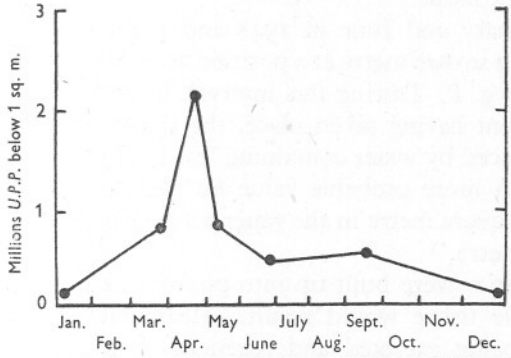


Fig. 5. Phytoplankton population on George's Bank, Gulf of Maine, in terms of units of plant pigment below a square metre. (After Riley, 1946.)

The standing crop in that deeper, and nutrient-rich, sea-area is about five times greater than the standing crop in the Plymouth area during 1949—a year when the water was notably poor in nutrients.

*The Annual Production of Phytoplankton*

In the Plymouth sea-area there is evidence that the majority of the larger phytoplankton organisms are eaten by zooplankton organisms. These discharge great numbers of green faecal pellets into the water when plant life is abundant. The pellets, the organic detritus resulting from them, and some few plants provide the vegetable food of the filter-feeding bottom-living animals. Deposition of organic detritus or dead plants on the floor of the open sea in this area appears to be negligible in quantity. Over the whole year, or over the first 6 months of the year, the quantity of phytoplankton produced approximates to the quantity grazed by zooplankton in the water column. Yet only a portion of the plants which are eaten in the water column are fully digested.

The standing crop of plants at any moment is the resultant balance between the rate at which they have been produced and the rate at which they have been eaten.

The rate of production is influenced by an array of factors, in addition to the number of growing plants in the photosynthetic zone. As the year advances the decreasing concentration of nutrient salts reduces the rate of multiplication progressively, until the rate of their replenishment in the water of the photosynthetic layer balances the rate at which they are being utilized. This rate of replenishment exercises a major control over the monthly production during the summer. If the nutrients were not being continuously replenished plant growth would not only be slowed but soon stopped through lack of nitrogen and phosphorus in available forms.

The reduction in quantity of nutrient salts in the water column between winter and summer is readily determined. This quantity, plus that which has been excreted by the animals or otherwise reformed, has meanwhile been built up into plant tissue.

Between February and June in 1948 and again in 1949, the decrease in phosphate below a square metre at a position 20 miles off-shore from Plymouth amounted to 0·49 g. P. During this interval, in both years, there is evidence of water movement having taken place, the richer water present in January having been replaced by water containing less total phosphorus (Armstrong & Harvey, 1950). A more probable value for the decrease in phosphate since January below a square metre in the water actually present in June is 0·40 g. P below a square metre.

If these quantities were built up into phytoplankton some 53–65 g. of dry ash-free vegetable tissue would result. Meanwhile, during the 5 months, phosphate was being excreted and regenerated in the water and this also utilized by plants. The 53–65 g. of vegetable tissue is an estimate of the

*minimum* quantity of plant tissue produced; in all probability it was greatly exceeded.[1]

Minimal estimates of production during the first half of the year have been made by Atkins (1928) and by Cooper (1933) in previous years, from the decrease in phosphate, in nitrate, in carbon dioxide and from the increase in dissolved oxygen. The values range from 85 to 190 g. of organic matter in the 6 months.

During the second half of the year the standing crop is less. In addition, the low concentration of nutrients slows the plants' growth rate. It is not until after mid-September that any material increase in nutrients occurs in the upper layers. By this time the quantity of light is half that in summer and is falling rapidly (Fig. 6). Thus, there is almost certainly less production during the second half of the year.

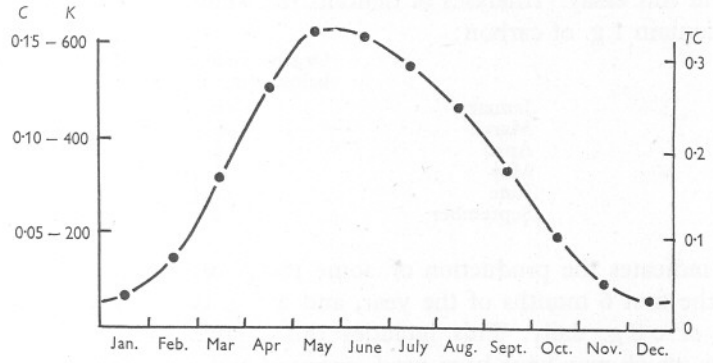


Fig. 6. Average illumination at Plymouth for the years 1930–37. *K*, kilolux hours per day; *C*, gram calories per cm.$^2$ per min., both for light within the range 380–720 m$\mu$ wavelength. *TC*, deduced total solar radiation, which includes infra-red, in g./cal. per cm.$^2$ per min. (From data by Atkins, 1938.)

These various considerations and minimal half-year estimates provide reason to expect that the total production throughout the whole of 1949 is unlikely to have fallen short of 120–200 g. of organic matter below a square metre (an average of 0·4–0·55 g. daily), and may have been considerably more.

It is of interest to compare this assessment of the annual production of organic matter by plants in this nutrient-poor area with an assessment based on entirely different premises in another sea area.

[1] Observations made in this area and in Loch Striven suggest that during March the diatom population in the whole water column divides on the average once in 36–38 hr., with the production of 50–70 % of its own weight of organic matter daily. From Fig. 6 it is seen that the incident light in March is roughly the average of that for the period January to June; the temperature is rather less than the average over this period. On the other hand, during April and May the concentration of nutrients in the upper layers falls rapidly. Hence for the first 5 months of the year there is suggested a daily production of rather less than 50 % of the biomass of the standing crop. If a value of 30 % daily is assumed, and the mean biomass over the first 5 months is 5–6 g. organic matter below a square metre (Fig. 4), then the production during this period amounts to 250–300 g.

A very rough assessment of the whole annual production of phytoplankton in the Gulf of Maine has been made by Riley in the following way. Transparent and black bottles were filled with the water, kept at sea temperature in a barrel of water for one or more days and the resulting difference in oxygen content of the light and dark bottles determined. This difference gives a direct measure of the gross production by the plants, that is the quantity of carbon synthesized, and takes no account of their losses meanwhile by respiration. The latter were calculated from the estimated quantity of plant life in the water and subtracted from gross production. From the depth of the photosynthetic zone, month by month, in the area and the relative light intensities, the carbon synthesized below a square metre was roughly estimated. In the following table, the quantity of organic matter has been substituted for the quantity of carbon, to make these readily comparable with the quantities already considered in this essay. Analyses of diatoms had shown that 2·24 g. of organic matter contain 1 g. of carbon:

| | Organic matter produced below 1 m.$^2$ in g. per day |
|---|---|
| January | −0·112 |
| March | +0·425 |
| April | 2·1 |
| May | 1·2 |
| June | 1·4 |
| September | 0·31 |

This indicates the production of some 160 g. organic matter below 1 m.$^2$ during the first 6 months of the year, and 270 g. during the whole year, an average of 0·8 g. daily. This includes the organic matter produced from nutrients which may have been used, excreted and used again.

### *Factors Affecting the Annual Production of Vegetation*

Having considered the sequence of plant life and the quantities involved, it is of interest to consider the major factors which determine the annual production of vegetable tissue.

The production taking place at any moment is the quantity of the standing crop multiplied by its *mean* rate of multiplication. Only those cells can grow which lie within the photosynthetic zone.

The quantity or *size of the standing crop* varies as it is either reduced by being eaten or is allowed to increase. Increase occurs when production exceeds losses due to grazing and losses due to respiration of those phytoplankton cells which are carried or sink below the compensation level, where they dwindle, being no longer able to make good their respiratory losses by photosynthesis. Observations on respiration by phytoplankton organisms indicate that at a sea temperature of 10° C., they lose some 4% of their organic matter daily when kept in the dark.

While phytoplankton cells are multiplying there appears to be little tendency

for them to sink, but as growth slows down owing to lack of nutrients, or light, or other ill-defined causes, the cells tend to lose buoyancy. Besides this, turbulence set up by rough weather, particularly between October and May, when a thermocline is absent, also carries cells to below the compensation level, thereby depleting the growing stock.

These losses may be small compared with those due to the continuous grazing by zooplankton, and, in shallow waters particularly, by filter-feeding bottom-living animals. Otherwise there would be a great accumulation of sinking organisms in the water column below the compensation level.

The *rate of multiplication* of the standing crop, or rather that portion of it within the photosynthetic zone, is most notably dependent upon the amount of light falling day by day upon the sea, and upon the concentration of nutrients. In some areas the availability of other microconstituents in the water probably affects the rate of multiplication.

The species composition of the standing crop will also influence its growth rate as a whole, since the different species composing the population have different light requirements for optimum growth rate, and these rates vary between different species. Smaller cells tend to grow faster.

The depth of the photosynthetic zone at any moment varies with the intensity of light falling on the sea, and in consequence so does that proportion of the standing crop which is making growth. Although the proportion of the light falling on the sea from month to month is much the same each year, the total quantity during any year varies materially. Thus from 1930 to 1937, the quantity of daylight falling on this laboratory varied between a daily mean of 307 kilolux hours in 1937 and 412 in 1930 (Atkins, 1938). Hence in a particular sea-area, changes in the quantity of incident light from year to year are likely to affect plant production.

The concentration of nutrients at any moment in the water in the photosynthetic zone, where it can be used by the plants, is the accumulated excess due to greater replacement than utilization. Replacement takes place by excretion from animals, by regeneration from dissolved organic nitrogen and phosphorus and by nutrients rising into the photosynthetic zone from below due to vertical mixing by turbulence. As far as we know, from experiments with one species only, the concentration of nutrient salts in the English Channel has, for several years, always been less than optimum, and in summer always acts as a powerful brake on the rate of growth.

A mathematical analysis of observations in the Gulf of Maine suggests that the availability of nitrogen and of phosphorus alternate in exerting the greater depressant effect upon growth rate during summer months.

It is helpful to consider the production of vegetation under simplified, hypothetical conditions, where the depth of water is similar to that of the photosynthetic layer. This implies little change in light intensity from season to season, a condition which may be approached in tropical areas. Plant pro-

duction throughout the year would be maximal if the standing crop kept the concentration of nutrients at such a low level that the daily increase in plant life, and never more, was grazed by zooplankton and the plants utilized the nutrients as quickly as they were being reformed. Thereby the dissolved organic nitrogen and phosphorus would be kept at a maximum, and the rate of replacement of nutrients both by regeneration from it, and by excretion from animals, at a maximum also.

In waters of depths greater than the photosynthetic zone replacements of nutrients, or their immediate precursors, by turbulent diffusion from below, plays an increasingly important part. Zooplankton rise by night to feed in the upper layers, then fall by day and excrete below the zone some of the combined nitrogen and phosphorus which they have collected. There is thus a continuous drain from the upper layers to the water below. Turbulence is the means by which this drain is compensated. Our observation of phosphorus compounds in the water column indicates that this drain downwards becomes pronounced only after the thermocline has formed. Throughout the period of spring diatom maximum, turbulence is sufficient to offset it. In this way turbulence contributes to production, while at the same time reducing production by carrying plant cells downwards.

Present knowledge shows that the production of plant tissue in the sea from day to day depends upon:

(i) The rate of regeneration of nutrients from dissolved organic compounds, particularly within the photosynthetic zone.

(ii) The quantity of nutrients rising by turbulent motion from below.

*On (i) and (ii) depends the continuance of growth.*

(iii) The population density of zooplankton eating the stock of growing plants.

(iv) The rate of loss of growing cells due to sinking below the zone. This is largely occasioned by turbulence, particularly in winter.

(v) The mean depth of the photosynthetic zone throughout each 24 hr. This varies with the quantity of light falling daily on the surface of the sea (Fig. 6) and with the transparency of the water.

*On (iii), (iv) and (v) depends the magnitude of the growing stock, or quantity of photosynthesizing phytoplankton.*

(vi) The considerable effect of temperature on the respiration rate of the plants, which tends to be offset by its effect upon the rate of regeneration of nutrients and upon the rate of photosynthesis.

(vii) The concentration of nutrients in the water within the photosynthetic zone. These consist of nitrogen in the form of ammonia, nitrate, nitrite and some amino-acids, and of phosphorus in the form of phosphate and probably of some organic phosphorus compounds.

(viii) The concentration of some other constituents of sea water (*vide infra*).

*On (v), (vi), (vii) and perhaps (viii) depends the growth rate of the growing stock of plants.*

In nature all these eight factors vary continuously, and most are interdependent upon one another.

Riley's analyses of survey data in several areas have indicated the relative influence of some of these factors and of how their influences change with the seasons. Before this valuable mathematical tool can be used in this area, a reasonably accurate technique of estimating the standing crop of phytoplankton needs to be evolved. However, a consideration of the rather complex and changing picture, which these eight factors presents, leads to a conclusion relevant to this thesis.

In comparing conditions from year to year in the area, small differences in the overall conditions of light, turbulence and temperature are likely to be subordinated to the big differences which may occur in the totals of all forms of combined nitrogen and phosphorus in the water. In the early 1920's there was twice as much as in recent years: one would expect that this difference alone doubled the regeneration and supply of nutrients to the growing plants, thereby doubling the production of vegetation except for a short period in the winter.

The possibility that microconstituents, other than nutrients, in the water may affect the growth rate of phytoplankton in nature is indicated by experiments *in vitro*. These have shown that very minute additions of salts, of iron, of manganese, of other elements, and of several organic compounds, increase the division rate of many species of plankton algae growing in sea water enriched with nutrient salts. Hence it is possible that varying concentration of some of these substances in the sea may affect the production of phytoplankton. Observations by Hart in the South Atlantic actually indicate that, in these nutrient-rich waters, the supply of some constituent derived from land drainage allows the much heavier development of plant life which occurs in some areas than in others. There are numerous observations which show that the multiplication rates of *particular* species of phytoplankton differ in different sea waters into which they have been introduced, due to microconstituents other than nutrients and iron. It is not known what constituent or constituents may be lacking, nor indeed whether there may be inhibitory organic compounds in the water. Somewhat indefinite evidence of the presence of inhibitors in some waters is provided by experiments by Allen & Nelson (1910) which showed better growth of diatoms after nutrient-enriched waters had been treated with hydrogen peroxide, chlorine or charcoal.

The list of substances which promote growth of marine plants is increasing. Concerning one of the more obvious essentials for growth the following is of interest. The quantity of manganese in an available form in the waters off Plymouth has been shown by experiment to be insufficient for a luxuriant growth of several species of autotrophic flagellates. Samples of water from an area in the Irish Sea, where flagellates are noticeably abundant, contained more than twice the concentration of available manganese found in this area. The inference

that in nature varying concentrations of this element influence the growth rate of these species seems justified.

In temperate seas, where low concentration of nutrients limits the annual production, a greater rate of multiplication of the plants would correspondingly increase production before and after the duration of the thermocline, and during these periods would allow the plants to keep down the concentration of nutrients to an even lower level. By so doing the dissolved organic nitrogen and phosphorus in the water column are increased, and the rate at which the phosphate and ammonia are released is increased also. In this way, the effect of a greater multiplication rate would be similar to the effect of more intense illumination in early spring and autumn, and would increase the turnover of nitrogen and phosphorus compounds.

## The Zooplankton Community

The wide variety of species in the zooplankton community differ greatly both in size and in their content of water. Moreover, there are considerable differences in the proportion of water in zooplankton from different areas, which are ascribed to differences in quantity of stored lipoids, this again being dependent upon the supply of phytoplankton food. It is, in consequence, desirable to express the quantity of such a mixed community in some one form. The content of dry organic matter is suitable and provides a measure of the value as food for other animals.

The population density of zooplankton organisms, expressed either as number or weight per *unit volume*, provides a measure of their *availability* as food for other animals. The quantity of zooplankton below a *unit area* of the sea is the *quantity maintained* by the vegetation produced in the water below that unit area. Moreover, the quantity below a square metre of the sea, expressed as weight, allows comparison to be made with observations made elsewhere. Comparable observations have been made, notably off the American Coast and in the Northern Sargasso, where quantitative catches have been dried and ashed, the loss on ignition providing a direct estimate of the organic matter.

The two ecological groups of which the zooplankton is composed—the plant-eating and the wholly predatory organisms—merge into one another; there is no sharp line of distinction between them. From limitations imposed by their size, the smaller organisms are likely to be herbivores. Many of those of medium size are omnivores, and the remainder, forming a small but very varying part of the community, are predominantly carnivores. Many of the latter are of relatively large size—ctenophores, medusae, arrow worms, *Tomopteris*, and the early planktonic stages of young fish. An exceptional group are the Salps which, although of relatively large size, are predominantly herbivorous. The effect upon the community of these purely predatory organisms is enhanced by the depredations made by pelagic fish, and by

omnivorous filter-feeding, bottom-living, organisms, more particularly in shallow water.

Almost always the bulk of the zooplankton is composed of the plant-eating group, and of these the bulk consists of juvenile copepods and their nauplii, with a variable, usually small, proportion of the larvae of bottom-living organisms. These latter spend a limited time, between a week and 2 months, forming the *temporary plankton*, whereas the life span of the copepods, from egg to adult, varies around 6 weeks, with the exception of the brood which lives over the winter months.

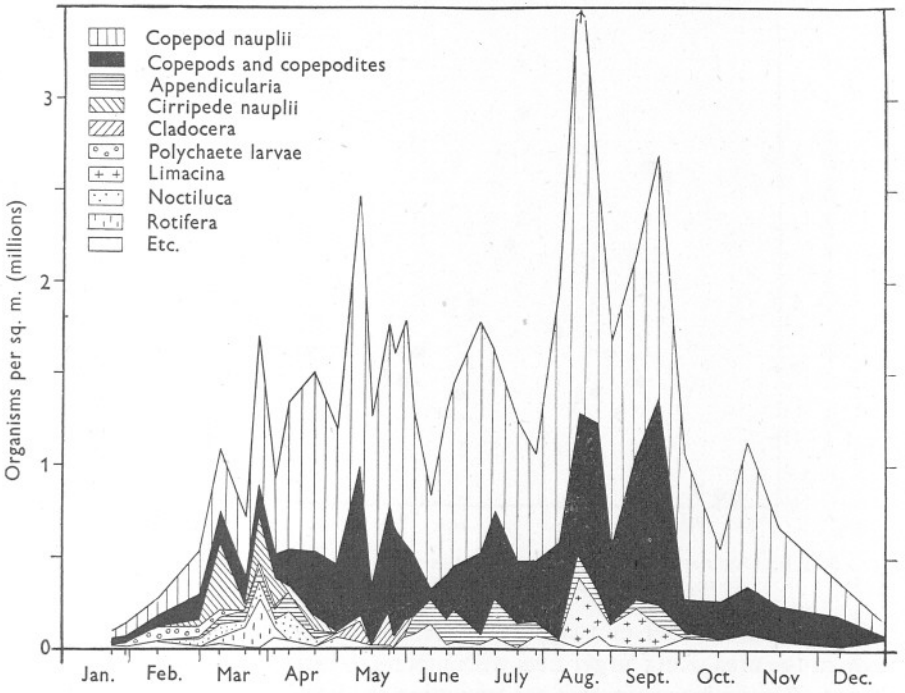


Fig. 7. Number of zooplankton organisms in millions caught in net, below a square metre in the sea off Plymouth, with a depth of 50 m., during 1934. (Harvey, Cooper, Lebour & Russell, 1935.)

Twice a month throughout 1934 several vertical hauls were made with a fine silk net at a position 4 miles off-shore from Plymouth, in 50 m. of water. The quantity of water filtered was registered by a meter, and the organisms in an aliquot of the combined catches were counted. The composition of the catch from the water at this position on the various dates is shown in Fig. 7.

The phosphorus content of the animals in a second aliquot of the catch was determined. From their phosphorus content an approximate value of their organic matter can be derived. Analyses of mixed communities, mostly copepods, show them to contain about 83% of water and 0·2% of phosphorus.

Analyses of zooplankton quoted by Fleming give a C : N : P ratio of 40 : 7·4 : 1 which implies 87 times more dry, ash-free, organic matter than phosphorus.

The values shown on the right of Fig. 8 are derived in this way. After attaining a maximum in early May, the summer population below a square metre fluctuates around a density containing some 2 g. of dry ash-free organic matter, with a significant increase in September. This autumn increase appears to be of frequent occurrence in other areas, and in some to occur before any autumn increase in phytoplankton would be expected, and before the summer population of predatory zooplankton is likely to have died away.

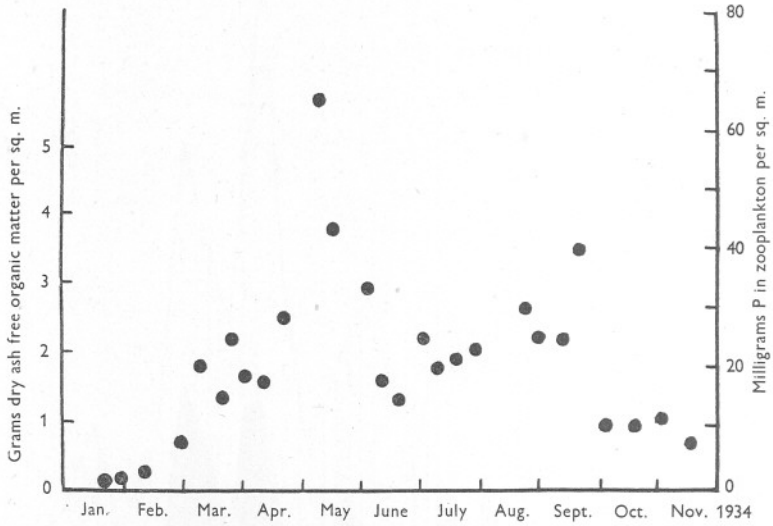


Fig. 8. Organic matter and phosphorus in zooplankton below a square metre, in 50 m. depth, off Plymouth. (Data from Harvey *et al.* 1935.)

During the summer of 1949, a considerable number of vertical hauls were made in the area using larger nets with meters to register the quantity of water filtered. The primary aim was to determine the patchiness of the distribution of the plankton. So far, it appears that the values shown in Figs. 7 and 8 are a reasonable rough approximation to the mean population density over the area. The catches in 1949 ranged from 1 to 1·7 g. dry weight (0·85–1·45 g. organic matter) below a square metre. These are significantly less than found in 1934, when the water contained more nutrient salts in solution at the beginning and at the end of the year.

In June 1947, a series of hauls were made at intervals throughout 24 hr. at two positions in the English Channel. These show the variation between one catch and another made in substantially the same body of water, and also indicate the proportion of the biomass which was present as macroplankton caught in the larger net. Vertical hauls between surface and bottom were made with a silk net having a mesh with openings 0·2 × 0·2 mm., and oblique hauls were made between 35 m. and surface with

a stramin net having meshes 1 × 1 mm. With the latter, the catches varied considerably in quantity, partly due to diurnal migration; hence, for purposes of comparison, the catches made at midnight, when the largest number of organisms have migrated into the upper layers, were chosen.

The composition of the catches shown in wet weight per cubic metre of water filtered is given in Tables I–III.

TABLE I. CATCHES MADE WITH SILK NET 20 MILES SEAWARD FROM PLYMOUTH. ALSO WITH 2 M. STRAMIN RING TRAWL, HAVING 1 MM. MESH IN OBLIQUE HAUL BETWEEN *C.* 35 M. AND SURFACE. 9 AND 10 JUNE 1947.

| | Wet weight in milligrams per cubic metre of water filtered | | | |
|---|---|---|---|---|
| | Copepods, mysids, euphausians, and decapod larvae | Medusae | *Sagitta* | Young fish |
| Silk net | | | | |
| Afternoon | 105 | 3 | — | — |
| Dusk | 85 | — | — | — |
| Midnight | 130 | 2 | — | — |
| Dawn | 145 | — | — | — |
| Midday | 195 | — | — | — |
| Afternoon | 115 | 2 | — | 1 |
| Mean wet weight | *130* | *2·5* | — | *0·02* |
| Stramin net | | | | |
| Midnight | 3·6 | — | 0·7 | 0·23 |

TABLE II. CATCHES MADE WITH SILK NET AND WITH 2 M. STRAMIN RING TRAWL AT 49° 22′ N., 6° 12′ W., BEING 30 MILES SOUTH OF THE SCILLY ISLES. 28 JUNE 1947.

| | Wet weight in milligrams per cubic metre of water filtered | | | |
|---|---|---|---|---|
| | Copepods, mysids, euphausians, and decapod larvae | Medusae | *Sagitta* | Young fish |
| Silk net | | | | |
| Morning | 172 | 35 | 19 | 0·2 |
| Midday | 201 | — | 48 | — |
| Afternoon | 165 | 18 | 26 | — |
| Dusk | 174 | 57 | 8 | 11 |
| Midnight | 140 | — | 0·5 | — |
| Mean wet weight | *170* | *22* | *20* | *2* |
| Stramin net | | | | |
| Midnight | 5·6 | 36 | 5·5 | 1·1 |

Subsequent analyses of the catches made with the silk net allow mean values of the population density below unit area to be calculated.

TABLE III. ORGANIC MATTER IN ZOOPLANKTON BELOW 1 M.$^2$ CAUGHT IN 0·2 × 0·2 MM. MESH NET (G.).

| | |
|---|---|
| 20 miles south of Plymouth | 1·6 |
| 30 miles south of Scilly Isles | 3·5 |

The estimates made in 1934 and 1949 indicate that the water off Plymouth maintained an average of some 2 g. of organic matter in the form of zooplankton

below a square metre, after the population peak in April 1934 until October, and a smaller quantity in 1949.

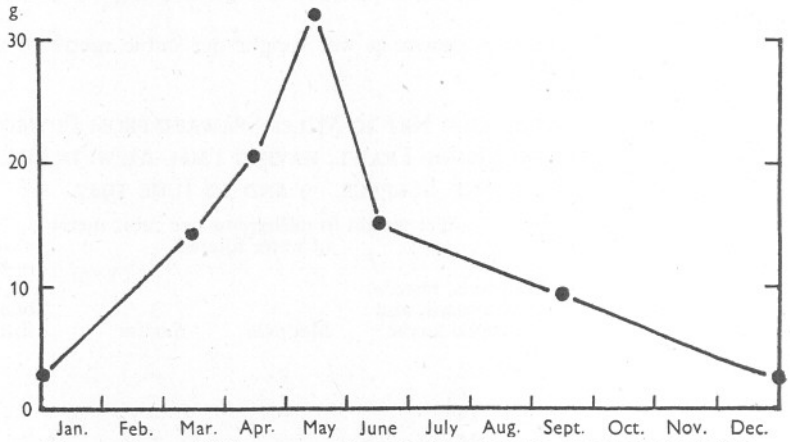


Fig. 9. Dry weight in grams of zooplankton below a square metre in the Gulf of Maine. (After Riley & Bumpus, 1946.)

It is of interest to compare these quantities with those found in other areas. The nutrient-rich waters of the Gulf of Maine, after the peak population in April or May, maintain some 12 g. dry weight of zooplankton, containing about 10 g. of organic matter, below a square metre. The waters of the Northern Sargasso between July and September were found to maintain zooplankton containing 1·4 g. organic matter. This quantity is rather less than that maintained off Plymouth in 1934; the standing crop of phytoplankton also appears to be less, or at least to contain less chlorophyll.

### *Food of the Zooplankton*

In general, the metabolic rate of small organisms is greater than that of larger ones; equal weights of vegetation will support the life of much less bacterial or small zooplankton tissue than, for instance, lamellibranch tissue.

Small animals not only need more food to make up for their greater metabolic rate than do larger animals, but, in general, weight for weight, they collect and partially digest a much greater quantity. For instance, the larvae of large bivalves, weight for weight, filter very much more water than the adults. They are stated, weight for weight, to digest and oxidize to carbon dioxide a hundred times more food.

In addition to requiring more food to make good their greater respiratory losses, the smaller animals are likely to be more wasteful of the primary vegetable food supply. When a plant is eaten, broken and only partly digested, a quantity of protein and carbohydrate dissolves and escapes into the water. Some of this is used by a sparse flora of bacteria, and possibly, a little by other micro-organisms. The solution is so dilute that the dissolved organic matter

is not at all readily available. Much of it is surely oxidized by oxygen in the water without being built into the bodies of bacteria. This is entirely lost to the food cycle. For this reason, the feeding habits of organisms in the zooplankton community is of interest.

Many wholly carnivorous species contain much more water than the herbivorous crustaceans—arrow-worms twice as much, ctenophores or medusae ten to twenty times as much—hence, although they may appear bulky, their organic content is usually small compared with that of the omnivores and herbivores forming the remainder of the community. The quantity of the latter which the carnivores succeed in catching and destroying is unknown, but on occasions their depredations appear to be great. During July 1949, an area was encountered in the mouth of the Channel, in 6° W., with a macroplankton fauna very considerable in comparison with that in the water off Plymouth, and consisting largely of medusae and the planktonic worm *Tomopteris*. Catches with a fine silk net consisted mostly of these worms, while copepods and other crustaceans were almost entirely absent; the quantity of these latter below a square metre was only a small fraction of that in the water off Plymouth. These facts indicate that *Tomopteris* is a voracious predator, and had succeeded in eating almost all the omnivores and herbivores. Of the other carnivores, the voracity of ctenophores is well known. Bigelow has noted that the smaller plankton animals are locally exterminated in the centres of abundance of *Pleurobrachia*, which is commonly found packed with copepods or euphausians as well as with larval fish.

The copepods, during their earlier stages, are probably from their very size mostly herbivorous, feeding upon phytoplankton. In their later stages many are omnivorous, eating whatever organisms they are able to catch. Some species, as *Temora* and *Centropages*, are notably voracious, and their stomach contents have been seen to consist of other crustaceans and of diatoms. If a *Calanus* is placed in a dense population of diatoms, it can be seen to extrude green faecal pellets at 20 min. intervals. For greed, voracity and wasteful feeding, many planktonic crustacea are unmatched.

During 1933 and 1934, when frequent observations of the population of the phytoplankton large enough to be caught in a net were made, great numbers of such green faecal pellets were found in the water at the time and immediately after the population of the larger diatoms had risen to high values. That this heavy grazing is not limited to the larger plants is indicated by an analysis of observations made in the Gulf of Maine, although it is perhaps the sudden changes in the population density of the larger plants which show the effect of grazing most clearly.

Although the biomass, or quantity of organic matter in the form of zooplankton does not change greatly during the summer, growth is proceeding all the time and providing a daily quota of food for other organisms.

There exist observations on the life history of *Calanus finmarchicus* which

allow a rough estimate of the rate of increase in the biomass of individuals of this species during the summer months. It is reasonable to consider this species as rather typical of other copepods, and it is copepods which constitute the bulk of the zooplankton population. A period of some 50 days between egg and sexually mature adult appears usual during the summer, a very much longer period during the winter. The diameter of the egg of *Calanus* is recorded by Gibbons as 0·172 mm., indicating a wet weight of 0·005 mg. The wet weight of sexually mature individuals appearing in the Plymouth waters in summer is recorded as around 0·8 mg. Hence in the 50 days there has been a 180-fold increase in wet weight. In order to proceed with a calculation, an assumption is made that the percentage of dry organic matter in the egg is roughly the same as in the adult. A further assumption is made that the daily percentage increase in weight remains constant during the whole period of 50 days; in actuality there is likely to be a short lag period before logarithmic growth starts and a slowing towards the end of the period. From the equation of geometrical increase, $Q_t = Q_0 \epsilon^{kt}$, $t$ being 50 days, the daily increase is 10% of the weight.

There is an independent method of arriving at a rough estimate of this daily percentage increase. During the 50 days between egg and adult, some sixty young are reduced in numbers to two, the two necessary to maintain the population. Meanwhile, the creatures are being eaten steadily. If they are eaten at a rate proportional to their population density, the fall in numbers from sixty to two in 50 days indicates that 7% are eaten daily. The two estimates (of the daily percentage increase in weight, and of the percentage eaten daily by other animals) are in reasonable agreement.

Concerning the food required by the zooplankton, it is helpful to distinguish between the quantity which is assimilated, and which is either burnt to carbon dioxide in the respiratory processes or is built up into the growing animal, and the quantity which is eaten in excess of that assimilated.

Experimental evidence provides a measure of how much of their body substance is required to be made good in order to compensate for the daily loss by indicated respiration.

Computations, shown in the previous paragraphs, indicate how much is built up daily into the growing animals—from 7 to 10% of their own weight.

A great variety of animals have been kept in closed containers and the oxygen used by them estimated after a short interval. They appear neither to have been starved nor heavily fed, nor to have been entirely inactive. It seems permissible to assume that the respiration rates found experimentally averaged those of animals growing normally, and, after adjustment for temperature, indicated their average rates when living in the sea.

Experiments with both *C. finmarchicus* and with a mixed community of crustacean plankton indicate that the animals 'burn' 4% of the carbon in their

tissues daily, at our summer sea temperature. From descriptions of the experiments the animals had not been starved. From this it is concluded that, of the food which they normally collect and pass through their guts, a quantity of vegetable tissue equal to about 4% of the animal's tissue is assimilated daily and broken down to carbon dioxide. In addition, a quantity equal to 7–10% of the animal's tissue is built up into the growing animal. It is unknown whether these lowly animals need the whole range of amino-acids required by mammals, and it is unknown whether phytoplankton protein is deficient in any one or more amino-acids required by the zooplankton. Thus it is possible that the animals need to digest and absorb more vegetable tissue than the sum of the quantities burnt in respiration and built into their own growing bodies.

For simplicity and in order to arrive at a rough calculation it is permissible to treat the whole zooplankton community as herbivores, and the plants as not being deficient in any necessary amino-acid.

It then follows that the population below a square metre of the sea, containing on the average 1·5 g. of organic matter will require to *assimilate* daily: 4% or 0·06 g. of vegetable organic matter to make good respiratory loss; 7–10% or 0·15 g. to build up into new tissue and provide the daily quota which is used by other animals.

Thus, in this single step in the food chain—vegetable tissue to small quick-growing animals—about 30% of the vegetable tissue assimilated is lost as carbon dioxide and 70% converted to animal tissue.

The zooplankton animals collect and eat more food than they assimilate. Judging by the habits and great voracity of many zooplankton organisms, and by the number of their faecal pellets to be found still coloured green in the sea, they succeed in collecting much more when phytoplankton is abundant.

Since plant life is sparse during periods in the summer, it is of interest to consider how the zooplankton succeed in collecting their ration.

Experiments by different observers with the large planktonic copepod, *Calanus finmarchicus*, have shown that it can filter very small diatoms from 4 to 5 c.c. of water daily.

This suggests that if the whole summer population were to consist of adult *Calanus*, the animals below a square metre could filter the very small plants from only about 100 l. of water daily. The weight of plant tissue in this quantity of water is negligible.

Experiment has shown that *Calanus* can catch larger diatoms very much more efficiently than they can filter very small ones. Kept in a suspension of medium-sized diatoms, in an hour each caught the number originally present in 3 c.c. of water. Kept in a suspension of large-sized diatoms each caught in an hour the number originally present in 8 c.c. of water. It is of course possible that in these experiments, where the diatom population was dense compared with that in the sea, the *Calanus* did not exert their catching power to its fullest extent.

The results of these experiments suggest that if the summer population below a square metre consisted of late-stage *Calanus*, it might catch the larger diatoms in 2000–3000 litres of water daily. Then, for the zooplankton to live entirely on plants, a cubic metre of the sea would need to contain 100 mg. of organic matter in plants large enough to be caught in a net.

A population density of plants such as this is of rare occurrence during the summer. We do not know how diatoms are distributed with depth in the waters off Plymouth, but, judging from other areas, they are most concentrated in the upper 30 m. Taking this into consideration, our records indicate that this population density of netable plant tissue occurred only on five occasions out of twenty-eight during the summers of 1934 and 1935.

During these years the average size of the organisms forming the zooplankton community was only a fraction of that of late-stage *Calanus*. The smaller animals are, weight for weight, probably more efficient in collecting food than the larger organisms, particularly in filtering the smallest plants.

It appears that the filter-feeding mechanism of the larger zooplankton organisms is not so highly developed that they can obtain much of their food by this method. Indeed experiment with *Hemimysis* has indicated that it could collect no more very small diatoms than an adult *Calanus*, which is about one-eighth of its size.

The zooplankton doubtless obtains some food by eating planktonic larvae, eggs, and sperm cells discharged into the water by lamellibranchs and other bottom-living animals. As each one spawns it discharges a considerable fraction of its own weight into the water. However, the daily supply from this source is not likely to contain on an average more than 0·05 g. of organic matter per square metre per day over the summer months, unless the quantity of bottom-living animals has been grossly underestimated.

During the periods of diatom scarcity the copepods' guts are often seen to contain pale brown matter, similar to the once-eaten plants which form most of the organic detritus then in the water. This detritus remains suspended in the water column for a considerable time, kept stirred by tidal streaming and wave action. It seems likely that this detritus, consisting of once-eaten plants, plays a considerable part in the food chain.

### *Fluctuations in Population Density*

Quite considerable fluctuation may occur from year to year in the average population of zooplankton maintained by the water occupying particular areas of the sea. Observations with the Hardy plankton recorder show this in various areas of the North Sea. It is pertinent to consider likely causes of these fluctuations.

Almost everywhere in the seas there is renewal of the water taking place from time to time, in some places frequently. Waters passing through any area are likely to have different biological histories in their immediate past, and in

consequence to have different contents of nutrients for plant growth or to have different rates at which these are being regenerated from dissolved organic nitrogen and phosphorus compounds. This in itself will bring about fluctuations from year to year in the plant food for the zooplankton. More zooplankton may be expected to be maintained where there is more phytoplankton over a sufficient period of time for temporary changes in the populations to be ironed out. Comparison of one area with another has long indicated this in a general way, and the more recent quantitative observations by Riley *et al.* all bear out this belief. Moreover, from observation of the changing populations of diatoms and copepods in a Scottish Loch, where the water is subject to little interchange with other water masses, Dr Marshall (1949) concludes that 'on the whole it does seem that the presence of diatoms increases the production of eggs and nauplii and helps the development of the younger stages' from time to time during the course of the year. Experiment indicates a similar relationship, since by enriching a tank of sea water with nutrient salts Clarke & Gross (unpublished) have induced a population density of copepods to develop in the water, amounting to several thousands per litre—a remarkable population density when compared with the 50 per litre found in the sea.

Another cause of fluctuations may be due to the copepod population being preyed upon to a different degree from year to year by migratory pelagic fish, or even due to the proportion of carnivorous zooplankton changing materially and for long enough to upset the balance seriously.

Of these two causes of fluctuations in a sea-area, supply of vegetable food appears to predominate. There may well be other circumstances which change from year to year and which play a part in controlling the copepod population, although these are not obvious. A rather remarkable distribution has been observed in the southern North Sea (Rae & Fraser, 1941). In 1920 and 1921 there occurred in January and December a considerable zooplankton population off the coast of East Anglia, and in the winter of 1933 off the Dutch coast. This has been attributed to heaping caused by the prevalent wind drift of the upper water layers, and presupposes that during the long winter nights the organisms spend most of the 24 hr. near the surface and a lesser period in the compensation current flowing in the deeper layers. These observations, and the inferences to be drawn from them, suggest a mechanism which may play an important part in regulating the distribution of zooplankton in some coastal areas.

When the population densities of two different areas are compared, another factor, and a potent factor, needs consideration. Vertical turbulence, and its effect on the production of plants, is unlikely to be the same. By renewing the nutrient salts in the photosynthetic zone in one area more rapidly than in another, plants are enabled to grow more rapidly so that a similar standing crop of plants can provide a greater daily supply of food for copepods. Yet, in

spite of this, and of differences in the depth of the photosynthetic zone, and of differences in temperature, the population per unit area of zooplankton does seem to follow roughly that of the phytoplankton in very different sea areas. Our present knowledge points to the average standing crop of plants usually predominating over other causes in controlling the average population density of zooplankton, provided the sea-areas compared with one another are of considerable extent. Within such areas there are liable to be extensive patches where diatoms abound, as in the southern North Sea, in which the zooplankton is less abundant than around the edges of the patches. These patches presumably arise and persist because the intensity of grazing within them is less than in the surrounding waters.

## Pelagic Fish

It is possible to make a rough estimate of the quantity of pelagic fish, mostly herring, in the North Sea, extending over some 170,000 square miles. During the 1930's roughly one million tons of herring were landed each year. Of the various year classes caught during any one year, about one-half the quantity is caught during the following year—the annual mortality of adult fish is 50% from all causes. About three-fifths of this mortality is ascribed to fishing, which is to say that 30% of all adult fish were caught annually. Hence the quantity of adult fish in the area is some three million tons. To this quantity there needs to be added the smaller fish not large enough to be enmeshed in the herring nets, that is, fish up to and including many 3-year-olds. It is only possible to guess that their weight may be a third or even more than that of the older fish.

If these two assumptions are accepted: (i) that fishing accounts for three-fifths of the natural mortality of the older fish, and (ii) that the younger fish, not enmeshed in the nets, aggregate one-third of the larger fish, then the total population amounts to four million tons.

The population would then, if evenly distributed, comprise 1·8 g. of dry organic matter below a square metre.

There are no data on which to base a similar estimate of the overall average population density of pelagic fish in the English Channel. All that can be done is to examine a presumption that it is not very different from that in the North Sea. The relative proportion of species is quite different; extensive and dense shoals of pilchard are encountered; great numbers of pilchard eggs are found in the water and further to the westward, in addition, an almost equal number of mackerel eggs. At first sight this suggests a mackerel population similar in over-all density to that of the pilchard. But this is not so, for pilchard eggs hatch out as larvae in a much shorter time than mackerel eggs. The herring fishery in the Channel has never been commensurate, area for area, with that in the North Sea. Although different shoaling habits of the fish could account for this, there is more reason to believe that the overall population density of

the fish is less in the Channel. The great difference between the two areas is the pilchard population, not present in the North Sea, and exploited in the Channel to only a limited extent on account of a restricted market for this fish. Recently a ship searching for shoals with an echo-sounder has encountered numerous shoals, some quite extensive, half a mile or more across. The fish, when shoaled, are sometimes so dense that they obliterate any 'trace' being recorded from sound reaching the sea bottom and returning to the ship. Furthermore, if a weighted wire is hung from a ship when over a shoal, fish are continually knocking against the wire. Fishing with a ring trawl, having a head rope 260 yards long and encompassing some 4600 m.$^2$ of water, catches of 4800 kg. of pilchard or more have been obtained. These observations suggest that when in shoals, the population density may well amount to about 1 kg. of fish per square metre, containing 170 g. of organic matter.

This tentative estimate of the density of shoaled fish permits a calculation which suggests that 1·8 g. of organic matter per square metre in pelagic fish in the North Sea may not be very different from the overall density in the English Channel. On this assessment the mouth of the Channel, extending to some 10,000 square miles, would contain some $5 \times 10^{10}$ g. of organic matter as pelagic fish. If these were all pilchard, and all in shoals at a density of 170 g. organic matter below a square metre within the shoal, the shoals together would cover 18 square miles. This computed 18 square miles of shoals assumes that all pelagic fish, mackerel, herring and pilchard of all sizes shoal with a similar density and are all present in shoals. They do not do so.

Since many shoals, composed of pilchard only, some extending over half a square mile or more, have been encountered by a single ship during the course of a few months, this total of 18 square miles is not wildly improbable.

The food required by the pelagic fish deserves consideration. Various experiments cited in the literature have shown that fish weighing 10 g. or more consume some 2 l. of oxygen daily per kilogram of body weight. Most of the experiments have been made at room temperature, which suggests somewhat less consumption at sea temperature. There is no indication that these fish were either starved or heavily fed, so their oxygen consumption under natural conditions, where they are slowly growing, is likely to be similar. The value indicates that 1–1$\frac{1}{4}$% of their tissue is consumed daily, and that a commensurate quantity of their daily intake of food is completely broken down to carbon dioxide. Presumably most of the food eaten in excess of this quantity will be returned to the water either in the form of solids or as partly digested and soluble organic matter, which will serve as food for other organisms and for bacteria. Hence the pelagic fish below a square metre, containing some 1·8 g. of organic matter will, on the average, assimilate daily a quantity of organisms containing about 1$\frac{1}{4}$% of this amount of organic matter, in order to make good respiratory losses. These fish do not live wholly on zooplankton, although this

constitutes a large part of their diet. For simplicity in this computation they are assumed to feed on zooplankton alone.

Experiments on the growth of plaice over protracted periods have a bearing upon these rough estimates. In order to maintain their weight, without loss or gain, they needed some $1\frac{1}{4}\%$ of their own weight of animal tissue to be supplied daily as food.

In nature the pelagic fish are growing very slowly indeed, compared with small organisms such as the zooplankton. A herring or mackerel, some few months old and weighing 5 g., will take some 3 years to attain a weight of 100 g., and thereafter increase in weight still more slowly. During the 3-year-period it will have lost by respiration some 750 g. of tissue and gained 95 g. by growth.

In this step in the food chain, herbivore to carnivore growing rather slowly to moderate size, only 10 or 11% of the assimilated food is converted to carnivore tissue, the other 90% being respired as carbon dioxide. Whereas in the previous step, phytoplankton to quick-growing herbivore, 70% of the assimilated food is converted to herbivore tissue, in spite of the more rapid respiratory loss.

These quantities relate to the quantity of food assimilated. In order to increase growth, progressively more food doubtless needs to be eaten than is assimilated. Dawes's (1930, 1931) experiments on the growth of plaice indicate this. A small female fish eating 1·9% of its own weight of mussel flesh daily gained an average of 0·06% daily; a small male fish eating $2\frac{1}{2}\%$ of its own weight of mussel flesh daily gained 0·25% of its own weight daily.

## Bacteria in Suspension

No observations have been made of the number of bacteria in the waters of the English Channel; at off-shore positions in other areas there are usually found some 100 or less per cubic centimetre which are capable of growth on nutrient media. Such plate counts give minimal values of their population density, because the bacteria tend to attach themselves firmly to suspended particles or organisms, and a particle with several attached bacteria would only 'count' as a single organism. Allowing for this, it appears unlikely that the number in off-shore waters exceeds about 1000 per c.c., and that no more than 0·2 g. wet weight occur below a square metre in a water column 70 m. deep. Such a quantity would contain some 0·04 g. of organic matter.

Their numbers in the sea are limited by the great dilution of dissolved organic matter serving as food in the water, probably no more than 5 or 10 mg. per litre, about half of which appears to be in forms unsuitable as bacterial food. Their growth is also probably limited by the presence of bacteriostatic substances, whose presence in the sea has lately been confirmed, and by their being ingested by other organisms.

Marine bacteria, at our mean sea temperature, lose by respiration some

30% of their own weight daily, varying from species to species. Their food requirements are great, although their biomass is small. This estimate indicates that no more than some 0·013 g. of dissolved organic matter below a square metre are broken down to carbon dioxide by bacteria daily.

### Demersal Fish

It is unknown what average weight of demersal fish lies below an acre of the English Channel, but it is possible to make a reasoned guess. The North Sea is not strikingly dissimilar in fertility to the English Channel, and for the North Sea extensive data are available.

Approximately half a million tons of demersal fish were landed each year during the 1930's. Of fish which were marked and put back in the sea, one-third were caught again within a year. Some lose their marks, others are not reported. This indicates that the total population of marketable demersal fish was about one million tons. Small fish of the same species which either passed through the meshes of the trawls or were thrown back perhaps amounted to an equal weight. In addition there are unmarketable species—particularly those which never grow big. A total population of three to four million tons of demersal fish of all species and sizes is not unlikely. This is equivalent to a mean population density of fish below a square metre containing $1\frac{1}{2}$ g. of dry organic matter.

The English Channel is almost certainly less populated than the North Sea. The landings of fish per acre are one-third of the landings from the North Sea, but it is less heavily fished. Statistics show that steam trawlers landed during the 1930's rather less demersal fish from the English Channel than from the North Sea per 100 hr. trawling.[1]

This suggests a mean population density in the English Channel containing $1–1\frac{1}{4}$ g. of organic matter, below a square metre, or some 50 lb. wet weight per acre.

Experiment has shown that demersal fish of moderate size completely consume and respire as carbon dioxide about $1\frac{1}{4}$% of their tissues daily, and further that they need to assimilate this quantity of tissue daily to maintain their weight. They feed very largely upon the bottom fauna, and therefore may be expected to assimilate daily a quantity of this containing some 0·015 g. of organic matter, and to eat rather more.

The relatively small consumption by fish compared with that by zooplankton (p. 129) is notable. Most of the planktonic animals reach maturity and die within a few weeks, except the brood which lives through the winter. Fish reach maturity in 1–7 years, and a very few individuals may attain a great age; cod and plaice as old as 24 years have been caught.

[1] During the course of an hour's trawling our research vessel sweeps about 10 acres of the sea floor and catches on the average rather more than 100 lb. wet weight of fish large enough not to escape through the meshes of the net.

## The Bottom Fauna

A considerable population of animals, live on, and buried in, the sea floor the majority obtaining food by creating a current of water from which plankton and detritus is filtered. The mechanisms for doing this are diverse in kind; many of the organisms lie buried and extrude a tube to the surface through which the water is passed. A smaller number live by passing soil through their guts and, from this, organic detritus and bacteria are utilized. A further small number, notably starfish and gastropods living on the surface, are carnivorous. In addition to these carnivores, demersal fish live on the epi- and in-fauna, and constitute perhaps the most effective group of predators. The crabs, prawns and amphipods living on the bottom are thought to be mainly scavengers, most of them making little demand on the living bottom fauna.

The population density of animals which live on, or burrow into, the bottom varies very much from place to place. There are areas where lamellibranchs such as *Spisula* or, near shore, where the common mussel cover the ground almost touching each other. Here there may be more than a kilogram of moist living tissue on a square metre, containing 150–200 g. or more of dry organic matter. On other areas there are found no more than 25 g. of living tissue containing some 5 g. of organic matter.

As methods of obtaining samples to a depth of about 6 in. have been developed, more and more animal life is being found in bottoms which contain only a rather sparse quantity on or near the surface. Large and aged bivalves are being found, buried, and having thick shells, not readily accessible to starfish and too well protected for their shells to be broken by most fish (N. A. Holme, private communication). The biomass of the fauna occupying sand, shell or gravel bottom appears to be composed largely of aged, slow-growing, buried individuals of the kind whose daily loss by respiration is slow.

With the exception of a small area near the land, where mud containing organic matter is deposited, there have been only a limited number of quantitative observations where the sea floor has been sampled to a depth of 6 in. or more. Based on these, an average of some 100 g. of living tissue in and on a square metre now seems a reasonable estimate. This will contain some 17 g. of organic matter. With the development of more efficient gear, and of under-water photography, a better picture of the biomass of the bottom fauna will be possible.

Of the many kinds of bottom-living animals, except the smallest, only a few are thought to be annual. Those constituting the major part of the biomass may live for several years. There is a worm in our aquarium 11 years old.

The results of numerous experiments on the respiration rate of various bottom-living animals provide data for a rough assessment of that part of their daily food which is completely consumed to form carbon dioxide. The food which is eaten but not completely consumed by an individual serves as food for other species. That part of it which is built up into living tissue of the

individual eventually provides food for predators or bacteria. One assumption has again to be made, namely that the animals used for experiment had not been starved, but contained or had recently contained food commensurate with that in their normal natural condition. This assumption would appear valid because the experiments did not aim at obtaining the basal metabolic rate and because the animals in many instances were collected shortly before the experiments.

The experiments, conducted between 16 and 23° C., show a very much greater respiration rate for small animals (around 200 c.c. of oxygen consumed per kg. of living tissue hourly) than for larger animals (around 80 c.c.). At our mean sea temperature the rates would be probably reduced to about two-thirds. Since the biomass of animals, when their population density is around 100 g. of living tissue per square metre, is mostly composed of larger slowly respiring animals, a mean rate of 80 c.c. oxygen consumed hourly per kilogram of tissue (170 g. of organic matter) is indicated. This implies the loss of $1\frac{1}{4}\%$ of their organic matter daily.

Hence organisms containing 17 g. of organic matter will assimilate 0·21 g. daily for their maintenance. There is no evidence that the population waxes and wanes with the seasons; however, the food to maintain the population will vary with the temperature of the water, although many of the organisms are likely to adapt their metabolism to slowly changing temperature.

It is remarkable that the population density of filter-feeding organisms on the sea floor should vary so greatly, often over extensive areas adjacent to each other, between which there is no reason to suppose the filter-feeders' food supply differs to any material extent.

Survival, particularly of the young, from predators, must play a considerable part in regulating the population density. For instance, an area in Plymouth Sound was heavily populated with mussels 4–5 cm. long in 1947, when *Asterias*, which had either settled there as larvae or had moved in from an adjacent area, decimated the population. However, it seems very improbable that the balance of life between carnivores and filter-feeding organisms can wholly account for the very different populations of the latter, except in isolated areas of limited geographical extent. Another instance of rapid change in bottom fauna in this vicinity does not allow any such simple explanation. An area of several square miles in Start Bay was very thickly populated with *Spisula*; within a period of some 2 months a heavy mortality took place, most of the *Spisula* shells sampled being then either empty or containing a dead organism; this catastrophic mortality had no obvious cause.

The nature of the sea floor has a marked influence not only on the species composition of the fauna, but also upon its density in terms of biomass. The former is readily understandable, the latter less so, for among the thousands of species of filter-feeding bottom-living organism, there must be many suited to life on or in all kinds of soils, with the exception of shifting sand which would

dislodge or bury their young. It is perhaps pertinent that under-water photography has shown ripple marks on sand at quite considerable depths, which suggests that the effect of gales may extend to depths hitherto unexpected.

The kind of sea bottom undoubtedly affects the settlement of larvae of particular species, and their metamorphosis. By partially filling bottles with soil from different sea bottoms and suspending them in the sea, Thorson concluded that planktonic larvae, which metamorphosed and settled, were able to choose their substratum. From experiment with the planktonic larvae of the worm *Ophelia*, Wilson showed that for metamorphosis and growth a clean sand was necessary with rounded grains about three times their own size. For these larvae, the size and shape of the interstices between the sand grains appears to render the bottom suitable or otherwise. Further investigation is now showing the influence of yet another factor. A species of the worm *Protodrilus* inhabits an area of shell-gravel. Remarkable experiments by Jägersten indicate that metamorphosis of these planktonic larvae is caused by a chemical substance which slowly dissolves out of this shell gravel, to which its distribution is limited. Experiment has also shown that low concentrations of copper promote the settlement and metamorphosis of ascidian larvae; these concentrations, though low, being several times greater than that usually occurring in sea water. The settlement, metamorphosis and subsequent growth of oyster larvae on different surfaces has been the subject of much investigation. This has led to the observation by Cole & Knight-Jones that they settle in greater numbers on surfaces where oysters have already settled than on comparable surfaces where settlement has not already taken place.

The distribution of the bottom fauna in soil communities, resulting in part at least from the exercise of choice by the larvae while members of the temporary plankton, causes another factor to affect the density of settlement or resettlement on the sea floor. Currents or drift of the water, which tend to change from time to time, may carry the larvae away from their suitable substratum. There is evidence of this happening in the Dogger Bank area.

In spite of these limitations to spreading and replacement of the population, it is still remarkable that the population density should vary so greatly.

## Bacteria in the Sea Floor

Several estimates have been made of the number of bacteria in marine muds containing organic detritus, in which they are likely to be more numerous than in clean open-sea deposits. Their numbers fall off rapidly below the upper layer of mud.

In the limited area of mud lying off Plymouth, investigated by Mare (1942), counts by dilution and plating indicate some $\frac{1}{2}$ g. wet weight of bacteria per square metre, containing about 0·1 g. of organic matter. Owing to their rapid respiration, bacteria lose some 30% of their substance daily at sea temperature, the rate varying with different species. Hence the complete combustion of 0·03 g. of organic matter daily per square metre due to bacterial activities is indicated.

## On the Quantity of Organisms Present, and their Daily Food Requirements

The mean quantity of organisms present throughout the year, per unit area over a considerable expanse of sea in the Plymouth sea-area, is set out in Table IV. Each quantity is deduced from the foregoing conclusions.

These rough estimates point to the pelagic organisms requiring vegetable food from which to assimilate some 0·23 g. of organic matter daily. There results from this intake zooplankton containing 0·15 g. of organic matter, a portion of which nourishes the pelagic fish, the remainder being eventually eaten by the bottom fauna.

Table IV. Mean Quantity throughout the Year of Plants and Animals below Unit Area, the Average Depth being 70 m.

| Wet weight of tissue containing 80% of water per acre (lb.) | Type of organism | Dry weight of organic matter, g./m.² | | | | |
|---|---|---|---|---|---|---|
| | | Quantity below a square metre (g.) | Daily production per square metre (g.) | Daily loss due to respiration | Food assimilated daily (g.) | |
| | | | | | Lost by respiration | Built into new tissue |
| ?180 | Phytoplankton | *c.* 4 | 0·4–0·5 | — | — | — |
| 70 | Zooplankton | 1·5 | 0·15 | 4% | 0·06 vegetable tissue | 0·15 vegetable tissue |
| 80 | Pelagic fish | 1·8 | [0·0016][1] | 1¼ | 0·025 animal tissue | — |
| — | Bacteria | 0·04 | — | 30 | 0·013 dissolved organic matter | — |
| 50 | Demersal fish | 1–1·25 | [0·001][1] | 1¼ | 0·015 animal tissue | — |
| 800 | Epi- and in-fauna | 17 | [0·03][2] | 1¼–2 | 0·2–0·3 | — |
| — | Bacteria | 0·1 | — | 30 | 0·03 | — |
| | | | | Total | 0·34 to 0·44 | |

[1] Based on a natural mortality of 30% per annum, due to being eaten.
[2] Based on a natural mortality of 60% per annum, due to being eaten.

Thus half of the deduced daily production of vegetable tissue appears to be assimilated by plant-eating organisms in the water column, leaving the other half, together with 0·12 g. of zooplankton organic matter, to maintain the bottom fauna, including the demersal fish feeding upon it.

In this table the zooplankton, assessed as containing 1·5 g. of organic matter per square metre on the average throughout the whole year, has been treated as entirely herbivorous. This it never is, and on rare occasions there may even be a considerable proportion of carnivores for short durations of time. On account of this alone, the relative proportion of plant to animal tissue available for the bottom fauna will vary. Furthermore, the ten per cent daily production is taken as persisting throughout the whole year, whereas it slows in winter. In consequence the estimate is more likely to be high than low.

Nevertheless, these observed and computed quantities shown in Table IV

indicate the dominant part played by zooplankton as consumers of vegetation and providers of food for animals higher in the food chain. They indicate that the production of zooplankton (0·15 g. daily or 2200 lb. wet weight per acre yearly) exceeds the production of all other animals.

The total daily loss by respiration of the whole animal community (0·34–0·44 g. of organic matter) is slightly less than the deduced daily production of organic matter. No significance is attributed to the total of the crudely estimated animal and bacterial requirements being rather less than the even more crudely estimated production of vegetable organic matter. Yet one might expect some loss of organic matter due to oxidation taking place in the sea without the agency of bacteria or other organisms. Experiments by Keys, Christensen & Krogh (1935) on the oxygen consumption by bacteria in stored sea water lends credence to an expectation of some non-vital oxidation in the sea.

The various estimates of production and losses have been arrived at in the following manner. On pages 118 and 124 computations have been made of the percentage of assimilated food which is converted into additional tissue in the growing animal. These relate to a steady population where the daily accretion is either eaten by other animals or fished by man—where growth equals the yield. Then

Food assimilated in unit time ($f$)
= growth in unit time ($g$) + respiratory loss in unit time ($r$).

The validity of these computations depends upon having chosen values of $g$ and $r$ for a sea temperature around 12° C. which are representative of whole populations, embracing all ages in terms of biomass, not of numbers. The premises have been stated from which these values, relating to a community of herbivorous zooplankton, were derived. Much the greater part of the biomass of a community of fish consists of individuals of moderate size—over 10 or 20 g.—such as have been found to lose $1\frac{1}{4}$% daily by respiration. There will be some fully grown, increasing not more than about 20% by weight annually (2–3% in linear dimensions) and respiring rather less rapidly. There will also be a small proportion by weight of quite small fish respiring more rapidly. For the whole community a loss by respiration of 1·25–1·5% daily appears a reasonable mean value. The growth rate, which, under the circumstances postulated, equals the rate of yield and the rate of mortality, is thought to lie in the region of 30–50% per annum for the major part of the biomass, much more for the small portion of it composed of quite small fish and less for the older larger fish. This indicates a growth rate of 0·08–0·14% per day. Observations of the bottom fauna indicate that most of the biomass is composed of well-grown organisms, many of considerable size. Even in the mud investigated by Mare, only 1% of the biomass consisted of micro- and meiobenthos. Well-grown bivalves and worms have been found to lose about 1–1·25% daily in respiration, quite small organisms very much more.

If, as a rough approximation, about a quarter or a third by weight of the bottom fauna is assumed to lose 4% daily on an average, and the remainder $1\frac{1}{4}$%, the whole community loses 2% daily. Concerning the rate of yield or mortality of this community, most of the biomass consists of long-lived animals feeding on vegetable and zooplankton detritus, many having attained an age of several years. A mortality rate of 60% of the biomass per annum seems a not unreasonable conjecture.

On these premises Table V is also constructed. It suggests that every 100 g. of vegetable tissue assimilated may yield:

70 g. of herbivorous short-lived zooplankton.
11 g. of herbivorous well-grown long-lived bivalves or worms.
4–7 g. (6–10% of 70 g.) of pelagic fish feeding on herbivorous zooplankton.
1 g. (6–10% of 11 g.) of demersal fish feeding on well-grown bivalves.
0·3 g. of carnivore feeding on carnivore, as fish on fish; or more if both are small and short lived.

It is implied that all the animal food eaten by carnivores is assimilated.

TABLE V. BALANCE SHEET OF ANIMAL PROTOPLASM

| | Percentage loss of biomass per annum 'Annual Mortality' | Percentage increase daily by weight ($g$) | Percentage loss daily by respiration ($r$) | Percentage of food assimilated, which is built into new tissue $\left(\frac{100g}{g+r}\right)$ |
|---|---|---|---|---|
| Zooplankton herbivores | — | 10 | 4 | 70 |
| Fish, community of all ages | 30<br>50 | 0·08<br>0·14 | 1·25–1·5<br>— | 5–6<br>$8\frac{1}{2}$–10 |
| Bottom fauna, most of the biomass being well-grown individuals | 60 | 0·16 | 2 | 11 |
| Full-grown fish, bivalves or worms, increasing in tissue weight not more than 20% per annum | — | <0·05 | 1–1·25 | <5 |

Although the premises on which these computations are founded are not sufficiently exact for definite quantitative conclusions to be drawn, they provide or expand a series of implications, most of which are self-evident without any such quantitative reasoning. Thus the yield, derived from the same quantity of primary vegetable food, will be still further reduced for every step in the food chain, if the food supply is inadequate. The average age, and the size, of individuals constituting an ecological group will have a profound effect upon this yield: if the respiration rate is doubled or the growth rate halved, the effect upon this yield will be the same, hence a higher sea temperature may be partially offset by an increased growth rate. The yield of pelagic

fish feeding on herbivorous plankton will be greater than that of demersal fish feeding on slowly growing bivalves, provided that both can collect a sufficiency throughout the whole year.

In addition to the losses which occur for every step in the food chain, there is a deterioration of food every time an organism is eaten or mutilated, due to organic matter passing into solution and becoming useless as food except for bacteria and possibly for some protozoa.

The estimates shown in Tables IV and V, and computations based on them, can only be accepted as pointers and not as conclusions, only as a first attempt to envisage the changing life in the sea as a whole and on a roughly quantitative basis. The estimates themselves are rude, but they are not notional, being founded on observation and experiment.

These estimates envisage the sea maintaining an average of 1000 lb. of animal tissue per acre. Is this quantity surprisingly great? The food chain leading up to many of the animals is long and this is not conducive to great fertility. On the other hand, it appears to be animals larger than bacteria and protozoa which convert most of the plants and each other into carbon dioxide. This constitutes a great difference between life in the sea and on land, where a proportion of the vegetation nourishes a considerable soil fauna of bacteria and protozoa. On the other hand, rich pastures may also maintain, out of sight, as much as 600 lb. per acre of worms and much insect life (Evans, 1948).

With a better 'balance of life' there is reason to suppose that the sea could maintain and yield an almost phenomenal quantity of animals compared with cattle on land. The Chinese have evolved a system where shallow sea-areas are banked off and filled with water from which predatory animals have been screened out. After the growth of algae has started, the 'ponds' are stocked with the fry of a quick-growing herbivorous fish. In the Phillipines, as described by Frey (1947), and also on the coast of India, this system is yielding as much as 5000–7000 lb. of fish per acre annually. At intervals of not more than 2 years, the ponds are drained and the mud bottoms allowed to bake in the sun; also, in India, they are ploughed. This treatment presumably affects the interchange of nutrient salts between soil and water, allowing more to pass into solution and preserve the pond's fertility.

## Evidence of Changing Fertility

The term 'fertility' of a sea-area, in its wide sense, implies the annual production of plants and the average quantity of animals maintained in it throughout the seasons. This quantity includes the bottom-living and migratory animals; neither of these allow quantitative sampling with any exactitude. It also includes the planktonic life in the water mass which does not usually remain in the area for any length of time, and is always subject to being replaced by another of very different biological history and potentialities.

The term 'fertility' comprises three concepts:

(i) The production of plants rather than their population density. Since, in most areas, production is directly dependent upon the supply of nutrients throughout a part of the year, the potentiality of the water to supply these nutrients is an almost direct measure of fluctuation in plant production from year to year. This potentiality to supply depends upon physical factors—as turbulence and temperature, changing with the seasons and varying from area to area—and the water's content of total combined nitrogen and phosphorus. Hence the concentration of one or other of these in the water provides a measure of the *potential fertility of the water mass* with respect to its production of plants.

(ii) The population of animal plankton living on the plants, changing with the seasons and providing food for the carnivorous plankton. This whole population of animals and plants moves in and out of a sea-area with the water masses. Short-term fluctuations in the phytoplankton and in the herbivorous zooplankton assuredly affect the early survival of most other animals, for which they are the only food during larval life. The quantity of planktonic life in the water also affects, or often affects, the movements of the migrating pelagic fish.

(iii) The population of longer lived animals which, once established, are able to withstand rather long periods of starvation. Where the bottom fauna is abundant it is notable that the greater proportion by weight is composed of relatively large and aged animals, and this also holds for the fish. This established population, which appears to comprise more than half the weight of living organisms, will be least subject to immediate changes from fluctuations in food supply due to changing water masses in the area. Their early stages, however, and the chances of this population maintaining itself by renewal, is very dependent upon the supply of planktonic food. The larvae need a population of food suited to their particular need, a population of organisms sufficiently dense for the larvae to be able to catch enough, a population present throughout the whole early life of the larvae. It is during their larval life that their respiration rate is greatest and they have not sufficient food reserves to live through an interval of starvation.

From general observations in the Plymouth area there is little doubt that the quantity of both pelagic and bottom-living organisms has decreased during the past 30 years. This opinion is not founded on measurement, but it is reinforced by the results of sampling and measuring particular populations and conditions.

Since 1924 comparable hauls have been made at weekly intervals with a stramin net, having meshes with openings around $1 \times 1$ mm., each haul filtering roughly 4000 m.$^3$ of water. During 1924, 1926 and 1929, consistently heavy catches were made, containing considerable quantities of late-stage copepods and euphausians. During 1925 and 1927 the catches were much less: during

subsequent years, particularly recently, catches have been very sparse indeed. It was soon observed by Russell that a relation existed between the size of the catches and the phosphate in the water at the beginning of each year.

The numbers of young fish in the catches were recorded. Of these, the number of clupeid fish varied in a very irregular manner in the daytime, and many more were caught at night (Russell, 1930). Hardy records catches of 2448, 27, 7, and 341 young herring in comparable vertical hauls, at intervals of a few hours, at substantially the same position in the North Sea. The numbers of young demersal fish, caught in each haul in this area, present a more regular picture.

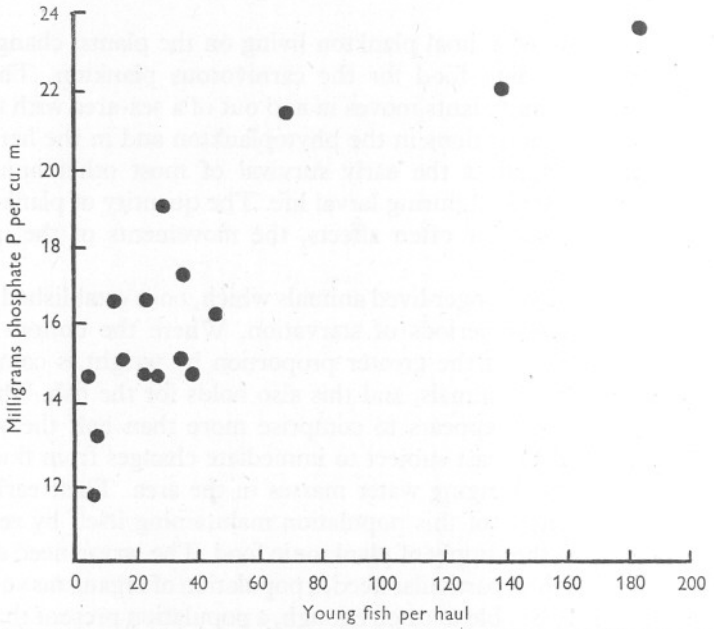


Fig. 10. Relation between the number of young fish caught per haul and the phosphate in the water occupying the area during the previous winter.

The average number caught between June and October are plotted against the concentration of phosphate in the water at the beginning of each year in Fig. 10. These numbers relate to fish spawned in summer, after the spring outburst of phytoplankton, and after the peak population of planktonic crustaceans which immediately follows it. These young fish lived their early life during a season when food was not at its greatest seasonal abundance.

At about the time when these fish larvae have absorbed their yolk sac, or very shortly after, they need to catch small crustacean or other larvae. This is a most critical period of their lives, when great mortality occurs. Observations by Rollefsen show that the food organisms need to be below a certain size. If unable to pass down a fish's gullet with an effective diameter of 0·2–

0·3 mm. they choke the fish. If organisms of small enough size are not sufficiently numerous, an increasingly large proportion of the larval or post-larval fish fail in their attempts to catch food during the critical period, and so perish. A major cause of good or bad survival years for young fish would appear to be the population density of zooplankton organisms of the right size at the right time.

There are three steps in the food chain between the young fish which have survived the post-larval stage and the quantity of plant nutrients. Furthermore, the quantity of nutrients in winter may sometimes bear no relation to the production of plants in the area during summer, on account of a different water-mass with very different potential fertility having meanwhile entered the area. In spite of this, *the highest winter concentrations of phosphate are seen to have marched with the most considerable survival of post-larval fish during the following summer, and the least winter concentrations of phosphate with the least survival.*

Another relation appeared during the course of these observations. The rich plankton populations found in the nineteen-twenties contained *Sagitta elegans* in considerable numbers, whereas in the sparse populations this species was replaced by *S. setosa*. During a cruise in 1935 there appeared to be a rather sharp line of demarcation between plankton-rich water containing *S. elegans* and plankton-poor water containing *S. setosa*. Thus it emerged that, like the winter concentration of nutrient salts, the presence of some plankton species marched with the quantity of the whole planktonic population.

There are observations made during 3 years which allow a comparison of the quantity of the larger phytoplankton organisms in the water. Frequent vertical hauls with a net of 0·05 × 0·04 mm. mesh, containing a meter, were made at the same position. The results expressed in terms of plant pigments per cubic metre (Harvey, Cooper, Lebour & Russell, 1935, p. 419, and fig. 12, p. 424) indicate a lesser population of these larger plants in 1949 than in 1934, and lesser in 1934 than in 1933. The quantity of phosphate in solution in the water during the previous winters varied in the same way (13, 15 and 16 mg. P per cubic metre respectively) although the differences were not great. The average number of post-larval fish, exclusive of clupeids, caught in 4000 m.$^3$ of water between June and October also varied in the same way (10, 16 and 23 fish per haul). Standing alone, this close relation between winter nutrients, larger plants, and summer-spawned young fish, would mean little, since it only embraces 3 years.

Observations of the population of smaller zooplankton (copepods and copepodites) extend over 2 years only, 1934 and 1939. Neither the quantity of zooplankton, the number of young fish in summer nor the winter phosphate were notably dissimilar.

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# THE SUSPENDED MATTER OF SEA WATER

By F. A. J. Armstrong and W. R. G. Atkins, F.R.S.

From the Plymouth Laboratory

Many chemical analyses have been made of the minor constituents of sea water which are utilized by plants and accordingly show definite seasonal variations. Analyses have also been made of the plankton strained out by fine-mesh silk nets. According to Harvey (1945) the finest bolting silk used, when wet and swollen, has a mesh of $42 \times 50 \mu$. This will let through the dwarf or nanoplankton, namely the smaller flagellates and diatoms, also bacteria, at least until the net is partially choked, as well as the finest clay particles, if any are still unprecipitated. Clay usually comes down close to the land, due to the action of the divalent magnesium and calcium ions of sea water as shown by Joly (1900).

## Method of Sampling

An attempt to measure the amount of these suspensions, living, dead and inanimate was made as follows. Carboys of sea water were filled at Station E 1, about 10 miles south-west of the Eddystone, in the English Channel, where the depth is 72–74 m. The water was taken in a carefully scrubbed and washed oak bucket, poured in through a clean wooden funnel, under the eye of the authors. The water surface was always free from oil and care was taken that the rim of the bucket should not touch the side of the ship, which sometimes had dried mud remaining on it above the wetted portion.

The carboys used were well washed with hot lime-free tap water and finally with distilled water, as customary here, and closed with a clean cork sealed in position. It was found that some of the suspended matter adhered to the glass, so during filtration it was loosened with a brush, which was then well washed. After the first four samples we considered that the customary cleaning of the carboy was likely to leave some of this matter on the glass. So from June 1948, inclusive, the carboys were cleaned with hot strong sulphuric acid in addition. The analyses for February to May 1948 show that this adherence of previous deposits gave results which were too high, but the matter removed was similar in composition to the usual suspension.

## Filtration and Determination of Dry Matter

The volume of sea water filtered varied, as some was used for other analyses, but lay between 15 and 29 l., with a mean close to 22. It was filtered through a Whatman No. 50 paper, 11 cm. diameter, the ash of which, 0·2 mg., was negligible. This was done on a Buchner funnel with the water pump. The first 10 l. was always re-filtered.

As a test of the efficiency of the filtration sea water collected 8 November 1949 was first filtered as usual; 25·0 l. gave 24·7 mg. or 990 mg./m.$^3$ of incinerated matter. Then 22·0 l. of the filtrate were filtered through 'Gradocol' membranes having an average pore diameter 1·09 $\mu$. As these became clogged four had to be used in succession. The washed residue and the filters were ignited and gave 0·9 $\pm$ 0·2 mg., or 40 mg./m.$^3$, of which gravimetric analysis showed that 60% was silica, and ferric oxide 13%, found colorimetrically using 2–2′-dipyridyl.

Thus the filter-paper, with re-filtration as described, allowed about 4% of the matter to pass through, which was later collected on the membrane. The appearance and composition of the fine suspended matter on the membrane were similar to that on the paper. Examination in the Tyndall beam showed that there was still matter in suspension in sea water filtered in succession through 'Gradocol' membranes 1·09, 0·61 and 0·2 $\mu$ A.P.D., but the amount must have been exceedingly small by weight.

After washing free from salts the residue was also washed with 20 ml. portions of acetone till colourless, and dried at 100° C. The net weight is that of organic and inorganic matter, insoluble in water and acetone. But only occasionally was there enough on the paper to render this weighing worth while, as it is necessarily less accurate than that of the incinerated residue.

The paper was incinerated below red heat till carbonaceous matter was destroyed. The ratio of the organic matter to the inorganic and ash was 0·68 in July 1948 and 1·01 in February 1949. In March, April and May 1948 the imperfectly cleaned carboys gave respectively the ratios 0·91, 1·82 and 0·31, but the March and April samples were not filtered till $4\frac{1}{2}$ and $3\frac{1}{2}$ months after collection.

The values for July 1948 and February 1949 give the insoluble organic matter as 1·77 and 1·62 g. dry weight for a cubic metre of water at the surface. This is a direct determination, but may be low on account of the loss of soluble substances.

The July 1948 ratio, 0·68, is moreover low, as on this occasion the inorganic matter was enriched with calcium carbonate which constituted 70% instead of about 20%. The high calcium content is probably due to high temperature and pH value, which combine to cause precipitation.

The incinerated dry matter is shown in the table as mg./m.$^3$ The constituents are shown both in mg./m.$^3$ to afford a comparison with analyses of the salts in solution and in percentages, using the oxide formulae as customary in the analyses of clays in agricultural work and in the Challenger analyses.

### Gravimetric Analysis of the Residue

Silica was determined by the loss of silicon tetrafluoride. The factor to correct to Si is 0·467.

Iron was found by fusion of the residue with potassium hydrogen sulphate, followed by acid extraction, formation of the cupferron complex and its extrac-

tion with chloroform. The solvent was removed and the complex destroyed with sulphuric acid and heat, followed by hydrogen peroxide, solution in acid and ammoniacal precipitation when just alkaline to methyl red. The precipitate was ignited and weighed as $Fe_2O_3$; the factor to convert to Fe is 0·700.

Aluminium was precipitated in the aqueous solution after the cupferron extraction by addition of ammonium chloride and then hydroxide till just alkaline to methyl red. The precipitate was ignited and weighed as $Al_2O_3$. The factor to convert to Al is 0·529.

The filtrate from the aluminium determination was freed from ammonium salts, organic matter if present being destroyed with hydrogen peroxide. Calcium was then precipitated as oxalate, and ignited and weighed as the carbonate. The factor to convert to Ca is 0·400.

One determination of phosphorus was made on a duplicate carboy of 30 November 1948. In view of the acid extraction necessary later on this was filtered on a Jena grade 3 (medium porosity) sintered glass crucible. With re-filtration of the first 10 l. this proved efficient, and gave 2100 mg./m.$^3$ residue dried at 100° C. Cold extraction with 0·28 N-$H_2SO_4$ gave 3·1 mg./m.$^3$, and hot extraction (in autoclave, Harvey, 1948) gave a further 2·2 mg. The residue when incinerated and extracted gave 0·2 mg., so total phosphorus in residue was 5·5 mg./m.$^3$

Since the other carboy gave 950 mg./m.$^3$ incinerated residue a further value for the organic/inorganic matter ratio is obtainable, namely 1·21 and the insoluble organic matter is 1·15 g./m.$^3$ The samples of water may not have been identical in the two carboys, but are likely to have been closely similar.

## Discussion of Results

The results are given in Table I. Neglecting results from inadequately cleaned carboys the incinerated dry matter ranges from 2·77 to 0·45 g./m.$^3$, namely parts per million, with silica as the main constituent in all but four cases. In one of these calcium carbonate, probably from the sea, constituted 70%.

The silica may have three origins: silica as such from diatom tests, silica fairly pure from small sand grains and apparently buoyed up by organic matter, and silicates of aluminium and iron, namely clay, brought down by rivers.

Incinerated dry matter varied from 100 to 16; the silica from 100 to 9; the iron oxide from 100 to 20; the aluminium oxide from 100 to 7. The greatest variation in silica was, very strangely, between 8 and 17 August 1949, with 80 and 880 mg./m.$^3$ respectively. As against this Atkins (1926) found silica in solution at E 1, 0 m., to vary from 240 to 40 mg. between 1923 and 1926. It appears, therefore, that the silica in suspension must—from the aluminium figures—be largely present as silicate and capable of enriching water depleted by diatom growth by slow solution. There is, however, no sign of any regular seasonal change in the silicate. The figures appear quite fortuitous. Nor do

TABLE I. WEIGHT OF SUSPENDED MATTER IN 1 M.$^3$ OF SEA WATER, SHOWN AS INORGANIC MATTER AND ASH, AFTER INCINERATION, IN MILLIGRAMS, EQUIVALENT TO PARTS PER THOUSAND MILLION

The major constituents are shown, also the percentage composition. The years are 1948, above, and 1949.

| | Weights (mg.) | | | | | Composition (%) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Total | $SiO_2$ | $Fe_2O_3$ | $Al_2O_3$ | $CaCO_3$ | Total | $SiO_2$ | $Fe_2O_3$ | $Al_2O_3$ | $CaCO_3$ | ° C. | Salinity (‰) |
| 11 Feb. | 1,060* | 465 | 96 | 81 | 250 | 85 | 44 | 9 | 8 | 24 | 10·1 | 35·27 |
| 10 Mar. | 6,770* | 3,700 | 740 | 1,300 | 630 | 95 | 55 | 11 | 20 | 9 | 9·3 | 35·35 |
| 12 Apr. | 6,900* | 3,100 | 650 | 810 | 1,360 | 86 | 45 | 9 | 12 | 20 | 10·2 | 35·33 |
| 10 May | 15,300* | 7,900 | — | 1,800 | 2,400 | 80 | 52 | — | 12 | 16 | 12·4 | 35·46 |
| 9 June | 1,140 | 520 | 130 | 70 | 200 | 89 | 54 | 11 | 6 | 18 | 12·6 | 35·34 |
| 15 July | 2,770 | 700 | 86 | < 20 | 1,900 | 99 | 25 | 3 | < 1 | 70 | 14·7 | 35·34 |
| 16 Aug. | 890 | 380 | 130 | 50 | 160 | 82 | 43 | 15 | 6 | 18 | 15·4 | 35·34 |
| 4 Oct. | 490 | 220 | 60 | 60 | 90 | 88 | 44 | 12 | 13 | 19 | 14·7 | 35·37 |
| 30 Nov. | 950 | 160 | 140 | 140 | 200 | 73 | 17 | 21 | 14 | 21 | 13·2 | 35·38 |
| 5 Jan. | 760 | 160 | 160 | 130 | 190 | 84 | 21 | 21 | 17 | 25 | 11·2 | 35·35 |
| 1 Feb. | 1,600 | 420 | 250 | 160 | 310 | 71 | 26 | 15 | 10 | 19 | 10·2 | 35·27 |
| 1 Mar. | 740 | 160 | 130 | 80 | 90 | 62 | 21 | 17 | 11 | 13 | 10·1 | 35·38 |
| 13 Apr. | 800 | 300 | 100 | 90 | 190 | 84 | 37 | 13 | 11 | 23 | 9·9 | 35·27 |
| 9 May | 800 | 250 | 180 | 80 | 110 | 77 | 31 | 23 | 10 | 13 | 11·5 | 35·32 |
| 9 June | 1,360 | 710 | 110 | 150 | 250 | 89 | 52 | 8 | 11 | 18 | 13·9 | 35·30 |
| 8 July | 1,880 | 770 | 300 | 270 | 310 | 88 | 41 | 16 | 14 | 17 | 16·5 | 35·41 |
| 8 Aug. | 450 | 80 | 120 | 70 | 110 | 89 | 18 | 28 | 16 | 27 | 15·3 | 35·43 |
| 17 Aug. | 2,020 | 880 | 260 | 160 | 490 | 89 | 44 | 13 | 8 | 24 | 16·0 | — |
| 29 Aug. | 800 | 340 | 120 | 90 | 240 | 98 | 42 | 15 | 12 | 29 | 19·4 | — |
| 6 Oct. | 590 | 260 | 150 | 60 | 100 | 92 | 43 | 24 | 9 | 16 | 16·4 | 35·25 |
| 8 Nov. | 1,190 | 520 | 210 | 190 | 310 | 103 | 44 | 17 | 16 | 26 | 14·0 | 35·26 |

* Inadequately cleaned carboys.

delays in the filtration of the carboys appear to cause any serious error, for filtration of the 8 August sample was begun on 16 August and that of 17 August on 20 August.

On the whole, the aluminium values appear to be low in the summer, giving the impression that it might be the more soluble. The amount of iron present in suspension was far more than that found in solution by Cooper (1935). Atkins (1945) showed that the reduction in silica in solution due to diatom production was only about 10% of that which should have been found had all the phosphate used gone to diatom production. The present demonstration of another source of silicate does tend to lessen this discrepancy, but can hardly be accepted as adequate to account for the great difference. One is thus justified in thinking that the non-siliceous phytoplankton may be quite important quantitatively.

## Summary

Sea water collected at Station E 1, surface, between June 1948, and November 1949, contained suspended matter from 2·77 to 0·45 g./m.$^3$ (or parts per million) dried and ignited. A few determinations of insoluble organic matter gave 1·77 to 1·15 parts per million dry weight at 100° C. The ignited residue contained from 55 to 17% silica, 28 to 3 of ferric oxide, 20 to under 1 of alumina and 70 (or excluding one high value 29) to 9 calcium carbonate. There was nothing in the records for temperature or salinity to suggest that the water mass had changed during the period of sampling.

The analyses reveal an unsuspectedly large amount of iron, compared with that found in solution. The ignited residue is rich in silicate, judging from the silica alumina ratio, but it is quite doubtful whether the additional supply of silicate available for diatoms is at all adequate to balance their requirements calculated on a phosphate utilization basis. It seems more probable that a considerable amount of the phosphate is available for non-siliceous phytoplankton.

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# THE CYCLE OF PHOSPHORUS IN THE WATERS OF THE ENGLISH CHANNEL

By F. A. J. Armstrong and H. W. Harvey, F.R.S.

From the Plymouth Laboratory

(Text-figs. 1–10)

A study of the distribution of phosphorus compounds—in solution in the water, in planktonic, in free-swimming and in bottom-living organisms, in detritus and in deposits on the sea floor—forms a natural sequence to two groups of observations which have been made in recent years. The one group has shown that water masses have been present in the mouth of the English Channel containing very different concentrations of phosphate in winter, when the phosphate concentration reaches a maximum—concentrations ranging from 10 mg. phosphate-P per cubic metre in some water masses to over 20 mg. in others. The second group of observations has shown a great difference in the population density of macroplankton between one water mass and another, and, also, more macroplankton and a better survival of young fish in the waters off Plymouth during years when the winter maximum of phosphate in the water was greatest.

The aim of this present study is twofold: towards finding a constituent of sea water which is unaffected by seasonal changes and whose concentration differentiates one water mass from another, and towards a further insight into those factors which affect the fertility of an area of the sea and cause fluctuations in population during the course of years.

Most of the data have been collected at a distance of 20 miles off shore from Plymouth in a depth of 70 m. The water occupying this area does not stay there; as shown by changes in salinity, it is replaced by other water masses at frequent and irregular intervals. Since it is impracticable to follow one particular water mass in its wanderings and intermingling throughout a year, seasonal changes in a particular water mass cannot be determined directly. From observations at one position small seasonal changes may not be apparent and could be demonstrated only by a series of observations taken at one position throughout many years, sufficient for fluctuations due to changing water masses to iron themselves out.

On the other hand, the considerable seasonal changes which occur in phosphate, nitrate, phyto- and zooplankton are quite apparent. They outweigh fluctuations arising from a succession of water masses passing through the area.

The earlier attempts to estimate organic phosphorus compounds in solution in the sea were vitiated by the use of a method of analysis which included in

the estimate any arsenate present (Kreps & Osadchik, 1933; Kalle, 1933; Seiwell & Seiwell, 1934).

This analytical difficulty was overcome by Kalle (1935, 1937), who then surveyed a considerable area of the southern North Sea in the winter of 1935. He envisaged the probability that the total phosphorus in dissolved compounds was a distinction between water masses—'Hilfsmittel zur Unterscheidung von Wasserkörpern'.

His investigation showed very different concentrations of total phosphorus and of phosphate in January in different areas of the North Sea. It also showed that the more turbid waters contained large quantities of this element in suspension.

During the same year, another analytical method was devised by Redfield, Smith & Ketchum (1937), which also eliminated interference by arsenic. They estimated phosphate in solution, total phosphorus and phosphorus in particulate matter retained on a filter, at a position in the Gulf of Maine on five occasions during a year, to a depth of some 250 m.

The position lay in a water mass which is considered subject to but little interchange with the surrounding water. During the course of the year, there was no marked difference in the total phosphorus in the water column between summer and winter.

| | May 1935 | Aug. | Nov. | Feb. 1936 | May |
|---|---|---|---|---|---|
| Total P, grams below a square metre | 9·4 | 10·1 | 10·7 | 9·8 | 11·0 |

Their research showed that the integral mean concentration of total phosphorus in a water column could be used to distinguish one water mass from another at any time of year.

A series of total phosphorus estimations have also been made in the nutrient-poor waters of the Adriatic, at intervals throughout a year, using Kalle's method (Nümann, 1941). The data provide no indication of any seasonal change in the total phosphorus content, but the quantity is very small, averaging 5 mg. P/m.$^3$, compared with over 30 mg. in the Gulf of Maine, 12 mg. off Plymouth during recent years and, by inference, over 20 mg. during the relatively rich period some 25 years ago.

The main difficulty in further investigation lay in the uncertainties inherent in the technique of estimation. Even the estimation of dissolved phosphate at great dilutions embraces reactions which are imperfectly understood; this is indicated by several papers appearing every year on modifications of the molybdenum blue method.

An examination has been made of the reactions involved in phosphate estimation and, also, a more simple and rapid variant of the method used by Redfield *et al.* to estimate total phosphorus in water samples has been developed (Harvey, 1948; Armstrong, 1949). The sample is acidified to 0·28 N and heated for 5 hr. at 130° C.; this treatment in the presence of chloride appears to hydrolyse all or almost all the organic phosphorus compounds; any

arsenate present is reduced with sulphite. Large quantities of arsenate may be added to the sea-water sample without showing any increase in the estimate of total phosphorus.

On the other hand when a sample of sea water is analysed for inorganic phosphate, the estimate by molybdenum blue includes the equivalent of any arsenate which may be present in the water. This amount is unknown.

Analyses of English Channel waters have shown the presence of some 19 mg. As per m.$^3$ (Orton, 1923), which compares with 7–24 mg. in more recent analyses of Atlantic waters (Rakestraw & Lutz, 1933) and 15–38 mg. in Pacific waters (Gorgy, Rakestraw & Fox, 1948). The latter authors found that from 8–16% of the whole existed as arsenate.

Based on the value of 19 mg. As/m.$^3$ in English Channel waters, this suggests that 1·5–3 mg. may be present as arsenate. These quantities would appear in the estimated concentration of phosphate as 0·6–1·2 mg. P of phosphate-P actually present.

Some experiments made during this investigation are of interest. When sea water is autoclaved with acid, as in the estimation of total phosphorus but *without added sulphite*, any added arsenite is oxidized to arsenate. This treatment would also be expected to disrupt any organic arsenic compounds, which are likely to be present in sea water because many marine organisms concentrate arsenic in their tissues.

Thus the difference in molybdenum blue developed in waters which have been acidified and autoclaved with and without added sulphite, gives an indirect measure of the arsenic present. Estimations in waters collected off Plymouth in 1947 gave values amounting to 3·1, 2·6 and 2·4 mg. As/m.$^3$, in a water collected in 1948 only 1 mg. As, and in a composite sample collected in 1949, 2·1 mg. As, there being less in the same water after filtration.

These were unexpectedly low values, in view of the direct estimations of total arsenic made in England and America by the methods of Marsh and Gutzeit respectively.

Some further observations made during this investigation suggest that little or no arsenite may be present as such in the sea. When a solution of sodium arsenite was added to samples of sea water at pH 8–8·2, increasing the concentration by 40 mg As/m.$^3$, it was oxidized to arsenate. This happened rapidly in some waters, slowly in others.

We do not know what proportion of the estimated values of phosphate-P are due to arsenate; there is conflicting evidence of how much to expect.

Since June 1947 samples taken from a series of depths, at the position 20 miles off-shore, have been analysed for phosphate and for total phosphorus.

### *Distribution of Phosphorus in the English Channel*

In winter, 20 miles off-shore from Plymouth and elsewhere in the English Channel, both phosphate and total phosphorus remained almost constant throughout the water column. Filtering the water had negligible effect—the quantity of phosphorus in particulate form is then very small indeed. Replicate samples taken from the same depth show only small differences between each other. The distribution shown in Fig. 1 is typical of winter conditions in this area; phosphate-P accounts for some 90% of the total.

Fig. 2 is derived from the data by Redfield *et al.* in the Gulf of Maine. Here there appears to be a different water mass below 170 m., in which practically all

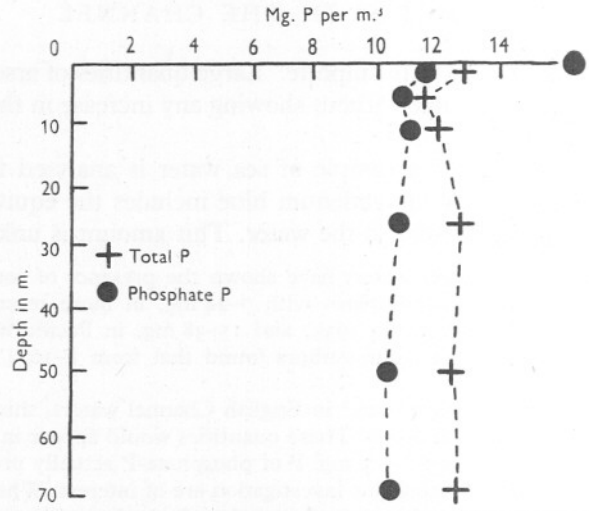


Fig. 1. Distribution of total and of phosphate-P in the water, 20 miles off shore, 5. i. 49. Depth 70 m.

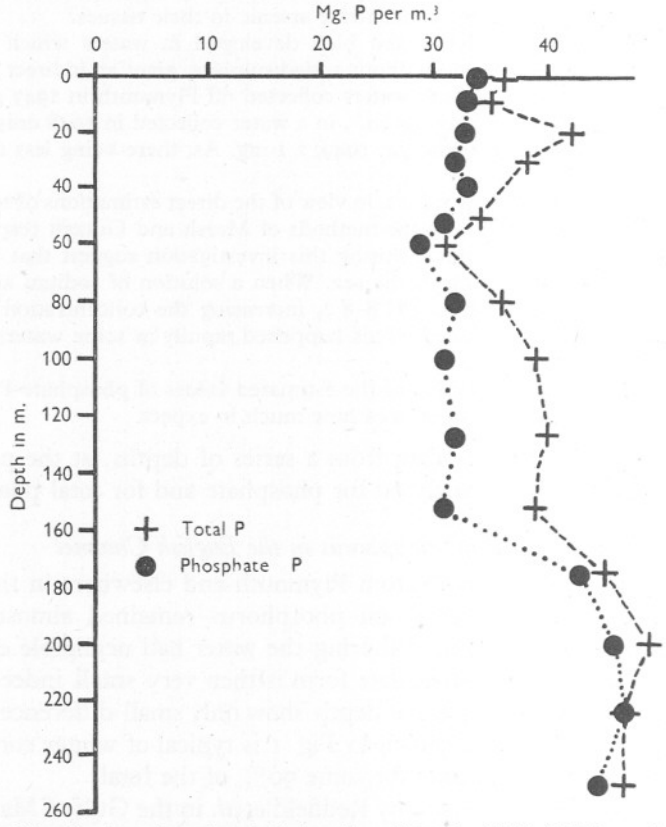


Fig. 2. Distribution of total and of phosphate-P in the Gulf of Maine, 26. ii. 36. From data by Redfield, Smith & Ketchum (1937).

the organic phosphorus has reverted to phosphate, whereas above 170 m. phosphate-P accounts for some 90% of the total.

In the waters so far investigated at the time of the winter phosphate maximum, the phosphate in the water columns amounts to 85–90% of the total phosphorus.

During the winter months, in particular, there is an odd phenomenon which we have frequently observed. If the water sample is taken from the surface, it often contains rather more total phosphorus and more phosphate than occurs in the water below. The cause is not obvious; possibly dust from the atmosphere may become trapped by surface tension at the air surface, or particles in suspension may attach to themselves minute bubbles of air during rough weather when waves are breaking, and these, rising to the surface, become entrapped. Both Söderstrom (1924) and Wilson (1932) have observed that when larvae of *Polygordius* and of *Owenia* come into contact with the surface they are held there and even torn apart by the surface forces. Suspended matter removed by filtration from water collected at the surface of the sea was rich in phosphorus. On two occasions it accounted for 5·5 and 2·2 mg. P/m.$^3$.

As the year advances, some redistribution takes place. Phosphate is used by the plants in the upper layers. Zooplankton, rising into these layers at night, graze on the plants and retiring by day excrete phosphate and soluble organic phosphorus compounds into the water below. Thus, until June, organic phosphorus compounds increase at the expense of phosphate. Most of this increase is in the form of dissolved organic P, since the quantity of phosphorus in the plankton never increases beyond a small fraction of that in solution. Also throughout the summer, there is less total phosphorus in the upper layers, due to vertical transport by plant-eating zooplankton, than in the water below. In several of our observations in summer there was a slight but significant accretion of phosphorus between 20 and 40 m. depth.

From February to June in 1948 and 1949 the dissolved organic plus particulate phosphorus increased from 10 or 12% to some 65% of the total in the 70 m. water column off Plymouth. A typical distribution is shown in Fig. 3, while Fig. 4 shows the distribution in the deeper water of the Gulf of Maine in August.

In order to determine the very small quantity of phosphorus present in particulate matter in suspension, samples were collected at regular intervals of depth and mixed to give a composite sample, representative of the whole water column. Part was filtered through No. 42 Whatman paper. From this and the unfiltered remainder, replicate subsamples were taken for analysis. The difference between the mean values for the filtered and unfiltered samples gave a measure of the phosphorus in particulate matter. Table I shows the results of these analyses; it also includes the calculated quantity of phosphorus present in zooplankton and plants. The data from which these values were derived are given in a separate communication (Harvey, 1950, pp. 97–137).

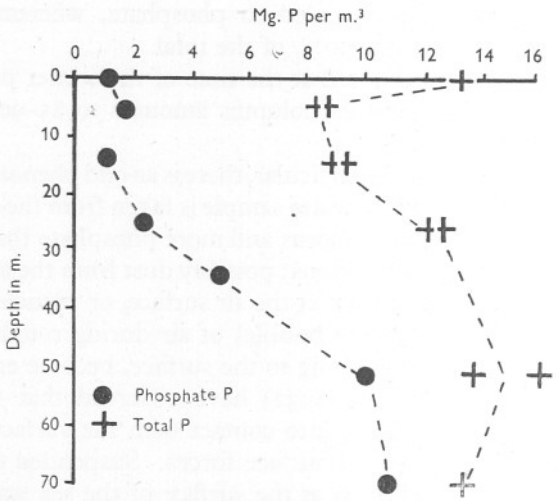


Fig. 3. Distribution of total and of phosphate-P in the water 20 miles off shore, 31. viii. 48. Depth 70 m.

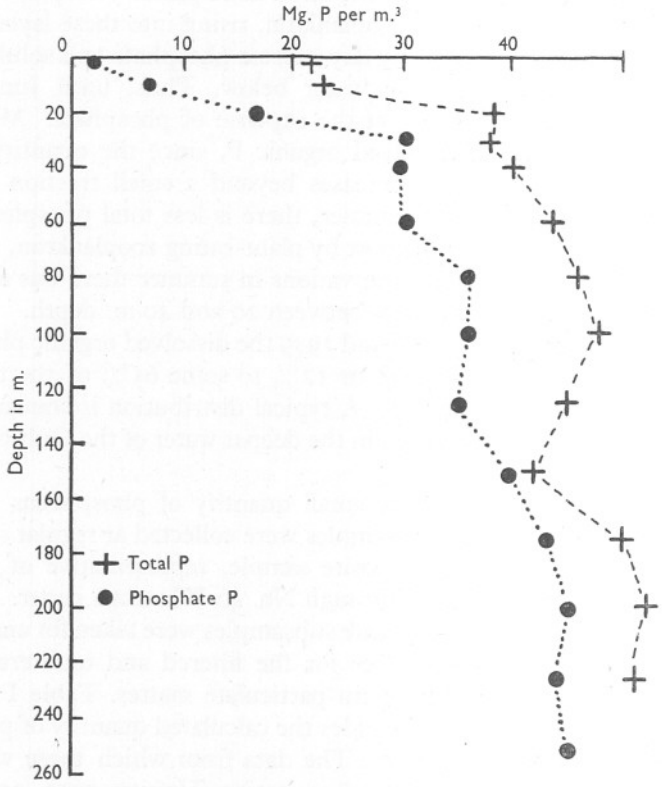


Fig. 4. Distribution of total and of phosphate-P in the Gulf of Maine, 21. viii. 35. From data by Redfield, Smith & Ketchum (1937).

By subtracting the quantity in living plankton from the total, a rough estimate is obtained of the quantity in detritus. This is thought to be mostly organic detritus, fragments of once-eaten diatoms and zooplankton, which can be seen present in the water after the spring flowering of diatoms in early April.

TABLE I. ANALYSES OF TOTAL P, MG. PER M.$^3$, IN COMPOSITE SAMPLES FROM 20 MILES OFF-SHORE

| | 1. iii. 49 | 13. iv. 49 | 9. v. 49 | 9. vi. 49 | 6. vii. 49 | 8. viii. 49 | 8. ix. 49 | 8. xi. 49 |
|---|---|---|---|---|---|---|---|---|
| Unfiltered | 15 | 16·4 | 14·9 | 11·6 | 11·7 | 11·0 | 12·8 | 12·1 |
| | 13·7 | 16·9 | 14·7 | 12·1 | 11·9 | 10·2 | 12·1 | 12·5 |
| | 13·3 | 15·6 | 14·1 | 11·9 | 12·0 | 9·6 | 12·9 | 12·6 |
| | | 15·5 | 12·6 | 11·8 | 11·6 | 10·3 | 12·4 | 13·1 |
| | | 16·3 | 14·6 | 12·0 | 12·4 | 9·0 | 12·3 | 15·5 |
| | | 16·2 | 14·6 | 11·9 | 12·5 | 10·4 | | 13·8 |
| | | | 14·6 | | | | | |
| Av. | 14·0 | 16·15 | 14·3 | 11·9 | 12·0 | 10·1 | 12·5 | 13·3 |
| Filtered | 13·3 | 14·8 | 11·3 | 9·7 | 10·5 | 9·1 | 11·9 | 13·1 |
| | 13·6 | 14·7 | 11·4 | 10·0 | 10·4 | 8·5 | 12·2 | 13·7 |
| | 13·5 | 14·6 | 11·7 | | 10·7 | 8·9 | 12·0 | |
| | | 14·9 | 11·2 | | 10·4 | 8·9 | | |
| Av. | 13·5 | 14·75 | 11·4 | 9·9 | 10·5 | 8·9 | 12·03 | 13·4 |
| P in particulate matter (by difference) | 0·5 | 1·4 | 2·9 | 2 | 1·5 | 1·2 | 0·45 | — |
| P in phyto-plankton | 0·13 | 0·42 | 0·78 | 0·5 | <0·5 | <0·5 | <0·4 | — |
| P in zooplankton | 0·2 | 0·8 | 1·0 | 0·5 | 0·5 | 0·5 | 0·4 | — |
| In detritus (by difference) | 0·2 | 0·2 | 1·1 | 1·0 | 0·5 | 0·2 | — | — |

The nature of the particles of inorganic phosphate likely to occur in turbid waters is of interest. Dietz, Emery & Shepard (1942) have described sedimentary deposits of calcium phosphate, containing fluoride, which were laid down off the Pacific coast of America. They conclude that sea water is fully saturated with respect to calcium phosphate. Cooper (1948*a*, *b*) considers that particles in suspension are likely to consist of ferric phosphate, which is one of the most insoluble phosphates, and that these particles, once formed, may hydrolyse somewhat slowly in sea water. As a statistical average, waters richer in iron were also richer in phosphate.

With regard to this possibility, the following experiment is of interest.

Ferric phosphate was prepared and very thoroughly washed. The addition of this to a culture of phosphate-starved diatoms was followed by a prolific growth; this also happened when it was enclosed in a cellophane sac and suspended in the culture.

When added to sea water in a stoppered vessel, the pH quickly fell to *c.* 7. The water was poured off and replaced, the pH of this fresh sea water fell in the same way. The fall in pH of successive replacements of sea water became progressively slower.

The conclusion arrived at was that hydrolysis takes place at pH 8, becoming infinitely slow at *c.* pH 7, and that the rate of hydrolysis is much greater the finer the particles.

In addition to the estimates made in waters 20 miles off-shore, estimations have been made from time to time at positions nearer Plymouth. Sometimes there was rather less phosphorus in the water and at other times more. The distribution in January 1949 is shown in Fig. 5, when a 'richer' water lay nearer the shore. The high concentrations occurring in water collected from the surface on this occasion are noteworthy.

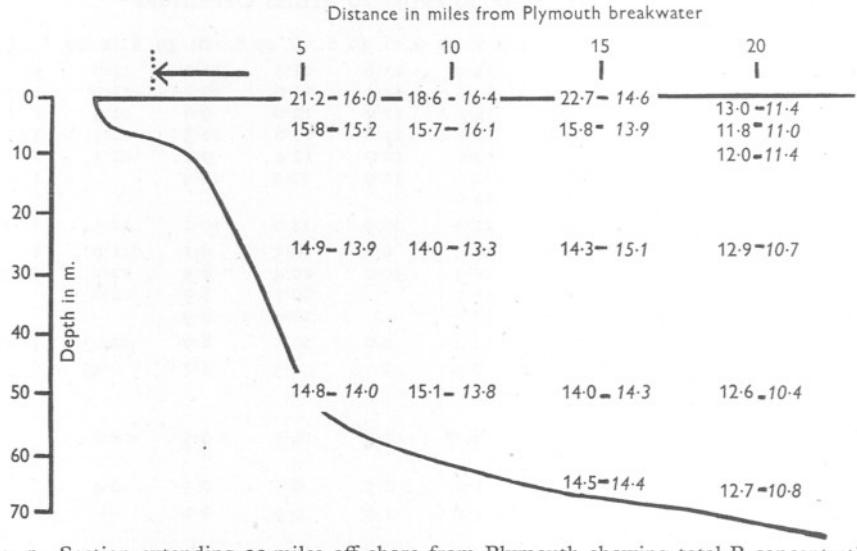


Fig. 5. Section extending 20 miles off-shore from Plymouth showing total-P concentration (upright type) and phosphate-P (italics) in mg./m.$^3$. 5 and 14. i. 49.

The integral mean concentrations of total and phosphate-P in the whole water column at the position 20 miles off-shore are shown in Fig. 6.

The total has fluctuated in an irregular manner between $9\frac{1}{2}$ and 16 mg. P/m.$^3$, while the salinity of the waters sampled fluctuated between 35·0 and 35·4 $^{o}/_{oo}$.

No relation is apparent between the fluctuations in total phosphorus and in salinity.

It is thought that the fluctuations in total phosphorus are almost entirely due to richer or poorer water moving into the area. Yet it is, of course possible that incursions of water have by chance masked a seasonal change phosphorus content. Only a series of observations extending over many years would rule out this possibility.

Further evidence bearing upon a possible seasonal variation was thereforesought in two directions: (1) whether organic detritus is deposited on the floor after the spring maximum of planktonic life and slowly regenerates phosphate; (2) whether the quantity of phosphorus locked up in living organisms which die during the autumn and winter months is at all considerable. Neither

inquiry provided evidence indicating a material seasonal change in the total phosphorus in the water.

It was considered that if any deposition of organic matter takes place, it would lie on the sea floor as a sludge or slurry. Therefore an apparatus was constructed which sucks in water from close to the bottom very rapidly. A strong spring is released when the foot of the apparatus touches bottom, retracting a piston which sucks in water with a rush. Fitting a longer foot allowed samples also to be taken from 35 cm. above the bottom.

Samples taken close to the bottom contained a little organic detritus and a little silt in addition to sand grains. Their phosphorus content was little greater than that in samples taken from water above (Table II). No evidence was found of any material deposition of detritus rich in phosphorus.

TABLE II. TOTAL PHOSPHORUS IN WATER SAMPLES OBTAINED BY 'PISTON SAMPLER' FROM CLOSE TO THE BOTTOM

| 12. v. 48 | | 23. vii. 47 | |
|---|---|---|---|
| 20 miles off-shore | mg. P/m.$^3$ | 13 miles off-shore | mg. P/m.$^3$ |
| 5–6 cm. above bottom | 16·5, 14·5 | 5–6 cm. above bottom | 18·0, 24·0 |
| 35 cm. above bottom | 12·4 | 35 cm. above bottom | 14·7 |
| 5 m. above bottom | 16·6, 11·6 | 3 m. above bottom | 14·2 |
| 25 m. above bottom | 9·6 | 8 m. above bottom | 13·1 |
| 50 m. above bottom | 10·3 | | |
| 29. ix. 47 | | 29. ix. 47 | |
| 13 miles off-shore | mg. P/m.$^3$ | 5 miles off-shore | mg. P/m.$^3$ |
| 5–6 cm. above bottom | 14·2, 11·4 | 5–6 cm. above bottom | 11·4, 15·7 |
| 35 cm. above bottom | 11·4 | 15 m. above bottom | 14·0 |
| 3 m. above bottom | 10·2 | 25 m. above bottom | 13·6, 12·1 |
| 16 m. above bottom | 10·7 | | |

Computations of the phosphorus in fish and bottom fauna, as incorporated in Fig. 10, amounted to a fifth of the whole below a square metre. Since these animals probably grow most rapidly in spring and early summer a quite small seasonal variation of phosphorus, dissolved and suspended in the water, is indicated.

The data for the mean integral concentration of total and of phosphate-P in the water column, presented in Figs. 6 and 7, permits the ratio of phosphate to organic phosphorus in the water column to be calculated on each occasion when a series of samples had been collected and analysed. This ratio is shown in Fig. 8. Except for a single occasion, the seasonal change in the ratio has followed a remarkably constant course.

On this exceptional occasion, 9 June 1949, the percentage of phosphate was greater than a month earlier or a month later. The changes in salinity and temperature which had occurred provided no explanation of this. It is thought that there had moved into the area a body of water in which plant life had been less abundant during the previous 3 months.

It is seen from Figs. 7 and 8 that, from the end of January until June, the

rate at which organic phosphorus compounds are being excreted is greater than the rate at which they are changing into phosphate. The most rapid increase in dissolved organic phosphorus took place in March and April, when production of plants was at its height; it ceased some time in June when the temperature was rising rapidly and organic detritus in suspension had reached

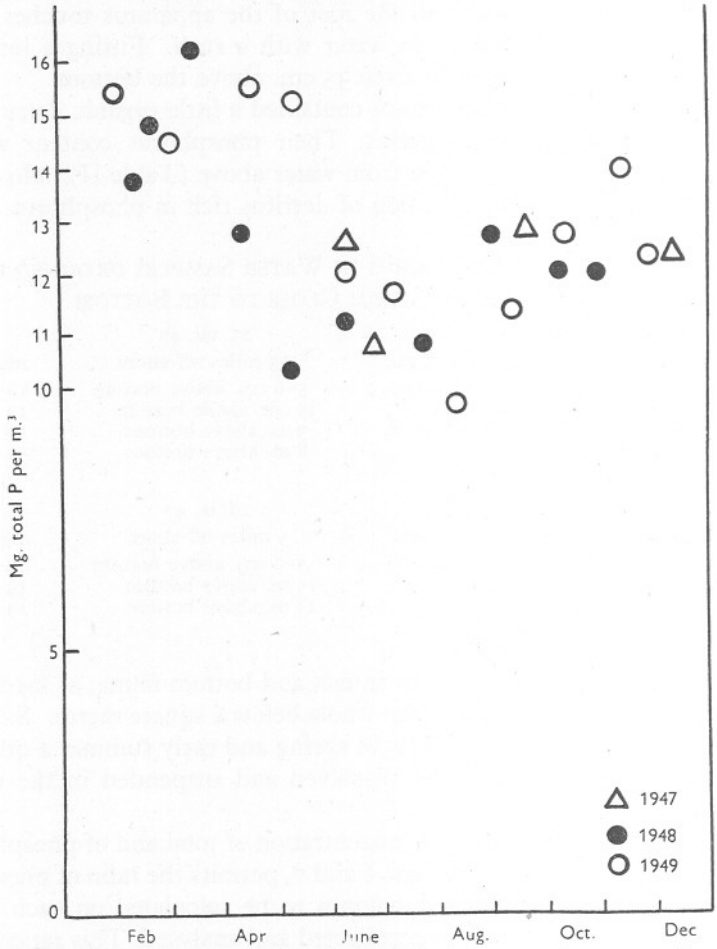


Fig. 6. The integral mean concentration of total-P in the water column 20 miles off shore.

a maximum. The increase ceased and phosphate started to increase long before the temperature of the sea reached its maximum in August.

There is no evidence whether breakdown of organic phosphorus compounds is mostly due to slow chemical decomposition or to bacterial action. If the latter, a seasonal variation in numbers of bacteria in the water would be indicated. This is not unlikely, because they grow rapidly on any surfaces such as those presented by particles of detritus in suspension.

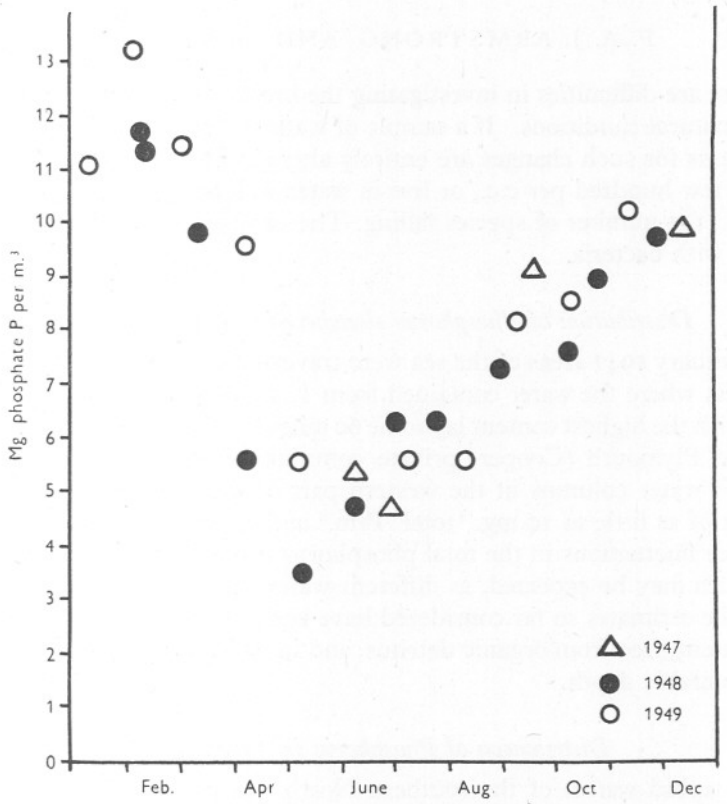


Fig. 7. The integral mean concentration of phosphate-P in the water column 20 miles off-shore.

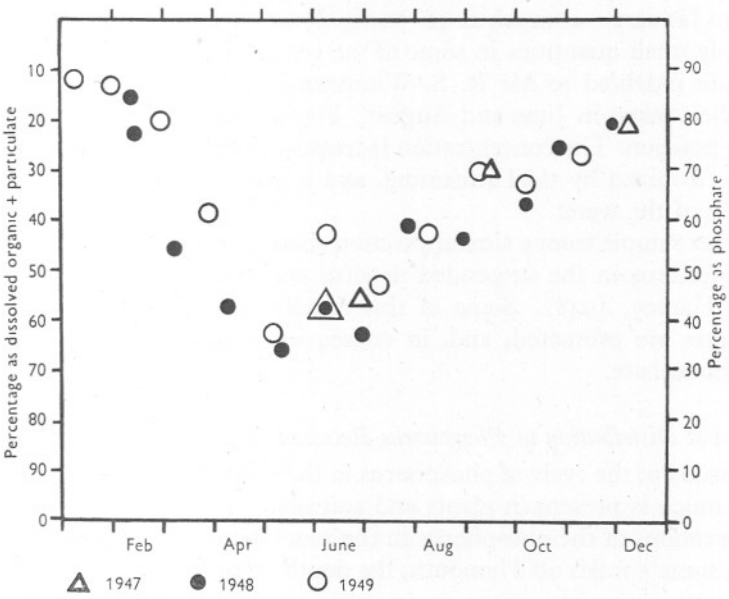


Fig. 8. Diagram showing the seasonal variation in the percentage composition of the phosphorus in the water column 20 miles off-shore.

There are difficulties in investigating the breakdown of organic phosphorus under natural conditions. If a sample of water is brought into the laboratory, conditions for such changes are entirely altered. The number of bacteria rise from a few hundred per c.c., or less in water well off-shore, to several million per c.c., the number of species falling. The surface of the container becomes coated with bacteria.

*Distribution of Phosphorus elsewhere in the English Channel*

In January 1947 areas of the sea were traversed during a cruise to the south and west where the water contained from 12 to 18 mg. phosphate-P/m.$^3$ The areas with the highest content lay some 60 miles and some 120 miles to the westward of Plymouth (Cooper, private communication). Since then we have sampled water columns in the western part of the Channel with an average content of as little as 10 mg. 'total' P/m.$^3$ and as much as 23 mg.

Hence fluctuations in the total phosphorus content of the water column off Plymouth may be expected, as different water masses drift through the area.

All the estimates so far considered have been in waters which are clear and transparent, free from organic detritus, and in which a Secchi disk is visible to a considerable depth.

*Distribution of Phosphorus in Turbid Waters*

The turbid waters of the southern North Sea present a different picture from those in the western English Channel. They contain a very material quantity of phosphorus in the form of detritus, as has been shown by Kalle (1937) in January—as much as 40–50 mg. P/m.$^3$ at some inshore positions, and negligibly small quantities in some of the central and of the least turbid areas.

We are indebted to Mr R. S. Wimpenny for samples from the southern North Sea, taken in June and August. Fig. 9 shows the large quantity at an inshore position. The concentration increases with depth, in spite of the water being well mixed by tidal streaming, and it increases hand in hand with the turbidity of the water.

Another sample from a similar position showed that a material proportion of the phosphorus in the suspended detritus consisted of solid inorganic phosphates (Harvey, 1948). Some of this dissolves in the dilute acid in which phosphates are estimated, and, in consequence, appears in analyses as dissolved phosphate.

*On the Distribution of Phosphorus Between Water, Animals and Plants*

Any study of the cycle of phosphorus in the sea necessitates some knowledge of how much is present in plants and animals.

Observations of the phosphorus in the zooplankton below a square metre of the sea, some 5 miles off Plymouth, the depth being 50–55 m., had been made

throughout 1934, and that of the larger net-caught phytoplankton throughout several years. The quantities present below a square metre were very similar to those 20 miles off shore, in a depth of 70 m., where most of the chemical data have been obtained. There were no observations concerning the smaller phytoplankton which escapes capture in a net having meshes of $42 \times 51\ \mu$ and a great capacity for entangling smaller diatoms, nor concerning the average population density of fishes or of bottom-living organisms.

This necessitated an inquiry, the results of which are presented separately (Harvey, 1950, pp. 97–137). Estimates, based on direct observation, of the quantity of phyto- and zooplankton below a square metre are incorporated in Table I (p. 151).

Fish are both migratory and unevenly distributed; available data allow no more than a conjecture of the average quantity in the western part of the English Channel.

The bottom-living animals are also very unevenly distributed, and the number of quantitative observations in the area are relatively few and over a limited area. These allow no more than a probable conjecture of the average population density—some 100 g. wet weight of living tissue below a square metre, the bulk of this being in animals having a life span of several years and living by filter-feeding on plankton organisms and organic detritus.

These estimates are incorporated in Fig. 10, which indicates the distribution of phosphorus in a water column, 70 m. deep, as investigated during 1947–49. This is roughly the average depth of the western part of the English Channel.

No seasonal change in the quantity of pelagic and demersal fish is shown, on the assumption that month by month the rate of replacement of the biomass by growth balances losses by mortality. The quantity of bottom-living organisms, the infauna and epifauna, is also delineated as constant throughout the seasons, on the same assumption.

However, a large proportion of these bottom-living animals discharge planktonic larvae during the spring and early summer, larvae which contribute to the zooplankton, although not forming a large part of it, having only a short planktonic period and being for the most part soon eaten by other planktonic organisms. This discharge of larvae into the water is accompanied by a material loss of the parents' body substance, and suggests that the water is likely to contain a little more dissolved phosphorus during the spring and early summer, perhaps as much as 1 mg. P/m.$^3$ This possibility is compatible with the values for total phosphorus shown in Fig. 5.

While considering the distribution between water and organisms, the state and quantity of phosphorus in bottom deposits deserves mention.

Muds rich in organic matter are laid down in estuaries, as those in the Clyde, Tyne and Tees which are rich in phosphate and, presumably, organic phosphorus. Their phosphate content decreases with depth, indicating slow solution into the overlying water. Conditions affecting solution in such a mud

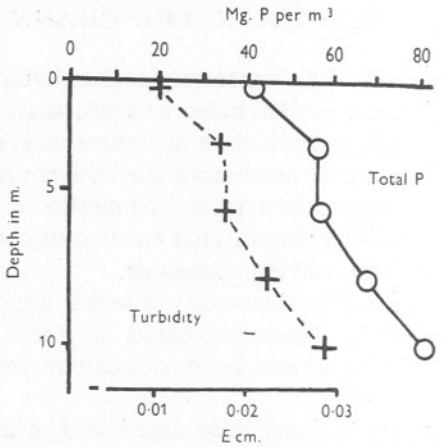


Fig. 9. Diagram showing change in total-P content and in turbidity with depth in turbid water. Samples collected off the Newcombe Bank, southern North Sea, June 1947. Depth 12 m.

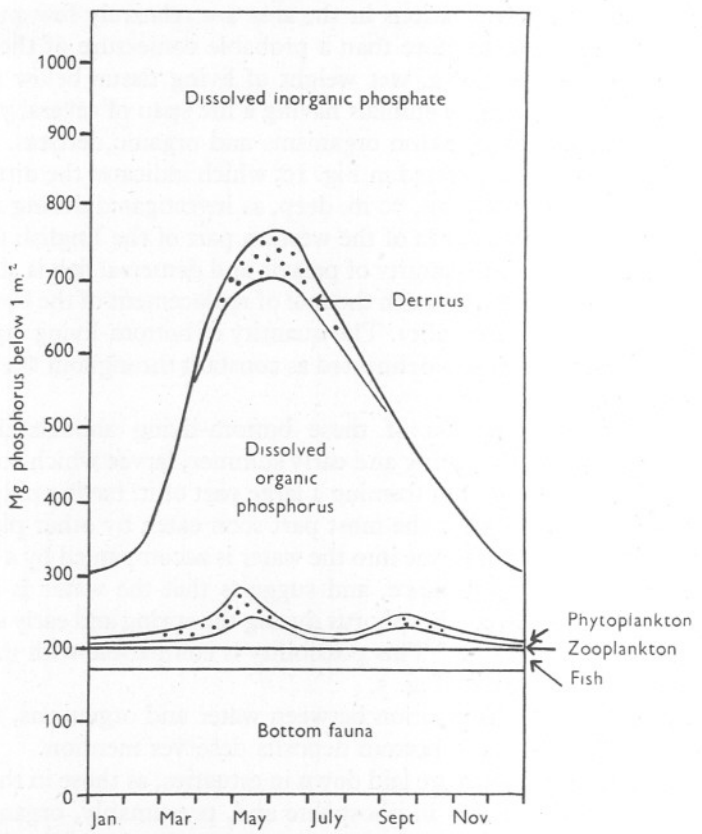


Fig. 10. Diagram showing distribution of phosphorus in water column 70 m. deep, Plymouth area. (Phosphorus in solution and in detritus based on observations made in 1948 and 1949, in zooplankton based on observations made in 1935 farther in-shore, in fish and bottom fauna on computations, Harvey, 1950, pp. 97–137.)

have been studied by Stephenson (1949). These mud deposits occupy very restricted areas and are quite different from the floor of the open sea.

Yet, well off shore, the deposits are not devoid of phosphate. A fine silt or grey mud collected several miles off shore was found to contain 0·03 % P—less than in soils, but a considerable quantity if any of it dissolves during the course of years.

The possibility of some small interchange between inorganic deposits and water cannot be dismissed.

*Phosphorus Content and Fertility of Water Masses*

The foregoing observations indicate that different water masses can be distinguished, one from another, by their total phosphorus content. Where, however, a water mass of less than 50 or 70 m. depth overlies a different water mass, the distinction may be difficult, since the zooplankton cause a redistribution in the upper layers during summer.

The observations also show that geographical distribution in terms of total phosphorus content does not coincide with the distribution in terms of salinity. There is also evidence that the total phosphorus content bears a relation to the productivity and general fertility of the water.

Evidences of the dependence of the animal population upon the supply or production of plant life, and of the latter upon the supply of nutrient salts, is reviewed on pages 132 to 135.

That the supply of phosphate varies with the total phosphorus in the water is implicit from the foregoing observations.

Hence it is expected that the mean concentration of total phosphorus in the water column denotes the potential fertility of the water occupying any particular area of the sea, its changing concentration providing a measure of changes from month to month and year to year in the supply of nutrient to the phytoplankton. It also appears to bear a broad relation to the population density of zooplankton which the water does maintain. An exact linear relation cannot be expected.

Observations of total phosphorus in the sea are limited, and comparable quantitative assessments of the population almost equally so. However, the observations summarized in the two following paragraphs point to this broad relation between total phosphorus in the water and the animal population maintained in it.

For a long period hauls have been made weekly off Plymouth with a ring trawl of 1 mm. mesh, each oblique haul filtering some 4000 m.$^3$ of water. It was observed that the catches of macroplankton, including young fish, were particularly heavy during 1924, 1926 and 1929, and that the winter maximum of phosphate at the beginning of each of these years was particularly high (Russell, 1935). This suggested that the water, rich in nutrient salts, was not displaced by noticeably poorer water during the first 8 or 9 months of each of

these years: it also suggested that a rich phytoplankton resulted in a rich zooplankton and good survival of young fish. In Harvey, 1950, fig. 10 (p. 134 of this *Journal*) is plotted the average number of young fish, exclusive of clupeoids, caught per haul from June to October, against the phosphate maximum at the beginning of each year. A marked relation is seen, in spite of water movements having assuredly taken place between winter and summer on many occasions.

During the summer months in the Gulf of Maine, where the water contains over three times more phosphorus than the water off Plymouth has contained since 1947, the average phytoplankton population during the summer months is considerably greater than in the water off Plymouth. The zooplankton below a square metre averaged during the summer months between 9 and 20 g. dry weight, compared with 1–2 g. in the waters off Plymouth (Riley & Bumpus, 1946).

Several other observations, which point towards this broad relation, are presented or are implicit in the considerations dealt with on p. 135.

We acknowledge with gratitude the assistance of Dr L. H. N. Cooper, Mr G. A. Steven and Mr P. G. Corbin, who collected for us many samples for analysis when on cruises in the Channel.

## Summary

Determinations of total phosphorus in water samples have shown areas in the western English Channel with water containing as little as 10 mg. P/m.$^3$, and other areas with double, and more than double, this concentration.

The integral mean concentration of total P in the water column, 20 miles off-shore from Plymouth, has fluctuated between 10 and 16 mg. P/m.$^3$ since June 1947.

The changes which have taken place in this integral mean concentration are attributed to different water masses, of different total phosphorus concentration, passing through the area, rather than to a seasonal change in the total phosphorus content of a water mass. No marked deposition of phosphorus-containing detritus could be found.

Changes in this integral mean were not coincident with changes in salinity. The geographical distribution of total phosphorus does not coincide with the geographical distribution of salinity.

In winter, 85–90% of the total phosphorus is in the form of dissolved inorganic phosphate, which fell to 45% of the total in the early summers of 1947–49.

The ratio of (dissolved inorganic) phosphate to organic phosphorus (in solution and in particles) has followed a regular seasonal change.

There is some diminution of total phosphorus in the upper 20 m. layer in

summer. This is attributed to zooplankton feeding in this layer by night and excreting some of their intake when they retire by day into deeper water.

Estimates have been made of the proportion of phosphorus in solution, in detritus, in plankton and in other animals.

At positions closer in-shore the water sometimes contained a little more and sometimes a little less total phosphorus.

Water collected from the surface of the sea was frequently richer in phosphate, and in total phosphorus, than water from below the surface.

Evidence is presented that the total phosphorus in the water distinguishes one water mass from another, is a measure of its potential fertility, bears a relation to the annual production of vegetation and of zooplankton, and also bears a relation to the survival of post-larval fish spawned in summer.

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## Table III. Determinations of Total and of Phosphate-P in Waters from the English Channel

### Position 50° 02′ N., 4° 22′ W., 20 miles SSW. from Plymouth breakwater (International Station E1)

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **9. vi. 47** | | | |
| 0·5 | 9·1 | 2·0 | 7·1 |
| 10 | 10·2 | 2·3 | 7·9 |
| 25 | 13·8 | 9·2 | 9·6 |
| 50 | 13·0 | 7·4 | 5·6 |
| **28. vi. 47** | | | |
| 0·5 | 8·3 | 3·2 | 5·1 |
| 5 | 8·5 | 1·9 | 6·6 |
| 10 | 7·9 | 2·5 | 5·4 |
| 15 | 9·5 | 2·1 | 7·4 |
| 20 | 12·3 | 3·6 | 9·7 |
| 30 | 10·2 | 4·2 | 6·0 |
| 40 | 12·3 | 5·6 | 6·7 |
| 50 | 10·0 | 7·9 | 2·1 |
| 60 | 10·1 | 5·8 | 4·3 |
| **18. ix. 47** | | | |
| 0 | 11·6 | 4·0 | 7·6 |
| 5 | 11·3 | 4·0 | 7·3 |
| 15 | 13·2 | 8·1 | 5·1 |
| 25 | 13·5 | 7·8 | 6·7 |
| 50 | 13·0 | 9·0 | 4·0 |
| 69 | 13·1 | 9·0 | 4·1 |
| **10. xii. 47** | | | |
| 0 | 13·3 | 10·0 | 3·3 |
| 5 | 13·3 | 9·5 | 3·8 |
| 25 | 13·2 | 9·8 | 3·4 |
| 50 | 13·5 | 10·1 | 3·4 |
| 70 | 13·3 | 9·5 | 3·8 |
| **12. ii. 48** | | | |
| 0 | 19·2 | 11·4 | 7·8 |
| 5 | 14·5 | 12·2 | 2·3 |
| 25 | 14·8 | 11·0 | 3·8 |
| 50 | 14·3 | 11·6 | 2·7 |
| 69 | 15·5 | 11·1 | 4·4 |
| **11. iii. 48** | | | |
| 0 | 15·0 | 7·5 | 7·5 |
| 5 | 15·8 | 8·7 | 7·1 |
| 15 | 16·6 | 10·9 | 5·7 |
| 25 | 17·0 | 10·9 | 6·1 |
| 50 | 16·0 | 10·1 | 5·9 |
| 70 | 16·5 | 10·6 | 5·9 |
| **12. iv. 48** | | | |
| 0 | 10·1 | 4·8 | 5·3 |
| 5 | 15·4 | 5·4 | 10·0 |
| 25 | 12·6 | 5·5 | 7·1 |
| 50 | 13·1 | 7·0 | 6·1 |
| 70 | 12·8 | 5·1 | 7·7 |
| **12. v. 48** | | | |
| 0 | — | 1·2 | — |
| 5 | 8·5 | 2·1 | 6·4 |
| 15 | 14·6 | 4·0 | 10·6 |
| 25 | 10·3 | 3·4 | 6·9 |
| 50 | 9·6 | 4·0 | 5·6 |
| 70 | 11·6 | 4·6 | 7·0 |
| **8. vi. 48** | | | |
| 0·5 | 8·5 | 1·5 | 6·0 |
| 5 | 10·7 | 2·2 | 8·5 |
| 25 | 10·3 | 2·8 | 7·5 |
| 50 | 12·4 | 8·4 | 4·0 |
| 70 | 11·8 | 8·4 | 3·4 |
| **1. vii. 48** | | | |
| 0·5 | 12·0 | 1·2 | 10·8 |
| 5 | 12·0 | 0·3 | 11·7 |
| 25 | 20·6 | 7·4 | 13·2 |
| 50 | 16·7 | 9·6 | 7·1 |
| 70 | 16·2 | 9·6 | 6·6 |
| **29. vii. 48** | | | |
| 0·5 | 16·1 | 1·8 | 14·3 |
| 5 | 7·8 | 1·3 | 6·5 |
| 25 | 9·1 | 4·7 | 4·4 |
| 50 | 13·0 | 9·5 | 3·5 |
| 70 | 12·1 | 10·0 | 2·1 |
| **31. viii. 48** | | | |
| 0 | 13·5 | 1·1 | 12·4 |
| 5 | 8·5 | 1·7 | 6·8 |
| 15 | 9·0 | 1·1 | 7·9 |
| 25 | 12·7 | 2·4 | 10·3 |
| 50 | 15·0 | 10·4 | 4·6 |
| 70 | 14·0 | 11·1 | 2·9 |
| **4. x. 48** | | | |
| 0·5 | 11·4 | 5·4 | 6·0 |
| 5 | 12·8 | 5·8 | 7·0 |
| 15 | 10·8 | 6·0 | 4·8 |
| 25 | 11·7 | 7·2 | 4·5 |
| 50 | 12·8 | 8·7 | 4·1 |
| 70 | 12·3 | 8·0 | 4·3 |
| **27. x. 48** | | | |
| 0·5 | 10·5 | 8·8 | 1·7 |
| 5 | 12·4 | 8·6 | 3·8 |
| 25 | 12·9 | 9·3 | 3·6 |
| 50 | 11·0 | 8·6 | 2·4 |
| 70 | 12·1 | 9·6 | 2·5 |
| **30. xi. 48** | | | |
| 0·5 | 15·5 | 10·2 | 5·3 |
| 5 | 11·3 | 9·9 | 1·4 |
| 10 | 12·3 | 9·5 | 2·8 |
| 25 | 12·7 | 9·6 | 3·1 |
| 50 | 12·0 | 9·1 | 2·9 |
| 70 | 11·9 | 10·6 | 1·3 |
| **5. i. 49** | | | |
| 0·5 | 13·0 | 11·9 | 1·1 |
| 5 | 11·8 | 11·0 | 1·8 |
| 10 | 12·0 | 11·4 | 0·6 |
| 25 | 12·9 | 10·7 | 2·2 |
| 50 | 12·6 | 10·4 | 2·2 |
| 70 | 12·7 | 10·8 | 1·9 |
| **1. ii. 49** | | | |
| 0·5 | 15·6 | 13·6 | 2·0 |
| 5 | 14·8 | 13·1 | 1·7 |
| 10 | 15·3 | 12·8 | 2·5 |
| 25 | 15·5 | 13·2 | 2·3 |
| 50 | 15·5 | 13·8 | 1·7 |
| 70 | 14·8 | 12·5 | 2·3 |
| **1. iii. 49** | | | |
| 0 | 16·7 | 13·3 | 3·4 |
| 5 | 13·8 | 11·6 | 2·2 |
| 10 | 14·4 | 11·4 | 3·0 |
| 25 | 14·6 | 11·3 | 3·1 |
| 50 | 14·7 | 11·6 | 3·1 |
| 70 | 14·5 | 11·3 | 3·2 |
| **13. iv. 49** | | | |
| 0·5 | 17·3 | 8·7 | 6·6 |
| 5 | 15·4 | 9·7 | 5·7 |
| 15 | 15·5 | 9·5 | 6·0 |
| 25 | 16·3 | 9·6 | 5·7 |
| 35 | 15·5 | 9·2 | 6·3 |
| 45 | 15·7 | 9·4 | 6·3 |
| 55 | 16·2 | 10·2 | 6·0 |
| 65 | 13·7 | 9·8 | 3·9 |
| **9. v. 49** | | | |
| 0 | 10·1 | 2·0 | 8·1 |
| 5 | 8·9 | 1·1 | 7·8 |
| 15 | 7·7 | 1·9 | 5·8 |
| 25 | 12·0 | 3·2 | 8·8 |
| 35 | 16·4 | 8·4 | 8·0 |
| 45 | 18·3 | 8·0 | 10·3 |
| 55 | 18·4 | 8·3 | 10·1 |
| 65 | 17·6 | 8·5 | 9·1 |
| **9. vi. 49** | | | |
| 0·5 | 9·7 | 4·8 | 4·9 |
| 5 | 9·0 | 4·7 | 4·3 |
| 10 | 10·5 | 4·7 | 5·8 |
| 20 | 12·7 | 5·7 | 7·0 |
| 25 | 14·6 | 10·8 | 3·8 |
| 30 | 13·4 | 10·8 | 2·6 |
| 40 | 12·5 | 10·8 | 1·7 |
| 50 | 12·9 | 10·8 | 2·1 |
| 60 | 13·3 | 10·1 | 3·2 |
| 68 | 13·0 | 10·0 | 3·0 |
| **6. vii. 49** | | | |
| 0·5 | 8·3 | 2·6 | 5·7 |
| 5 | 8·3 | 3·5 | 4·8 |
| 10 | 8·9 | 2·3 | 6·6 |
| 20 | 14·0 | 5·7 | 8·3 |
| 30 | 12·7 | 6·5 | 6·2 |
| 40 | 11·2 | 6·9 | 4·3 |
| 50 | 11·2 | 6·9 | 4·3 |
| 60 | 11·2 | 7·0 | 4·2 |
| 70 | 12·2 | 8·1 | 4·1 |
| **11. vii. 49** | | | |
| 5 | 5·8 | 3·9 | 1·9 |
| 20 | 7·6 | 3·1 | 4·5 |
| 30 | 11·9 | 6·8 | 5·1 |
| 70 | 10·5 | 7·1 | 3·4 |
| **8. viii. 49** | | | |
| 10 | 8·5 | 3·4 | 5·1 |
| 20 | 9·7 | 4·3 | 5·3 |
| 30 | 8·9 | — | — |
| 40 | 9·5 | — | — |
| 50 | 10·0 | 7·0 | 3·0 |
| 60 | 10·4 | — | — |
| 70 | 9·9 | 6·8 | 3·1 |
| **8. ix. 49** | | | |
| 0·5 | — | 4·8 | — |
| 5 | — | 3·6 | — |
| 10 | 8·1 | 4·2 | 3·9 |
| 20 | 13·9 | — | — |
| 30 | 11·3 | — | — |
| 40 | 11·3 | — | — |
| 50 | 11·5 | 9·2 | 2·3 |
| 60 | 12·2 | — | — |
| 70 | 10·8 | 9·9 | 0·9 |
| **6. x. 49** | | | |
| 0·5 | 12·9 | 7·1 | 5·8 |
| 5 | 12·7 | 5·9 | 6·8 |
| 10 | 12·2 | 5·4 | 6·8 |
| 25 | 12·7 | 8·9 | 3·8 |
| 50 | 12·7 | 10·1 | 2·6 |
| 70 | 12·7 | 9·1 | 3·6 |
| **8. xi. 49** | | | |
| 0 | 18·0 | 10·3 | 7·7 |
| 10 | 13·9 | 10·0 | 3·9 |
| 25 | 13·3 | 10·5 | 2·8 |
| 50 | 13·3 | 10·4 | 2·8 |
| 70 | 14·3 | 10·4 | 3·9 |

### Position 1–2 miles SW. of Eddystone, 10 miles SSW. of Plymouth breakwater

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **18. vi. 47** | | | |
| 0·5 | 11·9 | 2·2 | 9·7 |
| 5 | 12·3 | 2·5 | 9·8 |
| 10 | 12·4 | 4·2 | 8·2 |
| 15 | 11·8 | 2·9 | 8·9 |
| 20 | 12·5 | 3·1 | 9·4 |
| 25 | 13·3 | 3·8 | 9·5 |
| 30 | 12·5 | 4·8 | 7·7 |
| **23. vii. 49** | | | |
| 5 | 10·2 | 2·3 | 7·9 |
| 10 | 11·6 | 2·2 | 9·4 |
| 20 | 12·3 | 5·0 | 7·3 |
| 30 | 12·6 | 6·5 | 6·1 |
| 40 | 11·8 | 7·4 | 4·4 |
| 50 | 13·1 | 6·8 | 6·3 |
| 65 | 14·2 | 6·8 | 7·4 |
| **29. ix. 47** | | | |
| 5 | 10·7 | 4·7 | 6·0 |
| 15 | 10·1 | 5·1 | 5·0 |
| 25 | 10·5 | 5·1 | 5·4 |
| 50 | 10·7 | 6·1 | 4·6 |
| 63 | 10·2 | 6·1 | 4·1 |
| **24. xi. 47** | | | |
| 10 | 11·3 | 8·4 | 2·8 |
| 60 | 11·8 | 8·8 | 3·0 |
| **22. xii. 47** | | | |
| 10 | 11·5 | 9·4 | 2·1 |
| 60 | 11·5 | 9·5 | 2·0 |
| **16. i. 48** | | | |
| 10 | 16·0 | 13·6 | 2·4 |
| 50 | 14·7 | 12·1 | 2·6 |
| **10. i. 49** | | | |
| 0·5 | 22·7 | 14·6 | 8·1 |
| 5 | 15·8 | 13·9 | 1·9 |
| 25 | 15·1 | 14·3 | 0·8 |
| 50 | 14·3 | 14·0 | 0·3 |
| 58 | 14·4 | 14·5 | — |
| **29. ix. 47** | | | |
| 10 | 15·6 | 5·8 | 9·8 |
| 30 | 12·8 | 4·8 | 6·0 |
| 50 | 14·0 | 7·5 | 6·5 |
| **11. iii. 48** | | | |
| 5 | 16·7 | 9·9 | 6·8 |
| 50 | 19·4 | 13·3 | 6·1 |
| **14. i. 49** | | | |
| 0 | 21·2 | 16·0 | 5·2 |
| 5 | 15·8 | 15·2 | 0·6 |
| 25 | 14·9 | 13·9 | 1·0 |
| 50 | 14·8 | 14·0 | 0·8 |

### Position 49° 50′ N., 7° 15′ W. Sounding 120 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **18. i. 47** | | | |
| 5 | 22·9 | 18·6 | 4·3 |
| 25 | 22·6 | 19·8 | 2·8 |
| 50 | 22·6 | 19·6 | 3·0 |

### Position 49° 38′ N., 5° 20′ W. Sounding 90 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **28. vi. 47** | | | |
| 5 | 6·5 | 1·9 | 4·6 |
| 10 | 8·6 | 1·6 | 7·0 |
| 15 | 7·3 | 6·1 | 1·2 |
| 20 | 12·3 | 4·0 | 8·3 |
| 40 | 11·0 | 10·4 | 0·6 |
| 50 | 11·8 | 7·0 | 4·8 |
| 80 | 11·4 | 8·7 | 2·7 |

### Position 49° 22′ N., 6° 12′ W. Sounding 119 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **28. vi. 47** | | | |
| 0·5 | 8·8 | 1·9 | 6·9 |
| 5 | 7·2 | 1·1 | 6·1 |
| 10 | 7·5 | 2·2 | 5·3 |
| 15 | 7·5 | 1·9 | 5·6 |
| 20 | 7·2 | 1·6 | 5·6 |
| 30 | 13·2 | 7·6 | 5·6 |
| 40 | 11·4 | 9·4 | 2·0 |
| 60 | 11·5 | 8·5 | 3·0 |
| 80 | 11·9 | 8·1 | 3·8 |
| 110 | 12·1 | 8·8 | 3·3 |

### Position 50° 00′ N., 7° 10′ W. Sounding 110 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **30. vi. 48** | | | |
| 0·5 | — | 1·9 | — |
| 5 | 11·2 | 1·2 | 10·0 |
| 25 | 10·2 | 2·2 | 8·0 |
| 50 | 21·4 | 13·6 | 7·8 |
| 75 | 23·8 | 14·6 | 9·2 |
| 107 | 20·0 | 15·8 | 4·2 |

### Position 50° 05′ N., 03° 28′ W. Sounding 68 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **11. x. 48** | | | |
| 5 | — | 5·3 | — |
| 25 | — | 5·8 | — |
| 50 | 10·9 | 3·1 | 7·8 |
| 65 | 10·9 | 4·0 | 6·9 |

### Position 50° 00′ N., 2° 30′ W. Sounding 67 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **12. ii. 48** | | | |
| 25 | 16·3 | 11·5 | 4·8 |
| **12. x. 48** | | | |
| 5 | — | 8·4 | — |
| 25 | — | 8·0 | — |
| 50 | 11·4 | 10·0 | 1·4 |
| 64 | 11·4 | 9·2 | 2·2 |

### Position 49° 50′ N., 2° 22′ W. Sounding 184 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **27. vii. 48** | | | |
| 5 | 7·8 | 3·1 | 4·7 |
| 25 | 10·4 | 5·9 | 4·5 |
| 40 | 12·3 | 9·1 | 4·2 |
| **13. x. 48** | | | |
| 5 | — | 8·4 | — |
| 25 | 9·9 | 7·6 | 2·3 |
| 50 | 8·6 | 7·6 | 1·0 |
| 75 | 11·5 | 7·6 | 3·9 |
| 100 | 10·3 | 7·8 | 2·5 |
| 150 | 11·2 | 7·3 | 3·9 |

### Position 50° 36′ N., 8° 04′ W. Sounding 70 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **9. iii. 49** | | | |
| 5 | 21·4 | 15·8 | 4·6 |
| 25 | 23·6 | 15·5 | 8·1 |
| 60 | 24·5 | 15·2 | 9·3 |

### Position 3·5 miles N. of Longships lighthouse. Sounding 70 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **10. iii. 49** | | | |
| 0 | 17·0 | 11·5 | 5·5 |
| 5 | 16·4 | 11·8 | 4·6 |
| 20 | 16·8 | 11·8 | 5·0 |
| 40 | 18·0 | 11·5 | 6·5 |
| 60 | 18·3 | 12·1 | 6·2 |

### Position 49° 44′ N., 8° 50′ W. Sounding 89 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **3. v. 49** | | | |
| 0·0 | 11·7 | 3·1 | 8·6 |
| 5 | 10·4 | 5·2 | 5·2 |
| 20 | 10·4 | 3·6 | 6·8 |
| 40 | 14·0 | 4·7 | 9·3 |
| 80 | 19·4 | 12·5 | 6·9 |

### Position 49° 28′ N., 6° 30′ W. Sounding 119 m.

| Depth (m.) | Total-P (mg. P/m.³) | Phosphate-P (mg. P/m.³) | Difference |
|---|---|---|---|
| **12. vii. 49** | | | |
| 5 | 6·4 | 2·7 | 3·7 |
| 20 | 7·2 | 2·7 | 4·5 |
| 30 | 8·2 | 3·9 | 4·3 |
| 40 | 17·2 | 16·1 | 1·1 |
| 80 | 16·3 | 15·6 | 0·5 |
| 100 | — | 16·8 | — |
| 110 | 16·5 | — | — |

# THE BOTTOM FAUNA OF GREAT WEST BAY

By N. A. Holme, B.A.

Zoologist at the Plymouth Laboratory

(Text-fig. 1)

CONTENTS



## INTRODUCTION

At the end of the last century extensive investigations were made of the trawling grounds in the bay between Start Point and Portland, sometimes known as Great West Bay (see Stead, 1896; Holt, 1898; Garstang, 1903; Kyle, 1903; and Todd, 1903). Although these deal mainly with the food-fish of the area, Todd gives an account of invertebrates brought up in the trawl. Since the trawl mainly samples the 'epifauna' of the sea-bottom, no comparison will be made of Todd's results with those obtained in the grab surveys to be described.

In November 1923, Mr E. Ford made a survey of the bottom fauna of the Bay, using a $\frac{1}{10}$ m.$^2$ Petersen grab. With the exception of a number of stations in Start Bay (see Ford, 1925), the results were not published. Mr Ford has kindly lent me the notes on his collections, some of which are included in this paper.

In the summer of 1948 a cruise was made in the western side of the Bay, samples being taken at thirty-seven stations with the bottom-sampler described by Holme (1949). At each station between one and five hauls were made, each covering an area of $\frac{1}{20}$ m.$^2$. The results are in the main very similar to those of Ford, showing that it is possible to make a reasonably reliable qualitative survey of a fairly large area using these methods. They also show that the bottom-fauna has not changed to any extent in the past 25 years.

The survey was made during the term of a D.S.I.R. research grant at the

Plymouth Laboratory. I am grateful to the Director and staff for facilities afforded during this period.

I am indebted to Captain C. A. Hoodless and the crew of R.V. *Sabella* for their assistance in taking the samples, and to Miss U. M. Grigg for help in sorting and preserving specimens during the cruise.

The following have kindly identified certain species: Miss S. M. Davies (*Eone*), Mr G. M. Spooner (Amphipoda), Miss U. M. Grigg (some of the Mollusca), Mr H. G. Vevers (Echinodermata). The author is responsible for the other identifications.

## Methods

Except for a few dredge hauls, collections were made with the 'scoop-sampler', covering a nominal area of $\frac{1}{20}$ m.$^2$, and digging to a maximum depth of 15 cm. Many of the grounds are muddy and therefore fairly suitable for working with either the Petersen grab or the new sampler. Quantitative differences may be due either to changes in the density of the fauna over 25 years or to the relative efficiency of the two samplers.

On most grounds the scoop-sampler took a fairly adequate sample, but seldom came up full, the volume obtained corresponding to a 'bite' of depth 6–8 cm. It is unlikely that much soil was lost during hauling as all stations were worked in perfectly calm weather.

Positions were fixed by compass bearings on to the shore, which was in sight at all but one station. Station lists are given in Tables XI and XII (pp. 182–3). The writer's soundings have been reduced to chart datum.

Since tidal streams are weak the hauls at each station could be taken without the ship drifting more than perhaps 100 m., usually much less.

Collections at each station were put together and sieved through a mesh of 1, 2, or 3 mm., depending on the grade of soil. Smaller Crustacea and worms may have been lost when the larger-meshed sieves were employed. A soil sample from each station has been kept.

At certain stations, where the bulk of the sievings was great, only a proportion was kept for examination. To this was added any large or conspicuous animals seen in the rest of the sample. The numbers recorded at these stations are, therefore, not strictly quantitative, and can only be taken to represent the minimum numbers present in the sample. Owing to rather hasty preservation, inevitable when working through large quantities of material at sea, some of the smaller animals have not been identified further than the genus. Other specimens may, however, have been sufficiently well preserved to enable specific identification. Thus the recording of *Pectinaria koreni* and *Pectinaria* sp. from one station does not necessarilymean that more than one species was present.

Nomenclature usually follows the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931).

## Great West Bay

Great West Bay is 48 miles across from Start Point to Portland, and extends 20 miles inwards. Its area is about 650 square miles. The western side is sheltered from westerly winds by the coastline; this and the absence of Atlantic swell make the sea rather less rough than off Plymouth.

Tidal currents in the Bay are weaker than in the main English Channel, but reach over 2 knots (3·7 km./hr.) at Start Point and Portland Bill. Off Berry Head the current reaches only $\frac{3}{4}$ knot, while in Teignmouth Bay it is scarcely felt.

The bottom is variable, but coarse deposits are rare and localized. The most significant feature is the large amount of mud deposited, particularly off Berry Head and in Torbay. In parts of Start Bay and on 'the Corner', however, the soil is fairly clean, consisting of coarse sand or fine gravel.

The rivers Exe, Teign and Dart empty into the Bay, but do not affect the salinity outside their estuaries.

The area investigated will be considered under five headings: Teignmouth Bay, Torbay (worked only by Mr Ford), grounds off Berry Head, 'the Corner' fishing grounds, and Start Bay.

## Teignmouth Bay

Teignmouth Bay extends from the Orestone to Straight Point, and has a maximum depth of *c.* 22 m. Over much of the bay the depth is about 20 m. The bay is exposed to the south and east, but sheltered from the north and west by the coastline.

Three fairly distinct types of bottom are found: clean sand; mixed grounds of sand, mud and gravel; and mud.

### *Clean Sand*

This occurs in a belt parallel to the shore off Dawlish and Exmouth. Farther offshore the sand gives way to gravel deposits. The depth is less than 11 m. Towards Dawlish the sand is finer and slightly muddy.

In 1948 the following stations were worked in this area: 1, 2, 12 and 14–16 (Table I). The fauna off Exmouth (Stations 1 and 2) is poor, but becomes richer towards Dawlish.

Species characteristic of the area are: *Sigalion mathildae*, *Nephthys* sp., *Magelona papillicornis*, *Iphinoë trispinosa*, *Bathyporeia* spp., *Tellina fabula*, *Donax vittatus*, *? Spisula subtruncata* and *Ensis* sp.[1] *Echinocardium cordatum* is quite common at Station 16, but is rare or absent elsewhere.

Ford did not work this area.

[1] A note on the species of *Ensis* to be found in the area will be published shortly.

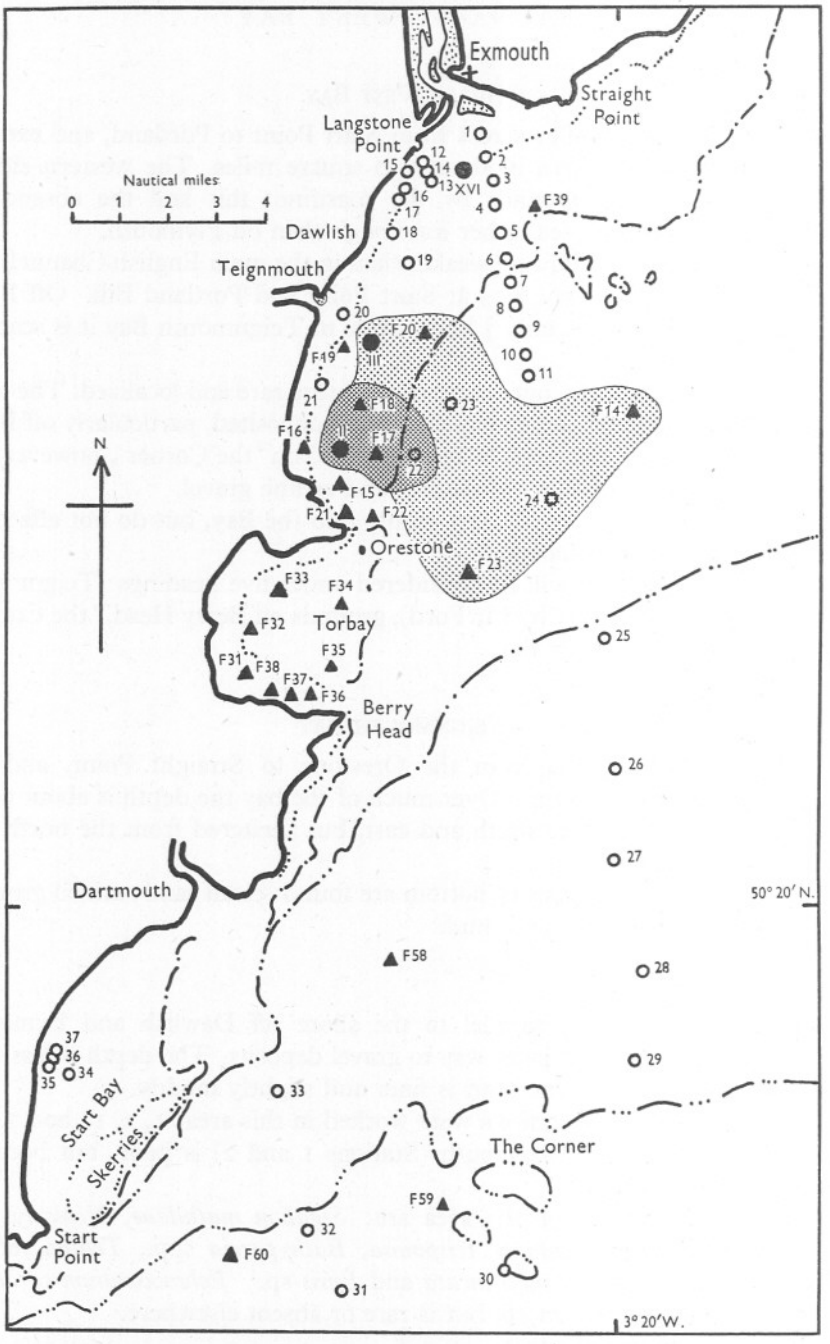


Fig. 1. Map of the western side of Great West Bay, showing stations worked by Mr Ford in 1923 and by the author in 1948. ▲, 1923 stations (Petersen grab); ○, 1948 stations (scoop-sampler); ●, 1948 dredge-hauls. ····, 5-fathom line; –·–, 10-fathom line; —·—, 20-fathom line; —···—, 30-fathom line. ⁘, area occupied by living *Turritella*; ▒, area where dead *Turritella* shells are abundant.

## Table I. Fauna of Fine Clean Sand in Teignmouth Bay

*Notes on Stations*

Station 1. 29. vii. 48. Exmouth Church, 349°, 1·2′. Clean sand.
Station 2. 29. vii. 48. Exmouth Church, 349°, 1·7′. Gravel and sand.
Station 12. 30. vii. 48. Langstone Point, 334°, 0·35′. Clean sand.
Station 14. 30. vii. 48. Langstone Point, 334°, 0·55′. Clean fine sand overlying gravel.
Station 15. 30. vii. 48. Langstone Point, 022°, 0·55′. Clean fine sand and some gravel. *Donax* picked out, and fauna sorted from two-thirds of total gravel.
Station 16. 30. vii. 48. Langstone Point, 013°, 0·9′. Sand.
The nominal area of each haul is 0·05 m.

| Station | 1 | 2 | 12 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|
| Depth (m.) | 5·5 | 10·5 | 5·5 | 7·5 | 5 | 10·5 |
| Area (m.²) | 0·15 | 0·05 | 0·1 | 0·05 | 0·05 | 0·2 |
| Sieve (mm.) | 1 | 3 | 1 | 1 | 1 | 1 |
| **Coelenterata** | | | | | | |
| ?*Peachia hastata* | .. | .. | .. | .. | .. | 3j. |
| ?*Sagartia* sp. | .. | .. | .. | .. | .. | 1 |
| **Nemertini** | | | | | | |
| Nemertine sp. | .. | .. | 1 | .. | .. | .. |
| **Polychaeta** | | | | | | |
| *Sigalion mathildae* | .. | .. | 2 | .. | .. | *c.* 4 |
| *Sthenelais boa* | .. | .. | .. | .. | .. | 1 |
| *Phyllodoce* sp. | 1 | .. | .. | .. | .. | 3 |
| *Nereis* sp. | .. | .. | .. | .. | .. | 1 |
| *Nephthys* sp. | *c.* 13 | .. | *c.* 3 | .. | .. | 4 |
| *Scoloplos armiger* | .. | .. | .. | .. | .. | 1 |
| *Nerine* sp. | .. | .. | .. | .. | .. | 1 |
| *Magelona papillicornis* | *c.* 40 | .. | 64 | 5 | 10 | 10 |
| ?*Owenia* tubes | .. | .. | .. | .. | .. | 3 |
| *Pectinaria koreni* | ?1 | 2 | .. | .. | .. | .. |
| ?*Lanice* tubes | .. | 1 | .. | .. | .. | 6 |
| Terebellid | .. | 1j. | .. | .. | .. | .. |
| Polychaeta indet. | 1 | 1 | 3 | .. | 1 | 1 |
| **Crustacea** | | | | | | |
| *Iphinoë trispinosa* | 20 | 1 | 3 | 1 | .. | .. |
| *Diastylis laevis* | 2 | .. | .. | .. | .. | 1 |
| *Diastylis* sp. | .. | .. | 1 | .. | .. | .. |
| *Pseudocuma cercaria* | 1 | .. | .. | .. | .. | .. |
| *Ampelisca brevicornis* | .. | .. | .. | .. | .. | 3 |
| *Bathyporeia guilliamsoniana* | 4 | .. | 3 | .. | 1 | .. |
| *Bathyporeia elegans* | .. | .. | 3 | .. | ?3 | ?1 |
| *Urothoë grimaldii* | .. | .. | 3 | .. | .. | .. |
| *Leucothoë lilljeborgi* | .. | .. | .. | .. | .. | 4 |
| *Nototropis swammerdami* | 1 | .. | .. | .. | .. | .. |
| *Gammarus locusta* | 1 | .. | .. | .. | .. | .. |
| Amphipoda indet. | .. | .. | 5 | .. | .. | .. |
| Prawn | .. | 1 | .. | .. | .. | .. |
| *Corystes cassivelaunus* | .. | .. | .. | .. | .. | 1j. |
| **Mollusca** | | | | | | |
| *Nucula nitida* | .. | .. | .. | .. | .. | 1 |
| ?*Pecten maximus* | 1j. | .. | .. | .. | .. | .. |
| *Chlamys opercularis* | 1j. | .. | .. | .. | .. | .. |
| *Montacuta ferruginosa* | .. | .. | .. | .. | .. | 2 |
| *Tellina fabula* | 2j. | .. | 1j. | .. | .. | 2j. |
| *Abra alba* | .. | .. | .. | .. | .. | 1 |
| *Abra* sp. | 4j. | .. | .. | .. | .. | .. |
| *Donax vittatus* | .. | .. | 2j. | .. | 1 | .. |
| ?*Spisula subtruncata* | 6j. | .. | .. | .. | .. | 1j. |
| *Lutraria* sp. (siphons) | .. | .. | .. | .. | .. | 2 |
| *Mysia undata* | .. | .. | .. | .. | .. | 1 |
| *Chione striatula* | .. | .. | .. | .. | .. | 1 |
| ?*Cardium aculeatum* | 1j. | .. | .. | .. | .. | .. |
| ?*Cardium tuberculatum* | 1j. | .. | .. | .. | .. | .. |
| *Ensis* sp. | 4j. | .. | 2 | .. | .. | 2 |
| Lamellibranchs indet. | 8 | .. | 4j. | .. | .. | 1 |
| *Philine aperta* | .. | .. | 1 | .. | .. | 1 |
| **Polyzoa** | | | | | | |
| *Cellaria* sp. | + | .. | .. | .. | .. | .. |
| **Echinodermata** | | | | | | |
| *Acrocnida brachiata* | .. | .. | .. | .. | .. | 2 |
| *Echinocardium cordatum* | .. | .. | 1j. | .. | .. | 3 |
| *Labidoplax digitata* | .. | .. | .. | .. | .. | 5 |

?, identity doubtful; j., small specimens; +, present, but numbers uncertain; ++, abundant.

*Mixed Grounds*

These occur off-shore in Teignmouth Bay in a depth of 10–23 m. Stations 3–11, 13 and 23 were worked in this area (Tables II and III). Deposits are of sand, fine shell fragments, and mud, sometimes mixed with fine gravel.

Characteristic species are: *Cerianthus lloydi*, *Melinna palmata*, *Phascolion strombi* (often in empty *Turritella* shells), *Eupagurus* spp., *Aloidis gibba*, *Cultellus pellucidus* and *Amphiura filiformis*.

Egg-clusters of *Turritella communis* were common at this time, and when trawling the meshes of the net came up covered with them. The presence of the Salcombe commensal, *Lepidasthenia argus*, at Station 3 is of interest. Although not taken in the grab hauls, *Gibbula magus* was found to be abundant off Langstone Point (dredge-haul XVI). A number of dredgings in the area showed that it was common only at this one station, where the bottom was of gravel.

Ford's Station 39, in this area, was evidently near a rocky ledge running southward from Straight Point. This is indicated by the presence of *Psammechinus miliaris* in the sample.

*Muddy Grounds*

These occur between Dawlish and the Orestone. Between Dawlish and Teignmouth the ground becomes progressively muddier, and north of the Orestone there is a deposit of mud in which *Turritella communis* is very abundant. The depth is between 10 and 22 m., and Stations 17–22 were worked in this area (Table IV).

Where living *Turritella* is abundant, only two or three other species are found. These include *Eupagarus bernhardus* which inhabits the empty shells. The estimated extent of the *Turritella* bed is shown in Fig. 1. At some stations living *Turritella* were abundant, at others large numbers of dead and worn shells were taken. In dredge-haul II living shells formed such a large proportion of the catch that they half-filled a galvanized iron bath. In dredge-haul III many white and dead shells were taken, but very few living ones occurred.

Mr Ford worked a number of stations in this bed, and the area shown on Fig. 1 is based on collections made on both cruises. There seems to be an area north of the Orestone where the animals live in abundance, from which dead shells are swept to the north and east by waves or currents.

It is of interest to note that Kyle (1903) records oysters (*Ostrea edulis*) from this area:

> 'From Hope's Nose to off Teignmouth there is a stretch of hard ground on which oysters are fairly abundant. As showing the trend of the currents in Teignmouth Bay, it may be mentioned that the empty shells congregate in masses behind the Orestone on the Torbay side.' (Hope's Nose is the headland opposite the Orestone).

Oyster shells are now rare or absent in Teignmouth Bay.

## TABLE II. FAUNA OF MIXED MUDDY AND GRAVEL GROUNDS IN TEIGNMOUTH BAY

*Note.* With most samples large animals were picked out, and a fraction of the sievings sorted (see p. 164). Numbers are those picked out, together with the subsample, which has not been multiplied by a factor.

Station 3. 29. vii. 48. Exmouth Church, 348°, 2·2′. Muddy sand and pebbles, overlying grey clay. One-quarter sorted.
Station 4. 29. vii. 48. Exmouth Church, 349°, 2·7′. Mud and a few pebbles. One-half sorted.
Station 5. 29. vii. 48. Exmouth Church, 349°, 3·3′. Fine shell fragments and sand. All sorted.
Station 6. 29. vii. 48. Exmouth Church, 349°, 3·8′. Muddy sand, gravel, and few shell fragments. Three-quarters sorted.
Station 7. 29. vii. 48. Exmouth Church, 349°, 4·3′. Fairly fine muddy sand. Small piece of red sandstone. One-quarter sorted.
Station 8. 29. vii. 48. Exmouth Church, 349°, 4·8′. Fairly fine muddy sand, with sandstone fragments. All sorted.

| Station | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|
| Depth (m.) | 14 | 17·5 | 19 | 19 | 20·5 | 21·5 |
| Area (m.²) | 0·15 | 0·1 | 0·1 | 0·15 | 0·1 | 0·15 |
| Sieve (mm.) | 3 | 3 | 3 | 3 | 3 | 3 |
| **COELENTERATA** | | | | | | |
| Hydroid | .. | .. | .. | + | .. | .. |
| *Cerianthus lloydi* | 1 | 2 | .. | .. | 4 | 2 |
| ?*Peachia hastata* | 1j. | .. | .. | .. | .. | .. |
| **PORIFERA** | | | | | | |
| Sponge | .. | .. | .. | .. | .. | 1 |
| **POLYCHAETA** | | | | | | |
| *Lepidasthenia argus* | 1 | .. | .. | .. | .. | .. |
| *Sthenelais boa* | 1 | .. | .. | .. | .. | .. |
| ?*Glycera convoluta* | .. | .. | .. | 3 | .. | 2 |
| *Glycera* sp. | .. | 1 | .. | .. | .. | .. |
| *Nematonereis unicornis* | 1 | .. | 1 | 1 | .. | .. |
| *Lumbriconereis* sp. | .. | .. | .. | 1 | .. | 1 |
| *Staurocephalus* sp. | .. | .. | .. | 1 | .. | .. |
| *Stylaroides eruca* | 1 | .. | .. | .. | .. | .. |
| *Scalibregma inflatum* | .. | .. | 1 | .. | .. | .. |
| ?*Owenia* tubes | .. | 1 | 1 | .. | .. | .. |
| *Pectinaria koreni* | .. | .. | .. | .. | .. | 1 |
| *Pectinaria auricoma* | .. | .. | 1 | .. | .. | .. |
| *Melinna palmata* | 2 | 16 | 4 | 6 | .. | 1 |
| Terebellid | .. | .. | 1j. | .. | .. | .. |
| Polychaeta | .. | 5 | 1 | 2 | .. | 1 |
| **GEPHYREA** | | | | | | |
| *Phascolosoma elongatum* | 2 | .. | .. | .. | .. | .. |
| *Phascolosoma vulgare* | .. | 3 | .. | .. | .. | .. |
| *Phascolion strombi* | .. | .. | 1 | 3 | .. | .. |
| **CRUSTACEA** | | | | | | |
| Amphipoda indet. | .. | .. | 1 | 1 | .. | .. |
| *Eupagurus cuanensis* | .. | .. | .. | .. | 1j. | .. |
| *Gonoplax rhomboides* | .. | .. | 1j. | .. | .. | .. |
| **MOLLUSCA** | | | | | | |
| *Abra alba* | .. | .. | 1 | .. | .. | .. |
| *Lutraria lutraria* | .. | .. | .. | 1j. | .. | .. |
| *Chione fasciata* | .. | .. | .. | .. | 1 | .. |
| *Cardium ovale* | .. | .. | .. | .. | .. | 1 |
| *Aloidis gibba* | .. | 1 | .. | 2 | .. | .. |
| *Cultellus pellucidus* | .. | .. | .. | .. | .. | 1 |
| *Turritella communis* | 4 | +* | 1 | .. | .. | 1 |
| *Aporrhais pes-pelicani* | .. | .. | .. | .. | .. | 2 |
| *Philine aperta* | 1 | .. | .. | .. | .. | .. |
| **POLYZOA** | | | | | | |
| *Cellaria* sp. | .. | .. | 1 | .. | + | 1 |
| **ECHINODERMATA** | | | | | | |
| *Amphiura filiformis* | .. | .. | .. | 1 | ?1 | 2 |
| *Cucumaria elongata* | .. | .. | .. | .. | .. | 1 |

* One egg-cluster of *Turritella*.

For abbreviations, see Table I.

## TABLE III. FAUNA OF MIXED MUDDY AND GRAVEL GROUNDS IN TEIGNMOUTH BAY (CONTINUED)

*Note*

Station 9. 29. vii. 48. Exmouth Church, 349°, 5·3′. Coarse muddy sand and a few shell fragments. All sorted.
Station 10. 29. vii. 48. Exmouth Church, 349°, 5·8′. Soil as at Station 9. One-tenth sorted.
Station 11. 29. vii. 48. Exmouth Church, 349°, 6·2′. Soil as at Stations 9 and 10. All sorted.
Station 13. 30. vii. 48. Langstone Point, 334°, 0·75′. Gravel and muddy sand. One-tenth sorted.
Station 23. 30. vii. 48. Orestone, 222°, 3·5′. Muddy sand with *Turritella* shells. All sorted.

| Station | 9 | 10 | 11 | 13 | 23 |
|---|---|---|---|---|---|
| Depth (m.) | 22 | 21·5 | 22 | 10·5 | 23 |
| Area (m.²) | 0·2 | 0·25 | 0·1 | 0·1 | 0·1 |
| Sieve (mm.) | 3 | 3 | 3 | 3 | 1 |
| COELENTERATA | | | | | |
| *Cerianthus lloydi* | 2 | 1 | .. | .. | .. |
| ?*Peachia hastata* | .. | .. | .. | 1 j. | .. |
| PORIFERA | | | | | |
| Sponge | .. | .. | .. | .. | 2* |
| NEMERTINI | | | | | |
| Nemertine sp. | 1 | .. | .. | .. | .. |
| POLYCHAETA | | | | | |
| *Phyllodoce* sp. | 1 | .. | .. | .. | .. |
| *Nereis longissima* | .. | .. | .. | .. | 1 |
| *Nephthys* sp. | 1 | 2 | 2 | 1 | 2 |
| *Hyalinoecia bilineata* | .. | 1 | .. | .. | .. |
| ?*Spiophanes bombyx* | .. | .. | .. | .. | 2 |
| ?*Owenia* tubes | 4 | 5 | 1 | .. | .. |
| *Pallasia murata* | .. | 1 | .. | .. | .. |
| *Melinna palmata* | 5 | 10 | 1 | 4 | .. |
| ?*Lanice* tubes | 1 | .. | .. | .. | .. |
| Polychaeta indet. | 10 | 6 | *c.* 8 | 2 | .. |
| GEPHYREA | | | | | |
| *Phascolosoma vulgare* | .. | 1 | .. | .. | .. |
| *Phascolion strombi* | .. | 1 | 2 | .. | 11 |
| CRUSTACEA | | | | | |
| *Coremapus versiculatus* | .. | .. | .. | .. | 1 |
| Amphipoda indet. | .. | .. | 1 | .. | .. |
| *Eupagurus bernhardus* | .. | 1 | .. | .. | .. |
| *Eupagurus cuanensis* | .. | 1 | .. | .. | .. |
| *Eupagurus* sp. | .. | .. | .. | .. | 1 j. |
| MOLLUSCA | | | | | |
| *Nucula radiata* | .. | 1 | .. | .. | .. |
| *Nucula nitida* | .. | 1 | .. | .. | .. |
| *Abra alba* | .. | .. | 1 | .. | 3 |
| *Abra nitida* | .. | .. | 3 | .. | .. |
| *Abra* sp. | .. | 3 | .. | .. | .. |
| *Spisula subtruncata* | .. | 1 | .. | .. | .. |
| *Lutraria* sp. (siphons) | .. | .. | 1 | .. | .. |
| *Dosinia lupinus* | 2 | .. | .. | .. | .. |
| *Aloidis gibba* | 1 | 1 | .. | .. | .. |
| *Cultellus pellucidus* | 1 | 7 | 3 | .. | .. |
| *Turritella communis* | .. | .. | 1 | .. | 1† |
| Nudibranch | 1 | .. | .. | .. | .. |
| POLYZOA | | | | | |
| *Cellaria* sp. | 1 | .. | 1 | .. | 1 |
| ECHINODERMATA | | | | | |
| *Ophiothrix fragilis* | 4 | 1 | .. | .. | .. |
| *Amphiura filiformis* | .. | 1 | .. | .. | .. |
| *Thyone roscovita* | 2 | .. | .. | .. | .. |
| *Labidoplax digitata* | 3 | 2 | .. | .. | .. |

* Attached to *Turritella* shells. † Also *c.* 250 dead worn shells.
For abbreviations, see Table I.

## TABLE IV. FAUNA OF MUDDY GROUNDS IN TEIGNMOUTH BAY

*Note*

Station 17. 30. vii. 48. Langstone Point, 017°, 1·15′. Fine slightly muddy sand, and some gravel. Sampler not digging deeply.
Station 18. 30. vii. 48. Teignmouth Pier, 229°, 1·7′. Fine muddy sand, overlying gravel. Large animals picked out, and half the sieved gravel examined.
Station 19. 30. vii. 48. Teignmouth Pier, 251°, 1·7′. Gravel and sand in first two hauls, last three of sand. Large animals picked out, and one-fifth of gravel examined.
Station 20. 30. vii. 48. Teignmouth Pier, 324°, 0·6′. Fine sand with little mud.
Station 21. 30. vii. 48. Teignmouth Pier, 004°, 1·9′. Very fine muddy sand.
Station 22. 30. vii. 48. Orestone, 210°, 2·2′. Mud, with old *Turritella* shells.

| Station | 17 | 18 | 19 | 20 | 21 | 22 |
|---|---|---|---|---|---|---|
| Depth (m.) | 10·5 | 12·5 | 16·5 | 9·5 | 10·5 | 21·5 |
| Area (m.²) | 0·2 | 0·1 | 0·25 | 0·1 | 0·15 | 0·1 |
| Sieve (mm.) | 1 | 1 | 1 | 1 | 1 | 1 |
| **COELENTERATA** | | | | | | |
| *Cerianthus lloydi* | .. | .. | 3 | .. | .. | .. |
| ?*Peachia hastata* | 1 | .. | .. | .. | .. | .. |
| Anemone | .. | .. | .. | .. | 1 | .. |
| **POLYCHAETA** | | | | | | |
| *Aphroditidae* (mainly polynoids) | 1 | .. | 1 | .. | 1 j. | .. |
| *Sigalion mathildae* | 1 | .. | 1 | 2 | .. | .. |
| *Sthenelais boa* | .. | .. | .. | .. | 1 | .. |
| *Phyllodoce* sp. | .. | .. | .. | .. | 1 | .. |
| ?*Eteone* sp. | 1 | .. | .. | . | .. | .. |
| *Nereis longissima* | .. | .. | .. | .. | .. | 1 j. |
| Nereid | .. | .. | 1 j. | .. | | .. |
| *Nephthys* sp. | 6 | .. | 2 | .. | *c.*8 | .. |
| *Glycera* sp. | .. | .. | 1 | .. | .. | .. |
| *Eone nordmanni* | .. | 1 | 1 | .. | ?1 | .. |
| *Nematonereis unicornis* | .. | .. | 1 | .. | .. | .. |
| *Lumbriconereis* sp. | 1 | .. | 1 | .. | .. | .. |
| Spionid | .. | .. | 1 | 1 | .. | .. |
| *Spiophanes bombyx* | .. | .. | .. | .. | *c.* 10 | .. |
| *Magelona papillicornis* | 17 | .. | 2 | 2 | 1 | .. |
| *Notomastus latericeus* | .. | .. | .. | .. | .. | 2 j. |
| ?*Owenia* tubes | 2 | .. | 2 | 2 | .. | .. |
| *Pallasia murata* | .. | .. | +* | .. | .. | .. |
| *Pectinaria* sp. | .. | 1 | .. | .. | .. | .. |
| *Melinna palmata* | 3 | .. | 12 | 1 | *c.* 25 | .. |
| *Amphitrite edwardsi* | 1 j. | .. | .. | .. | .. | .. |
| *Lanice* tubes | .. | .. | .. | 3 | .. | .. |
| Polychaeta indet. | 18 | 5 | 7 | 1 | *c.* 20 | .. |
| **GEPHYREA** | | | | | | |
| *Phascolion strombi* | .. | 1 | .. | .. | .. | .. |
| **CRUSTACEA** | | | | | | |
| *Iphinoë trispinosa* | .. | .. | .. | .. | 2 | .. |
| *Diastylis laevis* | .. | .. | .. | .. | 1 | .. |
| *Ampelisca brevicornis* | .. | .. | .. | .. | 3 | .. |
| *Ampelisca tenuicornis* | .. | .. | 1 | .. | .. | .. |
| *Bathyporeia* sp. | .. | .. | .. | .. | 2 | .. |
| *Urothöe grimaldii* | .. | .. | .. | .. | 2 | .. |
| Amphipoda indet. | .. | .. | .. | 2 | .. | .. |
| *Eupagurus bernhardus* | 1 j. | .. | .. | .. | .. | 1 j. |
| **MOLLUSCA** | | | | | | |
| *Nucula nitida* | .. | .. | .. | 2 j. | .. | .. |
| *Thyasira flexuosa* | .. | .. | .. | .. | 3 | .. |
| *Montacuta ferruginosa* | 1 | .. | .. | .. | .. | .. |
| *Tellina fabula* | 8 | .. | .. | .. | 5 | .. |
| *Abra alba* | .. | .. | .. | .. | 7 | .. |
| *Abra* sp. | .. | .. | .. | 1 | .. | .. |
| *Spisula subtruncata* | .. | .. | .. | .. | 1 | .. |
| *Lutraria* sp. (siphons) | 2 | .. | 1 | .. | 1 | .. |
| *Mysia undata* | .. | .. | 1 j. | .. | .. | .. |
| *Chione striatula* | 1 j. | .. | .. | 1 j. | .. | .. |
| ?*Mya truncata* | .. | .. | 1 j. | .. | .. | .. |
| *Ensis* sp. | 1 j. | .. | 4 | .. | .. | .. |
| *Cultellus pellucidus* | 1 j. | .. | .. | .. | .. | .. |
| Lamellibranch indet. | .. | .. | .. | .. | 1 j. | .. |
| *Gibbula magus* | .. | 2 | .. | .. | .. | .. |
| *Turritella communis* | 10 | 1 | .. | .. | 1 | 50† |
| *Retusa* sp. | .. | .. | .. | .. | 1 | .. |
| *Philine aperta* | .. | .. | .. | .. | 2 | .. |
| **ECHINODERMATA** | | | | | | |
| *Amphiura filiformis* | 1 | 1 | 7 | 1 | 2 | .. |
| *Echinocardium cordatum* | 1 | .. | .. | .. | .. | .. |
| *Cucumaria elongata* | .. | .. | .. | .. | 1 | .. |
| *Leptosynapta inhaerens* | 1 | .. | 1 | .. | .. | .. |
| *Labidoplax digitata* | 1 | .. | .. | .. | .. | .. |

* Piece of tube. † *c.* 2300 worn old shells.
For abbreviations, see Table I.

Outside the *Turritella* bed characteristic species are: *Sigalion mathildae*, *Melinna palmata*, *Lutraria* sp., *Chione striatula*, *Ensis* sp., *Turritella communis* and *Amphiura filiformis*.

Siphons of large specimens of *Lutraria* sp., probably *L. lutraria*, were taken at a number of stations. This mollusc digs to a considerable depth and the shell is out of reach of the 'bite' of the sampler.

### Torbay

Torbay was worked by Ford in 1923, but was not visited in 1948. Stations F31–38 (Table V) were worked, in a depth of 11–16 m. Torbay is sheltered on three sides, being open only to the eastward. The bottom is mostly fine muddy sand, and the fauna is rather similar to that off Teignmouth.

The main features are the presence of large numbers of *Nucula nitida* and *Lutraria lutraria* (?), the siphons only of the latter being taken in the Petersen grab. Ford notes that *Echinocardium* was more in evidence here than elsewhere in the Great West Bay.

Other typical species are: *Nephthys* sp., *Melinna* sp., *Ampelisca* sp., *Thyasira flexuosa*, *Abra alba*, *Cultellus pellucidus* and *Amphiura filiformis*.

### Grounds off Berry Head

Off Berry Head there is a deposit of very fine sand and mud. Stations 24–27 (Table VI) were worked about 6 miles from shore, in a depth increasing from 30 to 51 m. The soil is similar at all stations except 27, where it is rather coarser.

Characteristic species are: *Nephthys* sp., *Lumbriconereis* sp., *Notomastus latericeus*, *Pectinaria koreni*, *Callianassa subterranea*, ?*Abra alba*, *Chione striatula*, *Cultellus pellucidus*, *Turritella communis* (in small numbers), *Amphiura filiformis*, and *Leptosynapta inhaerens*. *Callianassa* occurs at all stations from 25 to 29, and evidently forms a bed of considerable density in this area. The average density is 13 per m.$^2$

### 'The Corner'

South of Station 27 the bottom becomes coarser and less muddy. Several species seem to reach a larger size than at previous stations. The area is trawled by Brixham fishing vessels, but is not very productive.

Stations 28–33 were worked in this area in a depth of 51–60 m. (Table VII). The bottom is of coarse slightly muddy sand, characteristic species being: hydroids, *Pectinaria koreni*, *Nucula nitida*, *Amphiura filiformis* and *Echinocyamus pusillus*.

*Echinocyamus* appears for the first time at Station 28, not having been taken at previous stations. Station 33 has a bottom of finer sand with a fauna similar to that found on similar soils in Teignmouth Bay.

## TABLE V. FAUNA OF TORBAY. SAMPLED BY MR FORD IN 1923 WITH TWO HAULS OF THE $\frac{1}{10}$ M.$^2$ PETERSEN GRAB AT EACH STATION

*Note*

Station F 31. 15. xi. 23. Saltern Cavern NW, Churston Point, SW by W½W. Sand.
Station F 32. 15. xi. 23. Red Cliff Hotel NW by N; Roundham Head NW by W½W. Silty sand.
Station F 33. 15. xi. 23. Orestone E by N; Torquay Pier N by W. Muddy sand.
Station F 34. 15. xi. 23. Orestone NE by N; Thatcher Rock N. Mud and sand.
Station F 35. 15. xi. 23. Berry Head S; Brixham Breakwater Light SW by W. Mud and sand.
Station F 36. 15. xi. 23. Berry Head SE; Brixham Breakwater Light WSW. Sand harder and cleaner than at Station 35.
Station F 37. 15. xi. 23. Old Battery SW; Brixham Breakwater Light SE by E. Sandy mud.
Station F 38. 15. xi. 23. Quarries WNW; Fishcombe Point S½E. Mud, with some *Zostera*.

| Station .. .. | F31 | F32 | F33 | F34 | F35 | F36 | F37 | F38 |
|---|---|---|---|---|---|---|---|---|
| Sounding (m.) .. | 11 | 15 | 14 | 16 | 15 | 12 | 12 | ? |
| COELENTERATA | | | | | | | | |
| Anemone | .. | .. | .. | .. | .. | .. | 1 | .. |
| PLATYHELMINTHES | | | | | | | | |
| Polyclad sp. | .. | .. | .. | .. | .. | .. | .. | 1 |
| NEMERTINI | | | | | | | | |
| Nemertine sp. | .. | 1 | 1 | .. | 1 | .. | .. | .. |
| POLYCHAETA | | | | | | | | |
| *Sigalion* sp. | .. | .. | .. | .. | .. | .. | 1 | .. |
| *Sthenelais limicola* | .. | 1 | .. | .. | .. | .. | 1 | 2 |
| *Phyllodoce maculata* | .. | .. | .. | .. | 1 | .. | .. | .. |
| *Nereis* sp. | .. | 1 | .. | .. | .. | .. | .. | .. |
| *Nephthys* sp. | 6 | 10 | 8 | 6 | 8 | 7 | 7 | 9 |
| *Ammotrypane* sp. | .. | 1 | .. | .. | .. | .. | 1 | .. |
| *Scalibregma* sp. | .. | .. | .. | .. | .. | .. | .. | 1 |
| *Notomastus latericeus* | .. | 1 | .. | .. | .. | .. | .. | .. |
| *Pectinaria auricoma* | .. | 1 | .. | .. | .. | .. | .. | .. |
| *Melinna* sp. | + | 5 | 3 | 2 | .. | .. | + | + |
| *Lanice conchilega* tubes | 3 | .. | 1 | .. | .. | 6 | .. | 2 |
| Polychaeta indet. | + | + | + | 6 | + | .. | + | + |
| CRUSTACEA | | | | | | | | |
| *Diastylis* sp. | .. | 2 | 1 | .. | .. | .. | .. | .. |
| *Ampelisca* sp. | 6 | 1 | 3 | 4 | .. | .. | 2 | 1 |
| ?*Maera* sp. | 1 | .. | .. | .. | .. | .. | .. | .. |
| Amphipoda indet. | .. | .. | .. | .. | .. | .. | 1 j. | .. |
| Caprellid | .. | .. | .. | .. | .. | .. | .. | 1 |
| *Porcellana longicornis* | 1 | .. | .. | .. | .. | .. | .. | .. |
| *Macropodia* sp. | .. | .. | .. | .. | .. | .. | .. | 2 j. |
| MOLLUSCA | | | | | | | | |
| *Nucula nitida* | 7 | 25 | 9 | 12 | 2 | 3 | 4 | 22 |
| *Thyasira flexuosa* | .. | 6 | 1 | .. | .. | .. | 1 | 5 |
| *Mysella bidentata* | .. | 3 | .. | .. | .. | 1 | .. | 2 |
| *Montacuta ferruginosa* | .. | .. | .. | .. | 4 | .. | .. | .. |
| *Tellina fabula* | 5 | 3 | .. | 1 | .. | .. | .. | 6 |
| *Abra alba* | .. | .. | 3 j. | 4 j. | 29 | .. | 1 | 6 j. |
| *Abra* sp. | .. | 7 j. | .. | .. | .. | .. | .. | .. |
| *Mactra corallina* | 1 j. | .. | .. | .. | .. | .. | .. | .. |
| ?*Spisula elliptica* | .. | .. | .. | 1 j. | .. | .. | .. | .. |
| ?*Lutraria lutraria* (siphons) | .. | 1 | .. | .. | 25* | 1 | .. | .. |
| *Chione striatula* | .. | 1 | .. | 2 | .. | .. | 2 | .. |
| *Cardium echinatum* | .. | .. | .. | .. | 2 | .. | .. | .. |
| *Aloidis gibba* | .. | .. | .. | .. | .. | .. | 1 j. | .. |
| *Cultellus pellucidus* | 1 | 1 | .. | 9 | .. | .. | .. | 2 |
| *Philine* sp. | .. | 5 j. | .. | 1 | .. | .. | .. | 4 j. |
| ECHINODERMATA | | | | | | | | |
| *Astropecten* sp. | .. | .. | .. | .. | 1 | .. | .. | .. |
| *Amphiura filiformis* | 1 | 13 | + | .. | 7 | .. | .. | .. |
| Ophiuroid | 1 | .. | .. | 2 | .. | .. | 1 j. | .. |
| *Echinocardium cordatum* | .. | 1 | 1 | .. | 13 j. | .. | .. | .. |

* In all but four specimens siphons only were taken.
For abbreviations, see Table I.

## Table VI. Fauna of Grounds off Berry Head. Soil: Fine Sand and Mud at all Stations

*Note*

Station 24. 4. viii. 48. Berry Head, 225°, 6·2′.
Station 25. 4. viii. 48. Berry Head, 254°, 5·7′.
Station 26. 4. viii. 48. Berry Head, 280°, 5·8′.
Station 27. 4. viii. 48. Berry Head, 297°, 6·4′.

| Station | 24 | 25 | 26 | 27 |
|---|---|---|---|---|
| Depth (m.) | 30·5 | 40·5 | 48 | 51 |
| Area ($m.^2$) | 0·1 | 0·1 | 0·15 | 0·25 |
| Sieve (mm.) | 1 | 1 | 11 | 1 |
| **Coelenterata** | | | | |
| Hydroids | .. | .. | + | + |
| ?*Sagartia* sp. | 9 | .. | .. | 1 |
| **Nemertinea** | | | | |
| Nemertine sp. | .. | 1 | 13 | 2 |
| **Polychaeta** | | | | |
| Aphroditidae | .. | .. | 1 | 1 |
| ?*Harmothoë lunulata* | .. | .. | 1 | .. |
| *Phyllodoce* sp. | .. | 1 | 1 | .. |
| *Nephthys* sp. | .. | 3 | 6 | *c.* 3 |
| *Glycera convoluta* | .. | .. | .. | 3 |
| *Glycera* sp. | .. | .. | 1 j. | .. |
| ?*Eone* sp. | .. | 1 | 1 | .. |
| *Lumbriconereis* sp. | 1 | .. | 2 | 2 |
| *Scoloplos armiger* | .. | 1 | 2 | .. |
| *Spiophanes bombyx* | 1 | .. | ?2 | .. |
| Cirratulid | .. | 2 | 6 | .. |
| ?*Stylaroides flabellata* | .. | .. | 2 | .. |
| *Scalibregma inflatum* | 1 | .. | .. | .. |
| *Scalibregma* sp. | .. | .. | .. | 1 |
| *Notomastus latericeus* | 3 | 10 | 3 | 1 |
| ?*Owenia* tubes | .. | .. | .. | 2 |
| *Pectinaria koreni* | 1 | .. | 4 | 22 |
| Terebellid | .. | ?3 j. | .. | 1 |
| Polychaeta indet. | .. | 11 | 7 | 4 |
| **Crustacea** | | | | |
| *Diastylis* sp. | .. | .. | .. | 1 |
| Cumacean | .. | .. | 1 | .. |
| *Ampelisca tenuicornis* | 1 | 1 | 1 | .. |
| *Harpinia antennaria* | .. | .. | 2 | .. |
| *Callianassa subterranea* | .. | 2 | 2+4 j. | 2 j. |
| Decapoda | .. | .. | 2 | .. |
| **Mollusca** | | | | |
| *Mysella bidentata* | .. | .. | .. | 5 |
| ?*Abra alba* | .. | 10 j. | 4 j. | 27 j. |
| ?*Dosinia exoleta* | .. | .. | .. | 1 |
| ?*Dosinia lupinus* | .. | .. | .. | 1 j. |
| *Chione striatula* | .. | .. | 3 j. | 1+6 j. |
| ?*Cardium aculeatum* | .. | .. | .. | 1 j. |
| *Aloidis gibba* | .. | .. | 3 j. | .. |
| *Cultellus pellucidus* | 1 j. | 1 j. | .. | 1+24 j. |
| *Psammosolen chamasolen* | .. | .. | 1 | .. |
| Lamellibranch indet. | .. | .. | 1 | .. |
| *Turritella communis* | 12* | +† | +† | .. |
| *Retusa* sp. | .. | 1 | .. | .. |
| **Echinodermata** | | | | |
| *Amphiura filiformis* | .. | .. | 10 j. | 51 |
| *Echinocardium cordatum* | .. | .. | .. | 2 |
| *Leptosynapta inhaerens* | .. | .. | 1 | 12 |

* Also two egg-clusters. † One egg-cluster only.
For abbreviations, see Table I.

## TABLE VII. FAUNA OF 'THE CORNER' REGION

*Note*

Station 28. 4. viii. 48. Berry Head, 310°, 8·2′. Muddy sand with shell fragments. Soil coarser and less muddy than at Station 27.
Station 29. 4. viii. 48. Berry Head, 319°, 9·4′. Coarse slightly muddy sand. One-quarter sorted after picking out large animals.
Station 30. 4. viii. 48. Start Point, 275°, 9·6′. Coarse slightly muddy sand, and shell fragments. Sampler not bringing up much soil.
Station 31. 4. viii. 48. Start Point, 282°, 6·3′. Coarse slightly muddy sand. One-quarter sorted.
Station 32. 4. viii. 48. Start Point, 270°, 5·4′. Coarse slightly muddy sand. One-quarter sorted.
Station 33. 4. viii. 48. Start Point, 240°, 5·6′. Slightly muddy sand.

| Station | 28 | 29 | 30 | 31 | 32 | 33 |
|---|---|---|---|---|---|---|
| Depth (m.) | 51 | 54·5 | 60 | 59·5 | 58·5 | 49 |
| Area (m.²) | 0·25 | 0·15 | 0·1 | 0·1 | 0·15 | 0·2 |
| Sieve (mm.) | 2 | 2 | 1 | 1 | 2 | ? |
| COELENTERATA | | | | | | |
| Hydroids | 1 | 1 | + | .. | ++ | .. |
| *Cerianthus lloydi* | .. | .. | .. | .. | 4 | .. |
| NEMERTINEA | | | | | | |
| Nemertine | .. | 2 | .. | .. | .. | .. |
| POLYCHAETA | | | | | | |
| Aphroditidae | .. | 1 | .. | .. | .. | 1 |
| *Sigalion mathildae* | .. | .. | .. | .. | .. | 1 |
| *Sthenelais limicola* | .. | .. | .. | .. | .. | 1 |
| Phyllodocidae | .. | .. | .. | .. | .. | 1 |
| Nereidae | .. | .. | .. | .. | 1j. | .. |
| *Nephthys* sp. | *c.* 3 | .. | .. | .. | .. | *c.* 6 |
| *Glycera convoluta* | .. | 1 | 1 | .. | .. | .. |
| *Glycera* sp. | .. | .. | .. | .. | .. | 3 |
| Eunicidae | 1 | .. | .. | .. | .. | .. |
| *Lumbriconereis* sp. | .. | 2 | 1 | .. | .. | 5 |
| *Magelona papillicornis* | .. | .. | 1 | .. | .. | 160 |
| *Scalibregma inflatum* | .. | .. | .. | .. | .. | 1 |
| ?*Owenia* tubes | *c.* 3 | 2 | 1 | .. | 1 | .. |
| *Pallasia murata* | 1 | .. | .. | .. | .. | .. |
| *Pectinaria koreni* | 10 | 4 | .. | 1 | 1 | 13 |
| *Pectinaria auricoma* | 1 | .. | .. | .. | .. | .. |
| ?*Lanice* tubes | .. | 4 | .. | .. | 1 | .. |
| *Dasychone bombyx* | .. | .. | .. | .. | 1 | .. |
| Terebellid | .. | 1 | 1 | .. | .. | .. |
| Polychaeta indet. | 10 | 6 | 2 | 4 | .. | *c.* 20 |
| CRUSTACEA | | | | | | |
| *Ampelisca spinipes* | .. | .. | .. | 1 | .. | .. |
| Caprellid | .. | .. | .. | .. | 1 | .. |
| *Callianassa subterranea* | 1 | 1 j. | .. | .. | .. | .. |
| *Upogebia stellata* | .. | .. | .. | 1 | .. | .. |
| *Corystes cassivelaunus* | 1 | .. | .. | .. | .. | 2 |
| MOLLUSCA | | | | | | |
| Chiton | .. | .. | .. | .. | 1 | .. |
| *Nucula nitida* | 1 | 1 | 1j. | .. | .. | 4 |
| *Diplodonta rotundata* | .. | .. | .. | 1 | .. | .. |
| *Tellina donacina* | .. | .. | .. | 1 | .. | .. |
| *Abra alba* | .. | .. | .. | .. | 10 | 15 |
| ?*Abra nitida* | 2 | 2 | .. | .. | .. | .. |
| *Abra* sp. | .. | .. | 1 | .. | .. | .. |
| *Gari ferroensis* | 1 | .. | .. | .. | .. | .. |
| *Dosinia lupinus* | 1 | 1 | .. | .. | .. | .. |
| *Chione striatula* | 2 | .. | .. | .. | .. | 1 |
| *Cardium* sp. | .. | .. | .. | .. | .. | 1j. |
| *Aloidis gibba* | .. | 1 | .. | .. | .. | .. |
| *Ensis* sp. | .. | .. | .. | .. | .. | 1j. |
| *Cultellus pellucidus* | 3 | .. | .. | .. | 1 | 3j. |
| Lamellibranch indet. | .. | .. | .. | .. | .. | 1 |
| *Dentalium* sp. | .. | .. | .. | 1 | .. | .. |
| *Turritella communis* | .. | .. | .. | .. | .. | +† |
| ECHINODERMATA | | | | | | |
| *Amphiura filiformis* | 33 | 7 | .. | 1 | 3 | 6 |
| *Ophiura texturata* | .. | .. | .. | .. | .. | 1 |
| *Echinocyamus pusillus* | +* | +* | +* | +* | 4* | .. |

* Empty tests of *Echinocyamus* common. † One egg-cluster.

For abbreviations, see Table I.

## Start Bay

A mile or so off Slapton the bottom is of fine muddy sand, with the following fauna:

Station 34. 5. viii. 48. Start Point 188°, 3·2′. Fine slightly muddy sand. Depth 18 m. 0·1 m.² sampled. Sieve: 1 mm.

| | | | |
|---|---|---|---|
| Phyllodocidae | 1 | ?*Mysella bidentata* | 2 |
| *Magelona papillicornis* | 1 | *Montacuta ferruginosa* | 1 |
| Polychaeta indet. | 13 | *Ensis* sp. | 1 |
| *Nucula nitida* | 3 | *Cultellus pellucidus* | 2 |
| *Abra alba* | 9 | *Natica catena* | 1 |

Closer in-shore a gravel bottom occurs, with *Spisula solida* as the main inhabitant. This ground has already been described by Ford (1925), who found that the bed of *Spisula* extended for about 4 miles along the coast, in a depth of about 10 m. The density exceeded 1000 per m.² in six out of nine stations. In 1948 Stations 35–37 were worked on the *Spisula* bed. The results may be summarized thus:

| | | |
|---|---|---|
| Station 35 | 0·1 m.² sampled | Empty *Spisula* shells only |
| Station 36 | 0·15 m.² sampled | *Spisula solida* 58 |
| | | *Chione fasciata* 1 |
| Station 37 | 0·05 m.² sampled | Empty *Spisula* shells only |

Bearings and distances from Start Point were:

35: 181°, 3·3′; 36: 181°, 3·5′; 37: 182°, 3·7′.

Dredge hauls confirmed the abundance of *Spisula*, although it may be noted that the density recorded, 387 per m.², is considerably less than all but one (no. 50) of the nine stations sampled by Ford.

## Comparison with Ford's Survey

The results of Ford's survey are given in Tables V, VIII, IX and X. From these it is clear that no major qualitative changes have occurred in the fauna. For example, the following were found in both surveys:

(1) The *Turritella* ground in Teignmouth Bay.

(2) The *Spisula* bed in Start Bay.

(3) A fauna with *Nephthys* sp., *Notomastus latericeus*, *Melinna palmata*, *Nucula nitida*, *Lutraria* sp., *Cultellus pellucidus* and *Amphiura filiformis* among the most abundant or widely distributed species.

Owing to the different types of sampler used and to the fact that the same stations were not revisited, a quantitative comparison of the fauna at the two different times is not possible. The *Spisula* bed may have declined in numbers, as shown above, and certain species, *Abra alba* for example, seem to have decreased in density. On the whole, however, there is no evidence of any overall change in the abundance of the fauna.

TABLE VIII. SAMPLES TAKEN BY MR FORD IN THE *TURRITELLA* BED IN TEIGNMOUTH BAY. TWO HAULS OF $\frac{1}{10}$ M.$^2$ PETERSEN GRAB AT EACH STATION

*Note*

Station F 14. 13. xi. 23. Hope Nose W½S, The Ness NW by W. Mud and *Turritella* shells. Sample with over 700 dead and worn *Turritella* shells.
Station F 17. 13. xi. 23. Orestone S½W, Babbacombe Point W by S½S. Black mud and brownish sand. Ten empty *Turritella* shells taken.
Station F 18. 13. xi. 23. Babbacombe Point SW½S, The Ness N½E. Dark sand and mud. Thirty empty shells of *Turritella*, but these were fresh and pink in colour.
Station F 20. 13. xi. 23. Orestone S by W, The Ness NW. Muddy shell gravel with *Turritella* shells. Over 600 dead and worn shells taken.
Station F 23. 14. xi. 23. Orestone NW by W½W, The Ness N by W¼W. Dark sandy mud and *Turritella* shells. Over 1200 white empty shells taken, but these were not badly worn.

| Station | F14 | F17 | F18 | F20 | F23 |
|---|---|---|---|---|---|
| Sounding (m.) | 30 | 19 | 17 | 21 | 32 |
| COELENTERATA | | | | | |
| Hydroid | 1 | .. | .. | .. | .. |
| Anemone | 1 | 1 | .. | .. | 2 |
| PLATYHELMINTHES | | | | | |
| *Cryptocoelis* sp. | 1 | .. | .. | .. | .. |
| POLYCHAETA | | | | | |
| *Aphrodite* sp. | .. | .. | .. | 1 | .. |
| Aphroditidae | 1 | .. | .. | .. | .. |
| *Sthenelais* sp. | 1 | .. | .. | .. | .. |
| *Nephthys* sp. | 3 | 22 | 2 | 2 | 4 |
| *Goniada maculata* | .. | 1 | .. | .. | .. |
| *Scalibregma* sp. | .. | .. | .. | 1 | .. |
| *Ammotrypane* sp. | .. | .. | 1 | .. | .. |
| *Notomastus* sp. | + | + | .. | .. | .. |
| *Owenia fusiformis* | .. | 1 | .. | 10 | .. |
| *Melinna* sp. | .. | + | 4 | 13 | 5 |
| *Lanice* sp. | .. | .. | .. | 1 | .. |
| Terebellid | .. | 1 | .. | .. | .. |
| Sabellid | .. | .. | .. | 1 | .. |
| Polychaeta indet. | 1 | + | .. | + | + |
| GEPHYREA | | | | | |
| *Phascolion strombi* | + | .. | 9 | .. | + |
| CRUSTACEA | | | | | |
| *Ampelisca* sp. | 1 | 1 | .. | 3 | .. |
| Amphipoda indet. | 1 | .. | .. | 1 | .. |
| Shrimp | .. | 1 | .. | .. | .. |
| *Eupagurus* sp. | 7 j. | .. | .. | 6 | .. |
| *Nika edulis* | .. | 1 | .. | .. | .. |
| *Gonoplax rhomboides* | .. | .. | .. | .. | 1 |
| *Porcellana longicornis* | 8 | .. | .. | 1 | .. |
| MOLLUSCA | | | | | |
| *Thyasira flexuosa* | 1 | 3 | .. | 3 | .. |
| *Abra alba* | ?25 | 2 j. | .. | 7 | .. |
| *Mactra corallina* | .. | 1 j. | .. | .. | .. |
| *Aloidis gibba* | .. | .. | .. | 1 | .. |
| *Cultellus pellucidus* | .. | .. | .. | 1 | .. |
| *Bullinella cylindracea* | .. | .. | 1 | .. | .. |
| *Nassa reticulata* | .. | .. | 1 | .. | .. |
| *Turritella communis* | 58 | .. | 70 | .. | 38 |
| ECHINODERMATA | | | | | |
| Ophiuroid | .. | 1 j. | .. | .. | .. |

For abbreviations, see Table I.

TABLE IX. SAMPLES TAKEN BY MR FORD ON VARIOUS GROUNDS IN TEIGNMOUTH BAY. TWO HAULS OF THE $\frac{1}{10}$ M.$^2$ PETERSEN GRAB AT EACH STATION

*Note*

Station F15. 13. xi. 23. Hope Nose S, Babbacombe Point W by S. Dark mud and sand.
Station F16. 13. xi. 23. Babbacombe Point S, Petit Tor NW. Fine red sand.
Station F19. 13. xi. 23. Hope Nose S by W, The Ness N. Fine red sand.
Station F21. 13. xi. 23. Black Head SW, Babbacombe NW by W. Very fine reddish sand.
Station F22. 13. xi. 23. Flat Rock SW½W, Black Head NW¼W. Coarse muddy shale (unsuitable for grab work).
Station F39. 16. xi. 23. Clerk Point W by N, Straight Pt. N by E. Coarse muddy gravel.

| Station .. .. | F15 | F16 | F19 | F21 | F22 | F39 |
|---|---|---|---|---|---|---|
| Sounding (m.) .. | 15 | 10 | 10 | 14 | 22 | 22 |
| COELENTERATA | | | | | | |
| Hydroid | .. | .. | .. | .. | .. | + |
| POLYCHAETA | | | | | | |
| Aphroditidae | .. | .. | .. | .. | .. | 1 |
| ?*Sigalion* sp. | .. | 1 | .. | .. | .. | .. |
| *Sthenelais boa* | .. | .. | .. | .. | .. | 1 |
| *Phyllodoce maculata* | .. | .. | .. | .. | .. | 1 |
| *Nereis* sp. | .. | .. | .. | .. | 1 | .. |
| *Nephthys* sp. | 7 | 1 | 6 | 10 | 1 | 1 |
| *Glycera* sp. | .. | .. | .. | .. | 1 | 6 |
| *Magelona sp.* | .. | .. | .. | .. | .. | 1 |
| *Scalibregma* sp. | .. | .. | .. | .. | 2 | 8 |
| *Ammotrypane* sp. | 1 | .. | .. | .. | .. | .. |
| *Notomastus* sp. | .. | .. | .. | + | + | .. |
| *Owenia fusiformis* | 5 | .. | 16 | 1 | 5 | .. |
| *Amphicteis* sp. | .. | 1 | .. | .. | .. | .. |
| *Melinna palmata* | + + | .. | .. | *c.* 9 | 2 | + |
| *Amphitrite* sp. | .. | .. | .. | .. | .. | 1 |
| *Lanice conchilega* | *c.* 10 | .. | 16 | 48 | .. | .. |
| Terebellid | .. | .. | .. | 1 | .. | .. |
| Polychaeta indet. | + | + | .. | + | .. | 3 |
| GEPHYREA | | | | | | |
| *Phascolosoma* sp. | .. | .. | .. | .. | 4 | .. |
| *Phascolion strombi* | .. | .. | .. | .. | .. | 2 |
| CRUSTACEA | | | | | | |
| *Ampelisca* sp. | 9 | .. | .. | 8 | .. | 6 |
| *Bathyporeia* sp. | .. | .. | 2 | .. | .. | .. |
| ?*Hippomedon* sp. | 1 | .. | .. | .. | .. | .. |
| *Eupagurus* sp. | .. | .. | .. | .. | .. | 1 |
| *Nika edulis* | .. | .. | .. | 1 | .. | .. |
| *Portunus* sp. | .. | .. | .. | .. | .. | 1 j. |
| MOLLUSCA | | | | | | |
| *Nucula nitida* | 4 | 1 | .. | 7 | 1 | .. |
| *Thyasira flexuosa* | 6 | .. | .. | 1 | 1 | 1 |
| *Diplodonta rotundata* | .. | .. | .. | .. | .. | 1 |
| *Mysella bidentata* | 2 | .. | .. | .. | .. | .. |
| *Tellina fabula* | .. | 1 | .. | 1 | .. | .. |
| *Abra alba* | 3 j. | 2 j. | .. | 7 j. | 2 j. | .. |
| *Abra nitida* | 2 | .. | .. | .. | .. | .. |
| *Donax vittatus* | .. | .. | 1 | .. | .. | .. |
| *Spisula* sp. | .. | 1 j. | .. | .. | .. | .. |
| *Lutraria lutraria* (siphons) | .. | 4 | .. | .. | .. | .. |
| *Chione striatula* | 1 | .. | .. | .. | .. | .. |
| *Aloidis gibba* | .. | 1 j. | .. | .. | .. | .. |
| *Ensis* sp. | .. | 1 j. | .. | .. | .. | .. |
| *Cultellus pellucidus* | 3 | .. | .. | 2 | .. | .. |
| *Turritella communis* | .. | .. | .. | .. | .. | 1 |
| ECHINODERMATA | | | | | | |
| *Amphiura filiformis* | 4 | .. | .. | 1 | .. | 3 |
| *Psammechinus miliaris* | .. | .. | .. | .. | .. | 1 |
| *Echinocardium cordatum* | .. | 1 | .. | .. | .. | .. |
| *Cucumaria elongata* | .. | .. | .. | .. | .. | 2 |
| *Synapta* sp. | 1 | .. | .. | .. | .. | .. |

For abbreviations, see Table I.

TABLE X. SAMPLES TAKEN BY MR FORD IN THE 'CORNER' REGION. TWO HAULS OF $\frac{1}{10}$ M.$^2$ PETERSEN GRAB AT EACH STATION

*Note*

Station F58. 20. xi. 23. Berry Head N 5 miles. Fine sandy mud.
Station F59. 20. xi. 23. Berry Head N 10 miles. Silty sand, gravel, and shells.
Station F60. 20. xi. 23. Start Point W by N$\frac{3}{4}$N, Downend Beacon N by E$\frac{3}{4}$E. Silty sand, gravel, and shells.

| Station .. .. | F58 | F59 | F60 |
|---|---|---|---|
| Sounding (m.) .. .. | 48 | 59 | 57 |
| COELENTERATA | | | |
| Hydroid | .. | .. | + |
| NEMERTINI | | | |
| Nemertine sp. | 1 | .. | .. |
| POLYCHAETA | | | |
| *Sthenelais limicola* | .. | 1 | .. |
| *Sthenelais* sp. | 3 | .. | .. |
| *Ophiodromus flexuosus* | 1 | .. | .. |
| *Nephthys* sp. | 3 | 1 | 2 |
| *Phyllochaetopterus* sp. | .. | .. | + |
| Chlorhaemid | 1 | 2 | .. |
| *Notomastus* sp. | 2 | .. | .. |
| *Owenia fusiformis* | .. | .. | 1 |
| Maldanid | .. | 1 | .. |
| *Lanice* sp. | .. | *c.*5 | .. |
| Polychaeta indet. | + | + | 2 |
| CRUSTACEA | | | |
| *Ampelisca* sp. | .. | 1 | 2 |
| Palaemonid | .. | .. | 1 |
| *Portunus* sp. | .. | 1 j. | .. |
| *Gonoplax rhomboides* | 2 | .. | .. |
| *Ebalia* sp. | .. | .. | 1 |
| *Macropodia* sp. | .. | 1 j. | .. |
| MOLLUSCA | | | |
| *Nucula nitida* | .. | 1 | .. |
| *Thyasira flexuosa* | 1 | .. | .. |
| *Tellina donacina* | .. | 1 | 2 |
| *Abra alba* | .. | 4 | .. |
| ?*Abra nitida* | 2 j. | .. | .. |
| *Chione striatula* | .. | 1 | .. |
| *Cultellus pellucidus* | 4 | 2 | .. |
| *Turritella communis* | .. | 1 | .. |
| ECHINODERMATA | | | |
| *Amphiura filiformis* | .. | 1 | .. |
| Ophiuroid | .. | .. | 1 |
| *Echinocardium cordatum* | 1 | .. | .. |

For abbreviations, see Table I.

## COMPARISON WITH THE PLYMOUTH FAUNA

Ford (1923) has outlined the communities to be found on the level sea bottom at Plymouth; he found that the main communities represented were *Venus* communities with Spatangidae. These were subdivided into two series: Series A, found in finer deposits and characterized by *Chione* (*Venus*) *striatula* and *Echinocardium cordatum*; and Series B, found in coarse deposits and characterized by *Chione* (*Venus*) *fasciata* and *Spatangus purpureus*.

Of forty species listed in Series A, thirty are recorded from Great West Bay; whereas of eighteen in Series B, only two have been taken (*Nucula radiata* and *Chione fasciata*), each occurring at only one station. (*Glycimeris glycimeris* and *Laevicardium crassum*, both from Series B, have, however, been taken in dredgings about 3 miles south of Straight Point.)

In general, the 'SpVf' communities of Series B are poorly represented and very localized, while the 'EcVg' communities of Series A are characteristic of the area. Ford has divided the 'EcVg' communities into subcommunities, but this has not been attempted for this area.

A number of species which are scarce or localized at Plymouth but common in the Bay may be noted: *Spisula solida*, *Turritella communis*, *Lutraria lutraria*, *Tellina fabula*, *Pectinaria* spp. and *Cerianthus lloydi*. Differences in the fauna of the two areas may be due to the greater shelter, deposition of large quantities of mud, or to the presence of a different type of bottom in the Bay.

With regard to the last, it seems possible that certain members of the fauna may prefer the type of sand found in the Bay to that off Plymouth. In the Bay much of the sand is derived from erosion of Permo-triassic red sandstone, of desert origin, which produces sand grains which, although angular, are more or less isodiametric (see, for example, Wilson, 1948, pl. XVI, fig. 3). Off Plymouth, however, one may assume that the sand is mainly derived from the marine-eroded Palaeozoic rocks, and the grains can be seen to present a more irregular outline, rather like the 'gritty sand' described by Wilson (1948, pl. XVII, fig. 3). It is possible that the distribution of *Pectinaria* spp., for example, is controlled by its preference for the type of sand found in Great West Bay, since it constructs its tube of sand grains.

Of species present at Plymouth but absent from the Bay one may merely list species of the 'SpVf' association. Their absence is due to the lack of coarse deposits which are associated with a strong tidal scour.

## Note on *Crepidula fornicata*

Although not taken in the bottom-sampler hauls, the spread of *Crepidula fornicata* (L.) to the area may be noted. Its occurrence in the Torquay-Paignton-Brixham area is mentioned by Cole (1950). In August 1948 a single specimen was found on a whelk shell taken south of Straight Point, and since then the species seems to have increased in numbers. Although the shores of Dawlish Warren and Exmouth have been frequently visited in the past few years, no shells of *Crepidula* were found until January 1950, when a number of empty whelk shells washed up on Dawlish Warren were found to have living *Crepidula* attached. Most were quite small, a centimetre or two in length, and several chains of three or four individuals were taken.

SUMMARY

An account is given of the bottom-fauna of Great West Bay from samples taken in 1948 with a new sampler. Comparison is made with a similar survey made by Mr E. Ford with the Petersen grab in 1923.

The deposits contain a fair proportion of mud, and the 'EcVg' communities defined by Ford dominate the area. Within the Bay are found fairly dense beds of *Turritella communis*, *Lutraria* sp., *Callianassa subterranea* and *Spisula solida*.

No marked changes in the fauna seem to have occurred since the earlier survey. The fauna is briefly compared with that of the Plymouth area.

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## Appendix

### Table XI. Mr Ford's Stations (1923). S.S. *Salpa*

$\frac{1}{10}$ m.² *Petersen grab.*

| | | |
|---|---|---|
| F 14 | 13. xi. 23 | Hope Nose W½S, The Ness NW by W |
| 15 | ,, | Hope Nose S, Babbacombe Pt. W by S |
| 16 | ,, | Babbacombe Pt. S, Petit Tor NW |
| 17 | ,, | Orestone S½W, Babbacombe Pt. W by S½S (Berry Head over Flat Rock) |
| 18 | ,, | Babbacombe Pt. SW½S, The Ness N½E |
| 19 | ,, | The Ness N, Hope Nose S by W |
| 20 | ,, | The Ness NW, Orestone S by W |
| 21 | ,, | Black Hd. SW, Babbacombe Pt. NW by W |
| 22 | ,, | Flat Rock SW½W, Black Hd. NW¼W |
| 23 | 14. xi. 23 | Orestone NW by W½W, The Ness N by W¼W |
| 31 | 15. xi. 23 | Saltern Cove NW, Churstone Pt. SW by W½W |
| 32 | ,, | Red Cliff Hotel NW by N, Roundham Hd. NW by W½W |
| 33 | ,, | Orestone E by N, Torquay Pier N by W |
| 34 | ,, | Thatcher Rock N, Orestone NE by N |
| 35 | ,, | Berry Hd. S, Brixham Breakwater Light SW by W |
| 36 | ,, | Brixham Breakwater Light WSW, Berry Hd. SE |
| 37 | ,, | Brixham Breakwater Light SE by E, Old Battery SW |
| 38 | ,, | Quarries WNW, Fishcombe Pt. S½E |
| 39 | 16. xi. 23 | Clerk Pt. W by N, Straight Pt. N by E |
| 58 | 20. xi. 23 | Berry Hd. N, 5 miles (log) |
| 59 | ,, | Berry Hd. N, 10 miles (log) |
| 60 | ,, | Start Pt. W by N¾N, Downend Beacon N by E¾E |

*N.B.* Ford's positions are compass bearings, magnetic variation in 1923 being 15′ 05″ W.

## TABLE XII. 1948 STATIONS. R.V. *SABELLA*

| | | | |
|---|---|---|---|
| | | $\frac{1}{20}$ m.² *Scoop-sampler* | |
| 1 | 29. vii. 48 | Exmouth Church | 349°, 1·2′ |
| 2 | ,, | ,, | 349°, 1·7′ |
| 3 | ,, | ,, | 348°, 2·2′ |
| 4 | ,, | ,, | 349°, 2·7′ |
| 5 | ,, | ,, | 349°, 3·3′ |
| 6 | ,, | ,, | 349°, 3·8′ |
| 7 | ,, | ,, | 349°, 4·3′ |
| 8 | ,, | ,, | 349°, 4·8′ |
| 9 | ,, | ,, | 349°, 5·3′ |
| 10 | ,, | ,, | 349°, 5·8′ |
| 11 | ,, | ,, | 349°, 6·2′ |
| 12 | 30. vii. 48 | Langstone Point | 334°, 0·35′ |
| 13 | ,, | ,, | 334°, 0·75′ |
| 14 | ,, | ,, | 334°, 0·55′ |
| 15 | ,, | ,, | 022°, 0·55′ |
| 16 | ,, | ,, | 013°, 0·9′ |
| 17 | ,, | ,, | 017°, 1·15′ |
| 18 | ,, | Teignmouth Pier | 229°, 1·7′ |
| 19 | ,, | ,, | 251°, 1·7′ |
| 20 | ,, | ,, | 324°, 0·6′ |
| 21 | 30. vii. 48 | ,, | 004°, 1·9′ |
| 22 | ,, | Orestone | 210°, 2·2′ |
| 23 | ,, | ,, | 222°, 3·5′ |
| 24 | 4. viii. 48 | Berry Head | 225°, 6·2′ |
| 25 | ,, | ,, | 254°, 5·7′ |
| 26 | ,, | ,, | 280°, 5·8′ |
| 27 | ,, | ,, | 297°, 6·4′ |
| 28 | ,, | ,, | 310°, 8·2′ |
| 29 | ,, | ,, | 319°, 9·4′ |
| 30 | ,, | Start Point | 275°, 9·6′ |
| 31 | ,, | ,, | 282°, 6·3′ |
| 32 | ,, | ,, | 270°, 5·4′ |
| 33 | ,, | ,, | 240°, 5·6′ |
| 34 | ,, | ,, | 188°, 3·2′ |
| 35 | ,, | ,, | 181°, 3·3′ |
| 36 | ,, | ,, | 181°, 3·5′ |
| 37 | ,, | ,, | 182°, 3·7′ |
| | | *Dredge hauls* | |
| II | 31. vii. 48 | Hope Nose | 177°, 1·6′ |
| III | 31. vii. 48 | Teignmouth Pier | 319°, 1·4′ |
| XVI | 3. viii. 48 | Langstone Point | 298°, 1·12′ |

*N.B.* The above are true bearings, and distances are in nautical miles.

# BIONOMICS OF THE POOR-COD (*GADUS MINUTUS* L.) IN THE PLYMOUTH AREA

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(Plates I and II and Text-figs. 1–16)

CONTENTS



The Poor-Cod, *Gadus minutus* L., is a very common gadoid off Plymouth, 'probably the commonest gadoid in the trawling grounds' (Mar. Biol. Assoc., 1931). McIntosh & Masterman (1897) and Ehrenbaum (1901–10) have described its development, and Schmidt (1902–07) has given a very detailed description of its larvae and post-larvae. Barring these, and a few other scattered works on its systematics, no detailed study has been made so far on the general life-history of *G. minutus*. The scope of this work is limited to the food, age and rate of growth, the length-weight relation and the spawning period of the Plymouth poor-cod population. The great availability of this fish in the Plymouth area has made the problem of collection of material for this study quite easy.

I am greatly indebted to Mr F. S. Russell and Mr E. Ford for suggesting this problem to me and for giving me much help and criticism in my work. I am extremely grateful to Mr G. A. Steven for kindly going through the manuscript of this paper and for offering valuable criticisms and suggestions for its improvement. My thanks are especially due to Dr T. J. Hart who encouraged and helped me most generously throughout my work. I am grateful to Mr P. G. Corbin for lending me several post-larval specimens of *Gadus minutus* from his collections and to Mr G. M. Spooner for kindly identifying the amphipods[1] contained in the food of the fish. I am grateful to Dr M. V. Lebour and Dr D. P. Wilson for helping me in the identification of some of the crustaceans and polychaetes in the qualitative analysis of the food of the fish. To Mr F. G. C. Ryder my thanks are due for making the otolith measuring scale and the vertical projector. Finally my thanks are due to the

[1] See also p. 193 of this *Journal*.

entire technical staff of the laboratory and the crew of the laboratory vessels for their help in collecting the specimens.

The work described here was undertaken while I was holding the Madras Government Scholarship.

## Methods of Collection and Treatment of Material

The whole material for this study has been collected from the Plymouth area outside the breakwater and around the Eddystone grounds by trawling from the Laboratory research vessels *Sabella* and *Sula*. The total number of fish thus collected and analysed is 5003 of all sizes ranging from 5 to 25 cm. Nearly all the specimens have been examined in the fresh state.

All specimens were measured to the nearest 5 mm., from the tip of the snout to the tip of the longest caudal ray (*total length*) and from the tip of the snout to the end of the caudal hypural (*standard length*).[1] It was apparent from the very beginning of the investigation that, because of the tearing and fraying of the caudal fin in trawled fish, all calculations had to be based on the standard length. All fish were weighed to the nearest gram in a Salter spring balance. The scales from the body of the fish which still retained them after trawling were removed by a scalpel and preserved in tissue-paper envelopes for later study. After measurements the specimens were dissected, the sexes were noted and the stomachs were then cut out and preserved in 5% sea-water formalin, sorted in 5 cm. body-length groups. A few random samples of specimens were boiled *in toto*. With other samples only the heads were boiled, for collecting the supra-occipital crest, which is the index that has been used for determination of age and rate of growth in this fish. During the early period of this study the specimens were collected by the ordinary otter trawl, and naturally a great amount of selective sampling by the gear has occurred. Towards the later period of the study Mr P. G. Corbin collected for me a fair number of O-group and I-group specimens of *G. minutus* by means of the otter trawl with attached sprat-net cod-end. The otoliths were collected by incising the skull dorsally behind the orbits and also by boiling the heads. All the otoliths were preserved in tissue-paper envelopes. A few specimens of the O-group from random samples were preserved in 5% sea-water formalin for later alizarine staining.

## Food of *Gadus minutus*

The food has been analysed qualitatively and volumetrically. The stomachs of each 5 cm. length group of fish were kept separate as they were collected. Each stomach was subsequently dissected and the contents washed out into a Petri dish. The different organisms were sorted and their volumes measured. The volumes were determined by the displacement method in a measuring cylinder graduated to 0·1 c.c. The organisms were identified to species whenever possible. But the effect of digestion often rendered only the generic or family

[1] All the lengths of the fish given in this paper are *standard lengths*, unless otherwise stated.

characters recognizable. *G. minutus*, like several other gadoids, sometimes everts its stomach and disgorges its contents during the course of trawling. But this occurred only in 0·8 % of the stomachs analysed, and so could be assumed to have not interfered with the general conclusions. Another factor which also has to be taken into account in the analysis of the food organisms is the fortuitous snatching of other organisms while the fish are in the trawl. When the stomachs contained a few organisms which were quite fresh in appearance and showed no evidence of action of the digestive juices, their presence must be disregarded because of this habit, which is well known among many other fishes.

In the first few months of the study, the fish were grouped into 5 cm. groups for food analysis. It was soon found that there was virtually no apparent difference in the food ingested by the various adolescent year groups and so the work was done on two separate groups only; O-group and all the rest together.

In counting the food organisms several precautions had to be taken to avoid the numerical difficulties arising out of the pieces and fragments resulting from the different stages of digestion. The method suggested by Brown & Cheng (1946) was followed. For amphipods and polychaetes the heads were counted and only recognizable specimens of other organisms were counted, the residue being treated as '*Galathea* remains', '*Processa* remains, Fish remains', etc. Volumetric analysis helps to tide over this difficulty to a great extent.

### *Food of the I- to V-Year Groups*

*G. minutus* of year-groups I to V is primarily a crustacean feeder, feeding on the bottom Crustacea. Day (1880–84) found that 'they live on small crustaceous animals...'. Thompson (1856) noticed chiefly Crustacea in their stomachs: 'In one was a full grown *Pagurus bernhardus* and fragments of marine plants also have occurred.' Fries *et al.* (1892) also make a more or less similar statement that 'it lives on small victims, consisting chiefly of crustaceans and mollusks'. In studying the food of the North Sea fishes, Franz (1910) found that the food of *Gadus minutus* consisted of fish (*Drepanopsetta*), crustaceans (*Pandalus* and *Eupagurus bernhardii*) and echinoderms.

In the analysis of the 3909 stomachs of Plymouth *Gadus minutus* (I to V year-groups) it was found that crustaceans form by far the greater part of the food consumed. Nine types of organisms form the principal food material of this fish in the Plymouth area. In the volumetric analysis (Tables I and II) these have been treated separately, and all the rest have been lumped together as 'others'. These nine principal organisms and their proportions of the total volume of food during the period under survey were as follows:

| | | | |
|---|---|---|---|
| *Processa canaliculata* | 21 % | *Porcellana* spp. | 6 % |
| Fish | 20 % | Crangonidae | 6 % |
| Polychaeta | 8 % | Amphipoda | 3 % |
| *Portunus* spp. | 8 % | Mysidacea and Euphausiacea | 3 % |
| *Galathea* spp. | 7 % | | |

Of the remaining 18% constituting the 'others', crustaceans formed 13%. Thus the total percentage of crustaceans consumed by the fish is 67 by volume.

When the number of fish that ingested particular organisms is considered, a different picture is obtained (Table III). *Processa canaliculata* occurs in more stomachs than any of the other food organisms, whose percentage frequency of occurrence is shown in the following list. Amphipods come second on the list, although as we have seen, they formed only a small percentage of the total volume of food. Conversely, Crangonidae and *Porcellana* spp., though forming a fair amount of the total volume of food, were found in a few fishes only. The reason is, of course, that whereas one *Porcellana* measured some 0·2 c.c., it requires 5–7 *Ampelisca spinipes* or 30–50 *Apherusa henneguyi* to make up the same volume.

| | | | |
|---|---|---|---|
| 29% | of the stomachs | contained | *Processa canaliculata* |
| 23% | ,, | ,, | Amphipoda |
| 16% | ,, | ,, | Fish |
| 16% | ,, | ,, | *Galathea* spp. |
| 14% | ,, | ,, | Polychaeta |
| 10% | ,, | ,, | *Portunus* spp. |
| 9% | ,, | ,, | *Porcellana* spp. |
| 8% | ,, | ,, | Mysidacea and Euphausiacea |
| 8% | ,, | ,, | Crangonidae |

The average volume of food per stomach for the period of investigation was 0·5 c.c. The percentage of empty stomachs (without taking the number of everted stomachs into consideration) was 10·5. The average volume of food per stomach in the respective months during the period of study was as follows:

| 1948 | c.c. | 1949 | c.c. |
|---|---|---|---|
| Apr. | 0·57 | Jan. | 0·34 |
| May | 0·59 | Feb. | 0·43 |
| June | 0·54 | Mar. | 0·42 |
| July | 0·73 | Apr. | 0·69 |
| Aug. | 0·46 | May | 0·77 |
| Sept. | 0·49 | June | 0·59 |
| Oct. | 0·47 | | |
| Nov. | 0·42 | | |
| Dec. | 0·46 | | |

Because the fish were collected at about the same time of the day throughout the investigation, it is probable that most of the food in their stomachs had undergone the same amount of digestion. The volume of food in the stomachs does not represent the volume consumed during feeding, because different food organisms will be digested at different rates. But on the general assumption that the food in most stomachs had reached the same state of digestion the results can roughly be treated as a fair guide to the feeding activity of the fish. On this basis three definite phases of feeding activity could be distinguished.

## Table I. Volumetric Analysis of the Stomach Contents per 100 Stomachs (Volumes in c.c.)

| | 1948 | | | | | | | | | 1949 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Food organisms | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June |
| Fish | 2·4 | 24·0 | 28·0 | 36·1 | 2·6 | 3·1 | 4·7 | 3·2 | 5·8 | 2·8 | 8·6 | 6·9 | 9·8 | 12·1 | 19·3 |
| Amphipoda | 2·0 | 2·6 | 3·2 | 2·0 | 1·7 | 1·4 | 0·7 | 1·7 | 1·5 | 0·6 | 0·5 | 1·0 | 1·4 | 1·4 | 1·7 |
| Polychaeta | 16·0 | 4·6 | 1·3 | 1·5 | 1·0 | 6·7 | 2·1 | 1·9 | 2·5 | 4·1 | 5·3 | 5·5 | 2·4 | 2·9 | 1·2 |
| Schizopoda (*sens. lat.*) | 2·4 | 3·0 | 2·8 | 1·0 | 1·0 | 1·0 | 1·0 | 1·0 | 1·0 | 1·0 | 0·5 | 0·4 | 0·8 | 1·4 | 2·2 |
| *Processa canaliculata* | 6·2 | 14·0 | 7·4 | 11·5 | 16·7 | 14·2 | 15·7 | 10·8 | 9·6 | 5·5 | 7·6 | 11·6 | 5·6 | 5·6 | 16·3 |
| Crangonidae | 8·1 | 2·2 | 2·0 | 3·0 | 2·9 | 2·1 | 1·1 | 4·5 | 5·6 | 3·3 | 1·8 | 0·7 | 1·0 | 2·6 | 1·1 |
| *Galathea* spp. | 2·4 | 3·6 | 4·0 | 4·3 | 3·8 | 2·2 | 3·1 | 1·3 | 3·5 | 1·9 | 3·2 | 3·8 | 14·2 | 4·6 | 4·8 |
| *Porcellana* spp. | 1·1 | 0·5 | 2·1 | 8·3 | 2·5 | 2·3 | 0·7 | 5·1 | 5·0 | 1·4 | 2·5 | 3·6 | 3·4 | 3·8 | 2·0 |
| *Portunus* spp. | 3·9 | 2·2 | 1·5 | 3·4 | 5·4 | 5·7 | 4·1 | 2·9 | 3·1 | 3·4 | 3·1 | 2·9 | 6·5 | 5·2 | 6·1 |
| Others | 12·0 | 2·0 | 1·6 | 1·6 | 8·4 | 9·9 | 13·9 | 9·9 | 8·2 | 9·7 | 9·4 | 5·5 | 24·2 | 36·9 | 4·6 |
| Total volume | 56·5 | 58·7 | 53·9 | 72·7 | 46·0 | 48·6 | 47·1 | 42·3 | 45·8 | 33·7 | 42·5 | 41·9 | 69·3 | 76·5 | 59·3 |
| No. of stomachs examined | 160 | 486 | 470 | 195 | 242 | 266 | 189 | 215 | 155 | 189 | 308 | 330 | 302 | 252 | 150 |
| No. of empty stomachs | 20 | 54 | 61 | 21 | 18 | 14 | 15 | 10 | 16 | 24 | 52 | 40 | 26 | 18 | 16 |

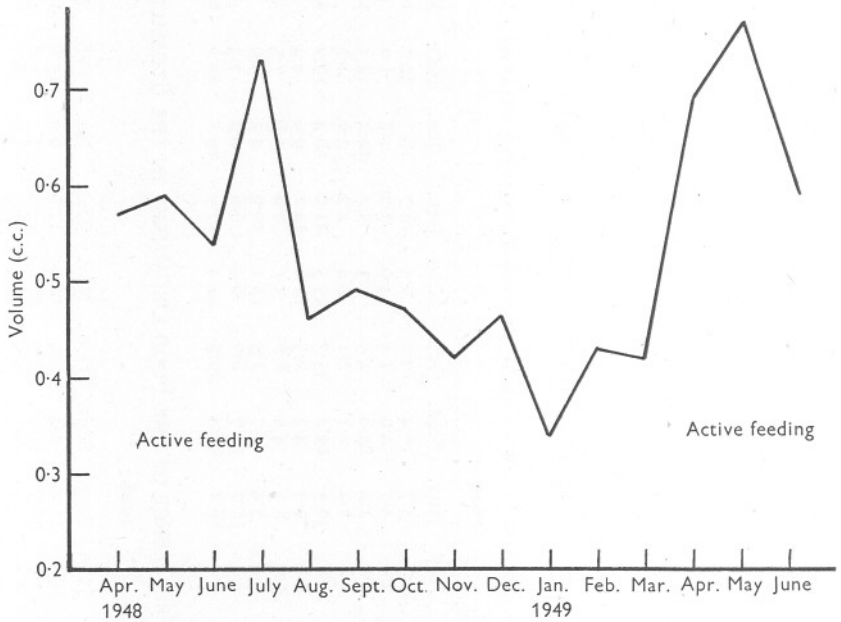
## Table II. Percentage Composition of the Stomach Contents

| | 1948 | | | | | | | | | 1949 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Food organism | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June |
| Fish | 4·2 | 40·9 | 51·9 | 49·7 | 5·7 | 6·4 | 10·0 | 7·5 | 12·7 | 8·3 | 20·2 | 16·5 | 14·1 | 15·8 | 31·6 |
| Amphipoda | 3·5 | 4·4 | 5·9 | 2·8 | 3·7 | 2·9 | 1·5 | 4·0 | 3·2 | 1·8 | 1·2 | 2·4 | 2·0 | 1·8 | 2·9 |
| Polychaeta | 28·4 | 7·8 | 2·4 | 2·1 | 2·2 | 13·8 | 4·5 | 4·5 | 5·5 | 12·2 | 12·5 | 13·1 | 3·5 | 3·8 | 2·0 |
| Schizopoda (*sens. lat.*) | 4·2 | 5·1 | 5·2 | 1·4 | 2·2 | 2·1 | 2·1 | 2·4 | 2·2 | 2·9 | 1·2 | 1·0 | 1·2 | 1·8 | 4·1 |
| *Processa canaliculata* | 11·0 | 23·9 | 13·7 | 15·8 | 36·3 | 29·2 | 33·3 | 25·5 | 21·0 | 16·4 | 17·9 | 27·7 | 8·1 | 7·3 | 27·5 |
| Crangonidae | 14·2 | 3·7 | 3·7 | 4·2 | 6·3 | 4·3 | 2·3 | 10·6 | 12·2 | 9·9 | 4·2 | 1·7 | 1·4 | 3·4 | 1·9 |
| *Galathea* | 4·2 | 6·1 | 7·4 | 5·9 | 8·3 | 4·5 | 6·6 | 3·1 | 7·6 | 5·6 | 7·5 | 9·1 | 20·5 | 6·0 | 8·1 |
| *Porcellana* | 1·8 | 0·9 | 3·9 | 11·4 | 5·4 | 4·7 | 1·5 | 12·1 | 10·9 | 4·2 | 5·9 | 8·6 | 4·9 | 5·0 | 3·4 |
| *Portunus* | 7·1 | 3·6 | 2·8 | 4·7 | 11·7 | 11·7 | 8·7 | 6·9 | 6·8 | 10·2 | 7·3 | 6·9 | 9·4 | 6·8 | 10·3 |
| Others | 21·3 | 3·4 | 3·0 | 2·2 | 18·2 | 20·4 | 29·5 | 23·4 | 17·9 | 29·1 | 22·1 | 13·1 | 34·9 | 48·2 | 7·8 |

## Table III. Percentage of Prevalence of the Food Organisms in the Stomachs Examined

| | 1948 | | | | | | | | | 1949 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Food organism | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June |
| Fish | 9·4 | 27·2 | 35·0 | 61·5 | 5·4 | 3·8 | 9·0 | 11·7 | 11·6 | 6·3 | 15·6 | 13·3 | 9·4 | 6·0 | 14·6 |
| Amphipoda | 9·4 | 39·5 | 36·6 | 27·7 | 20·7 | 15·0 | 8·5 | 23·3 | 9·0 | 9·5 | 5·8 | 10·9 | 8·7 | 16·3 | 27·0 |
| Polychaeta | 43·8 | 19·1 | 4·7 | 6·2 | 4·1 | 23·3 | 5·8 | 14·0 | 10·3 | 23·8 | 12·3 | 9·7 | 10·3 | 18·3 | 7·2 |
| Schizopoda (*sens. lat.*) | 12·5 | 30·3 | 11·1 | 8·7 | 9·1 | 6·0 | 4·2 | 9·3 | 5·2 | 4·2 | 5·2 | 3·6 | 1·7 | 1·2 | 9·3 |
| *Processa* | 28·1 | 34·6 | 43·8 | 24·6 | 48·8 | 45·1 | 26·5 | 34·9 | 22·6 | 20·6 | 11·7 | 19·4 | 13·2 | 20·6 | 38·5 |
| Crangonidae | 12·5 | 7·8 | 7·2 | 11·8 | 9·9 | 8·3 | 3·7 | 9·3 | 7·7 | 6·3 | 3·9 | 4·8 | 5·0 | 12·3 | 8·2 |
| *Galathea* | 9·4 | 16·7 | 12·1 | 13·8 | 14·5 | 15·8 | 12·2 | 14·0 | 13·5 | 7·9 | 7·1 | 31·5 | 33·7 | 24·2 | 10·7 |
| *Porcellana* | 3·1 | 2·9 | 2·3 | 7·7 | 4·1 | 6·0 | 4·2 | 16·3 | 12·3 | 7·9 | 11·0 | 18·2 | 16·2 | 14·7 | 5·6 |
| *Portunus* | 9·4 | 8·8 | 6·6 | 10·8 | 16·8 | 5·3 | 9·0 | 7·0 | 11·6 | 15·9 | 4·5 | 4·8 | 12·3 | 10·7 | 9·3 |

The average volume of food per stomach has been plotted against the respective months as a curve (Text-fig. 1). The spawning period of the fish is from February to May. Text-fig 1 makes clear that there was a period of very active feeding from April to July, synchronizing with the end of spawning and the period just after spawning when the fish was recovering from the strain. This was followed by a period, from August to December, when the average volume of food per stomach was more or less the same as the annual average volume per stomach. For practical purposes this period could be




Text-fig. 1. Stomach contents of *Gadus minutus*. The average volume in c.c. per stomach in successive months.

distinguished as 'the period of average feeding', and it coincided with the latter part of summer, autumn and early part of winter. This period was succeeded by a period of 'low feeding'. During the months just prior to spawning and during the earlier part of the spawning period, i.e. from the latter part of December to early part of March, the abdominal cavity of the fish is very much distended and filled by the gonads. At this time the fish shows a much reduced feeding activity. Just after spawning the fish feeds voraciously. Newly spawned and fully spent specimens with their stomachs gorged with food were common in the April and May samples. In May 1949 two specimens, measuring 19·5 and 20 cm., had ingested 6 and 5 c.c. of food material respectively. Both were emaciated and completely spent, and in each of them the supra-occipital stood out like a skin-covered crest on the top of the head. Such specimens were frequent in April and May.

This conclusion is substantiated further by the number of empty stomachs occurring in the various months. The percentage of empty stomachs that occurred in the respective months are given below:

| 1948 | % | 1949 | % |
|---|---|---|---|
| Apr. | 10·0 | Jan. | 12·7 |
| May | 11·1 | Feb. | 17·5 |
| June | 13·0 | Mar. | 12·1 |
| July | 10·5 | Apr. | 8·6 |
| Aug. | 7·5 | May | 7·1 |
| Sept. | 5·3 | June | 10·6 |
| Oct. | 7·5 | | |
| Nov. | 5·0 | | |
| Dec. | 10·0 | | |

The percentage of fish with empty stomachs was greatest just prior to, and during, the spawning period. During the period of growth, i.e. from August to November, the percentage was small. Almost all the fish which had empty stomachs during the spawning months were fully mature specimens with ripe and enlarged gonads about to spawn.

The percentage of empty stomachs, if calculated for the three different periods of feeding activity, can be seen to average 10·1 % during the period of active feeding from April to July, 7·1 % during the period of 'average feeding' from August to December, and 14·1 % during the period of low feeding from January to March.

Considering the part that each of the principal food organisms plays in the food and feeding of the poor-cod, we find that *Processa canaliculata* is the commonest organism, forming a very large proportion of the food throughout the year. It is most predominant in the months following spawning, especially from August to November (Text-fig. 2A).

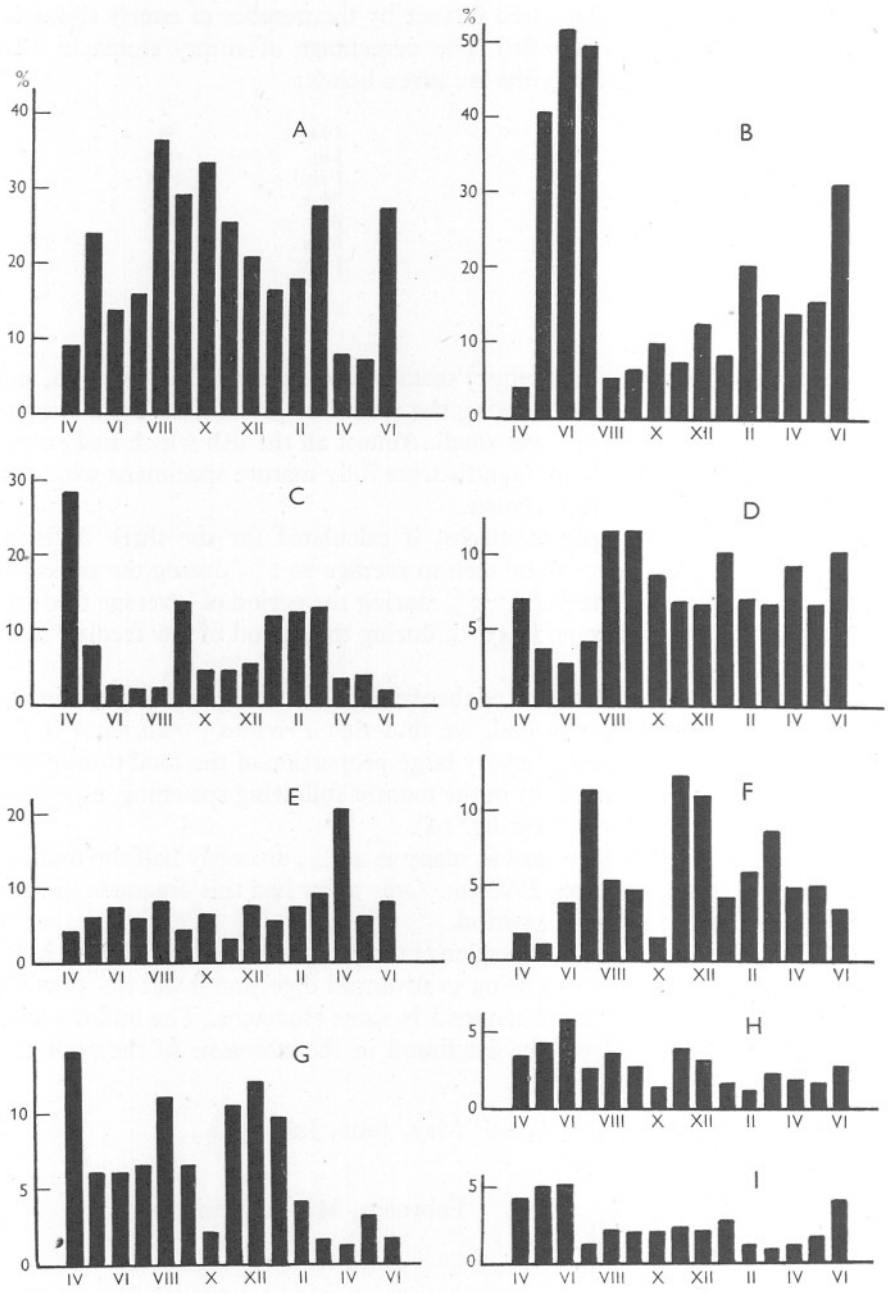
In August and September 1948 as many as 46 %, or nearly half the number of fish analysed, had ingested *Processa*. Only a few had this organism in their stomachs during the spawning period.

*Fish.* Fish forms an important portion of the diet of the poor-cod during May, June and July (Text-fig. 2B). Owing to advanced digestion it was not possible to identify the species of fish consumed in some stomachs. The otoliths were the best aid to identification. The fish found in the stomachs of the poor-cod were:

*Crystallogobius nillsoni* May, June, July 1948

*Callionymus* sp.
*Trigla* sp.
*Ctenolabrus* sp.
*Gadus minutus*? } February, March, April 1949

In July 1948 as many as 61 % of the stomachs analysed had fish in them. In June of the same year about 35 % had ingested fish.




Text-fig. 2. Histograms showing the relative percentage composition of the nine principal food organisms taken by *Gadus minutus* in the different months during 1948–49. For comparison all values are expressed as the percentage in volume of 100 c.c. of food material. A, *Processa canaliculata*; B, fish; C, Polychaeta; D, *Portunus* sp.; E, *Galathea* sp.; F, *Porcellana* sp.; G, Crangonidae; H, Amphipoda; I, mysids and euphausiids.

*Polychaeta.* Polychaetes have presented considerable difficulty in identification as they were in an advanced state of digestion in most of the stomachs. They were largely present in the food during the spawning months (Text-fig. 2C). *Amphitrite* sp. and *Goniada* sp. formed the commonest of the identifiable worms in the food. In September 1948 there was one stomach which contained a *Pallasia murata* with a portion of the worm in a part of the tube. In April 1948 nearly 40% of the stomachs examined had polychaetes in them.

*Portunus* sp. Portunidae were present in the food throughout, forming a fairly consistent proportion of it (Text-fig. 2D). In August and September 1948 they formed nearly 12% of the food in the stomachs analysed. The common species were *P. pusillus* and *P. depurator*. In August 1948 about 17% of the stomachs analysed had Portunidae.

*Galathea* sp. Galatheids form an important element of the crustacean part of the food, especially during the latter part of the spawning period, from March to May (Text-fig. 2E). Many of the spent fish in April 1949 had their stomachs distended and gorged with nothing but *Galathea*. *G. intermedia* was the commonest species, *G. dispersa* was also found fairly often, while *Munida bamffica* occurred twice. In March and April 1949 as many as 30% of the stomachs examined had *Galathea* in them.

*Porcellana* sp. *Porcellana* forms a small yet consistent part of the food, being most common in the months just prior to spawning (Text-fig. 2F). *P. longicornis* is the common species found in the stomachs of *Gadus minutus*, though occasionally *Porcellana platycheles* has been observed in fish of the younger year groups in April and May 1949. In November 1948 *Porcellana* was found in about 16% of the stomachs examined.

*Crangonidae. Crangon vulgaris* and *Philocheras bispinosus* were the two species usually found in the food. Crangonidae were especially common just before and after spawning (Text-fig. 2G). In April 1948 and May 1949 nearly 12% of the fish had ingested Crangonidae.

*Amphipoda.* Caprellidea (mainly *Phtisica marina*) were found in the stomachs more often in the months of April, May and June than in the other months, but Gammaridea formed a larger proportion of the amphipods consumed. The Gammaridea commonly found in the food were *Apherusa ovalipes*, *A. henneguyi*, *Ampelisca spinipes* and *A. diadema*. Mr G. M. Spooner informs me that *Phtisica marina* lives exclusively amongst hydroids and sponges and *Ampelisca* spp. are burrowers, usually lying buried under a surface layer of sand or gravel.

The occurrence of these amphipods in such large numbers in the stomachs of the poor-cod suggests a deliberate search on the part of the fish to ingest these forms and it further emphasizes the bottom-feeding nature of the fish.

Big specimens of *A. spinipes* measuring between 8 and 18 mm. in length were common in the stomachs in August and September 1948 and in March and April 1949. In August 1948 two specimens had in their stomachs

152 and 131 *Apherusa* spp. respectively. The proportion of amphipods in the total volume of food in the stomachs was comparatively small; yet a large number of fish had fed on them. In the latter part of the spawning season and in the months just following spawning the proportion of amphipods was larger than in other months (Text-fig. 2 H). Gammaridea were most common in July, August and September 1948. In May 1948 amphipods were found in about 40 % of the stomachs examined.

*Mysidacea* and *Euphausiacea*. Schizopods form only a small proportion of the food of the fish, but were fairly consistent in their occurrence in the stomachs (Text-fig. 2 I). *Leptomysis gracilis* was the species most commonly ingested, and a few *Anchialina* were occasionally observed. In April and May 1948 a fairly large number of stomachs contained mysids and euphausiids (13 % in April and 30 % in May).

*Others*. Of the other organisms special mention should be made of *Upogebia* sp. and small Paguridae (mainly *Eupagurus bernhardus*). In May 1949 *Upogebia* formed as much as 36 % of the total volume of food, and about 10 % of the fish had them in their stomachs. Paguridae also formed a large proportion in the food (26 % of the total volume) in April 1949 and as many as 15 % of the fish had ingested them.

Isopoda, Mollusca and Echinodermata formed only a negligible proportion of the food throughout the year. Occasionally they formed a large proportion in the food of a few individual stomachs. But such instances were very rare.

The various organisms that were found in the analysis of the food of the poor-cod of the adolescent years are given in the Appendix (p. 238).

Thus *Gadus minutus* in its adolescent and adult stages is primarily a crustacean feeder, feeding on the bottom-living forms and showing differential feeding activity depending on spawning and growth.

### *Food of the O-Group of* Gadus minutus

Comparatively few specimens of the O-group were available for study of the food and they have been obtained during seven months only, viz.:

| | Specimens | | Specimens |
|---|---|---|---|
| Oct. 1948 | 5 | March 1949 | 22 |
| Nov. 1948 | 159 | Apr. 1949 | 3 |
| Jan. 1949 | 21 | May 1949 | 55 |
| Feb. 1949 | 364 | | |

All these specimens were between 7 and 9 cm. long (standard length). The numbers for October 1948 and April 1949 are negligible. The February 1949 and November 1948 collections alone are of any comparative value. The analyses of the food of O-group in the different months are not therefore strictly comparable. This food analysis is therefore restricted to an enumeration of the food organisms and a comparison with the food of the older age groups.

The poor-cod of the O-group also is primarily a crustacean feeder. Copepods, small *Galathea intermedia*, small *Porcellana longicornis*, and amphipods formed a large proportion of the food in all the seven months. Lebour (1919) also noted that the food of the poor-cod of a length from 40 to 160 mm. 'is chiefly crustacea—copepods, especially *Calanus* and *Temora*, *Podon*, decapods and their larvae....' But the earlier post-larval stages are evidently still plankton feeders.

The average volume of food per stomach was 0·12 c.c., compared with 0·5 c.c. in the older fish. Empty stomachs were found only in November 1948 and February 1949, and their percentages were only 3% in November and 5% in February.

The majority of the stomachs contained fine sandy gravel mixed with empty shells of very small *Natica* sp. and *Nucula* sp.

The volumetric analysis of the food and the percentage composition of the stomachs containing the respective food organisms have been tabulated in Tables IV and V.

The various organisms that were found in the food of the O-group are given in the Appendix (p. 239).

Copepods were taken in all the 7 months. About 90% of the stomachs examined had copepods in them. *Calanus finmarchicus* and *Acartia clausi* were the commonest. The others were *Temora* sp., *Pseudocalanus elongatus*, and *Centropages typicus*. When the stomachs had a large copepod content they usually presented a reddish colour. Copepods were especially noticeable in November 1948, February, March and May 1949.

Amphipods formed a great proportion of the food in November 1948, February and May 1949. Caprellidea were very rare. They were found only in 1·9% of the stomachs examined in the 7 months. Gammaridea formed almost the whole of the amphipodan element in the food. The species found were *Apherusa* sp. and juvenile forms of *Ampelisca diadema* and *A. spinipes*.

*Galathea intermedia* formed the greatest proportion of the food in January, February and March 1949. In January and March 1949 as many as 60% of the stomachs examined had *G. intermedia* in them. All the *G. intermedia* were small and juvenile forms. The other decapod crustacea found in the food were *Pandalina brevirostris*, *Philocheras bispinosus*, *Crangon vulgaris*, small *Porcellana longicornis*, small *Portunus* spp., *Eupagurus bernhardus* and small *Processa canaliculata*.

Mysids and euphausiids were found mainly in January 1949, when as many as 55% of the stomachs contained them. *Leptomysis gracilis* and *Nyctiphanes couchi* were the species taken.

In January 1949 many stomachs contained polychaetes mostly unrecognizable. The only identified species was *Goniada* sp.

Among Isopoda, *Conilera cylindracea* was taken from a few stomachs in November 1948 and February, March and May 1949.

TABLE IV. VOLUMETRIC ANALYSIS OF THE STOMACH CONTENTS PER 100 STOMACHS (VOLUME IN C.C.)

| Food organism | O-group Oct. | Nov. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|
| Polychaeta | .. | 0·2 | 1·5 | 2·4 | 0·5 | 3·3 | 0·6 |
| Mollusca | .. | 0·1 | 0·1 | 0·1 | 0·1 | .. | 0·2 |
| Isopoda | .. | 0·4 | .. | 0·2 | 0·4 | .. | 0·4 |
| Amphipoda | 2·0 | 2·4 | 0·8 | 1·4 | 0·8 | .. | 1·8 |
| *Processa* | 4·0 | 0·4 | 0·8 | 0·4 | 1·0 | .. | 0·4 |
| Crangonidae | 3·0 | 0·6 | 1·0 | 0·1 | .. | .. | 0·2 |
| *Galathea* | 6·0 | 2·8 | 5·0 | 4·1 | 3·0 | 6·6 | 1·0 |
| *Portunus* | .. | .. | 0·4 | 0·6 | .. | .. | 0·6 |
| *Porcellana* | .. | 0·2 | 2·1 | 1·9 | 0·7 | .. | 0·8 |
| Baguridae | .. | .. | .. | 0·2 | .. | .. | .. |
| Copepoda | 0·2 | 0·2 | 0·1 | 0·4 | 0·2 | 0·1 | 0·2 |
| Schizopoda (*sens. lat.*) | .. | 0·4 | 0·4 | 0·3 | 0·2 | .. | 0·2 |
| Sandy gravel and stone | 0·8 | 0·2 | 0·5 | 0·1 | 0·4 | 0·6 | 0·2 |
| Others | 0·4 | 0·8 | 0·9 | 1·0 | 1·7 | .. | 0·7 |
| Total volume in c.c. | 16·4 | 8·7 | 13·6 | 13·2 | 9·0 | 10·6 | 7·3 |
| No. of stomachs examined | 5 | 150 | 21 | 350 | 22 | 3 | 55 |

TABLE V. PERCENTAGE OF PREVALENCE OF THE FOOD ORGANISMS IN THE STOMACHS EXAMINED

| Food organism | O-group Oct. | Nov. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|
| Polychaeta | .. | 2 | 55 | 12 | 23 | 66 | 9 |
| Mollusca | .. | 10 | 20 | 3 | 23 | .. | 46 |
| Isopoda | .. | 3 | .. | 1 | 20 | .. | 8 |
| Amphipoda | 100 | 16 | 75 | 18 | 70 | .. | 32 |
| *Processa* | 20 | 3 | 10 | 1 | 15 | .. | 4 |
| Crangonidae | 20 | 3 | 10 | 2 | .. | .. | 4 |
| *Galathea* | 60 | 28 | 60 | 40 | 65 | 100 | 10 |
| *Portunus* | .. | .. | 5 | 4 | .. | .. | 4 |
| *Porcellana* | .. | 2 | 20 | 10 | 25 | .. | 6 |
| Paguridae | .. | .. | .. | 1 | .. | .. | .. |
| Copepoda | 100 | 72 | 100 | 92 | 95 | 100 | 76 |
| Schizopoda (*sens. lat.*) | .. | 12 | 55 | 6 | 20 | .. | 8 |
| Sandy gravel and stone | 100 | 66 | 80 | 29 | 85 | 66 | 62 |

Lebour (1917, 1919) examined the food of 144 post-larvae measuring 6–14 mm., and fifty-three specimens of the O-group of *Gadus minutus* in 1917 and 1919. The records of her analysis of the food of these fish were as follows:

140 specimens of *G. minutus* post-larvae measuring 6–14 mm., from the Young Fish Trawl of 1914, were examined (Lebour, 1917, p. 455). Of these 4 stomachs were empty, 1 contained ova, 1 contained *Dinophysis*, 134 contained *Pseudocalanus elongatus*, with *Acartia*, *Euterpina*, *Metrida* and *Podon* each occurring once.

In 1919, 4 specimens of 6–13 mm. long post-larvae and 53 specimens of the O- and I-groups of *Gadus minutus* were examined (Lebour, 1919, pp. 283–5).

Analysis of the post-larvae: one empty, two contained copepod remains, one contained 1 *Pseudocalanus* and one young *Temora*.

Analysis of the O-group and I-group:

| No. of specimens | Length in mm. | Food |
|---|---|---|
| 1 | 40 | *Crystallogobius*, many *Podon*, *Calanus*, *Temora*, remains of decapod larvae |
| 3 | 60–70 | Crustacean remains, many *Acartia*, *Candacia*, *Temora*, decapod larvae, young amphipods and isopods |
| 5 | 70–80 | *Temora*, *Candacia*, decapod larvae remains, *Calanus* and one empty |
| 5 | 80–90 | Copepod remains, *Calanus*, *Pseudocalanus*, decapod larvae, *Candacia* and *Eupagurus* larvae. |
| 8 | 90–105 | Copepod remains, annelid remains, *Pandalus montagui* and decapod remains |
| 19 | 73–105 | Indistinguishable |
| 5 | 69–110 | *Crangon* remains |
| 1 | 135 | *Labidocera wollastoni*, many *Calanus* |
| 1 | 143 | 4 *Crystallogobius*, mysid, and many *Calanus* |
| 5 | 83–160 | Decapod remains (*Leander*?) |

Only three post-larvae of *Gadus minutus* occurred in the present material and all of them contained *Pseudocalanus* in their stomachs. Lebour's analysis of the food of 144 post-larvae quoted above showed that the great majority contained copepods, amongst which *Pseudocalamus elongatus* was always present. Other species each occurred once only. It is quite evident, as Lebour emphasizes, that *Pseudocalanus* is the favourite food of *Gadus minutus* in its post-larval stages.

Lebour's analysis revealed that the food of *G. minutus* contained fish and crustacea at the respective stages as follows:

| 6–14 mm. (total length) | 40–105 mm. (total length) | 105–160 mm. (total length) |
|---|---|---|
| Copepods, ova, *Dinophysis* | Copepods, amphipods, isopods decapod larvae, *Pandalus montagui*, *Podon*, *Crystallogobius*, *Crangon* | *Crystallogobius*, *Leander*?, *Crangon*, mysids |

Lebour further stated that *Gadus minutus* 'in their young stages eat *Pseudocalanus* more than anything else, *Acartia* and other small copepods also being taken, probably when *Pseudocalanus* is not so abundant. *Calanus* is taken by the larger but rarely by the smaller fish.'

The present analysis also reveals this fact well. The O-group (7–9 cm. standard length) contained copepods, amphipods and small decapods like *Galathea intermedia*, *Porcellana longicornis* and small *Portunus* spp. besides occasional inclusions of polychaetes, mysids, and isopods. There was a complete absence of fish in the food analysed. Even Lebour found fish in only two specimens of the sample, one of which was 14·3 cm. in total length and therefore belonged to the I-group. Thus copepods, amphipods and *Galathea* formed the bulk of the food of the poor-cod of the O-group.

In the food of the I–V groups the bigger decapods like *Processa canaliculata*, *Portunus* sp. and *Galathea* spp., and fish like *Callionymus* sp., *Trigla* sp. and *Crystallogobius* sp., and polychaetes formed the major portion throughout the year. Copepods were observed only in four stomachs in the food analysis of

these age groups. It is quite evident that copepods do not play any important part in the food and feeding of the fish at this adolescent and adult period of its life.

The food of *G. minutus* can thus be divided into three categories depending on the three phases of its life cycle, as follows:

| Stage | Length in mm. (Standard length) | Food |
|---|---|---|
| Post-larval | 6–14 | Copepods, mostly *Pseudocalanus elongatus* |
| O-group | 40–80 | Copepods, mostly *Calanus finmarchicus*, *Acartia* and *Temora*; small decapods like *Galathea intermedia*, *Porcellana longicornis*, etc.; amphipods, mostly Gammaridea; isopods and polychaetes |
| Adolescent and adult stages | 80–230 | Decapods, mostly the larger like *Processa canaliculata*, *Galathea* sp., *Portunus* sp., *Porcellana* sp., *Upogebia*; fish like *Crystallogobius* and *Callionymus* sp.; polychaetes, mostly *Amphitrite* and *Goniada*, amphipods like large *Ampelisca* spp., *Apherusa* spp. and *Phtisica marina* |

## Age and Growth Determination in *Gadus minutus*

In his studies of the rate of growth of Plymouth fishes Cunningham (1891) made some observations on the growth rate of *Gadus minutus* from length measurements. He examined 246 specimens collected between 1889 and 1891. After that J. S. Thomson (1904) used the scales of *G. minutus* in his investigation on the validity of scales as an index of age in Gadidae. Apart from these two early investigations there is no other reported work on the age determination and growth rate of this species.

The scales of *G. minutus* are very deciduous and get scraped off from the body of the fish very easily during trawling. Even with specimens which retain a few scales, it is quite impossible to collect them from the same region of the body in all of them. Again, very often the retained scales turned out to be the minute scales which Stuart Thomson (1904) has described in his paper. Harold Thompson (1922) has shown in his treatise on haddock scales how essential it is to collect the largest scales, and that too from one and the same region in all the specimens, if any assessment of age and if any valid and reasonable comparison between the several specimens can be made. In the present work the scales were used for deciphering the age only in the relatively few specimens where this was possible. They could not be used for any assessment of back-calculation and growth rate. For age determination in *G. minutus*, the otoliths at first were used. The otoliths are very massive and thick structures, and to reveal the 'year rings' they had to be broken transversely and sometimes even sectioned before the rings could be distinguished. Though the zones were quite clear in most of them there was no uniformity in the width of the zones, and it was not practically possible to make sections at the same sagittal plane in all the otoliths. For these reasons it was impossible to utilize the otolith for critical comparisons and for purposes of back-calculation. Therefore some other structure had to be selected for a satisfactory

estimation of the age and growth rate, possessing all these necessary traits of an 'age index'. The supra-occipital crest was selected with this in view.

Bones have rarely been used for age determination of marine fishes and even when they have, there have been differences of opinion on the validity of the zones, as is clear from a survey of the literature (Menon, 1950). The main objection against utilizing bones for age assessment has been that the zones are ill-defined. This difficulty can usually be overcome by finding out the optimum temperature for cooking the specimens when collecting the bones. Overcooking always blurs the zones. When the bones are prepared without overcooking it is found that age assessments can be based on them with at least as much confidence as on scales or otoliths.

*Growth rate from scales*

Scales were collected from all specimens in which they were available. Only those scales which were firmly lodged in the scale pockets were collected as, being extremely deciduous, there was a possibility of scales from different specimens getting intermingled on the fishes when they came up in the trawl. These scales were removed with a scalpel and stored in labelled envelopes. Altogether scales were collected from 294 specimens, from whichever region of the fish they were remaining in their pockets. The scale of *G. minutus* has a thin shining dermal tissue covering it, often with big stellate chromatophores. These obscure the sclerites and it is necessary to clean the scale before it can be read under the microscope clearly. The best method of cleaning the scale is to put it in a solution of 10% caustic potash for 5 min. and then to scrape it in water in a watch-glass with a forceps and a needle. All the dermal tissues and chromatophores can easily be removed by this method. The scale is then mounted on a slide. The treatment with caustic potash imparts a deep black tinge to the sclerites, which thus become clearly defined and visible in the general field of the scale. Alizarine stain also enhanced the clarity of the sclerites and 'rings'. After removal of its chromatophores and dermal tissues the scale is placed in alizarine staining solution for 5 min.[1] The excess stain is washed off by leaching the scale in 2% caustic potash solution, and then the scale is mounted in glycerine. The 'annual rings' become very clearly defined. This method was better, easier and quicker than that suggested by Graham (1929*a*).

The scale of *G. minutus*, like the scales of most Gadidae, is oval in shape, with several sclerites arranged around a central nucleus (Pl. II, fig. 1). The sclerites are arranged in alternating bands of widely separated ones, which constitute the so-called 'summer zone' and of closely approximated ones, which constitute the 'winter zone or ring'.

[1] Alizarine staining solution: 5% caustic potash, 1000 c.c.; alizarine dye solution, 1 c.c. Alizarine dye solution: glacial acetic acid, 0·5 c.c.; glycerine, 3 c.c.; chloral hydrate 10 c.c. and alizarine sulphonate 0·1 g.

The difficulty of getting scales from the same region of the fish in all specimens has been explained in the preceding paragraphs. They are therefore not comparable in size. The measurements of these scales made with a micrometer scale verified that there is no regularity in the measurements of scales from the different specimens. The zones are very clearly defined in stained scales and fairly distinguishable in unstained ones. Unfortunately, no data of blank scales were kept and so a probable or approximate percentage of them

TABLE VI. ANALYSIS OF THE SCALES OF *GADUS MINUTUS* ACCORDING TO THE LENGTH- AND AGE-GROUPS

| Length in cm. | Year groups: Male 1− | 1+ | 2+ | 3+ | 4+ | Female 1− | 1+ | 2+ | 3+ | 4+ | 5+ | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7·5 | 3 | .. | .. | .. | .. | 3 | .. | .. | .. | .. | .. | 6 |
| 8·0 | 3 | .. | .. | .. | .. | 4 | .. | .. | .. | .. | .. | 7 |
| 8·5 | 5 | 2 | .. | .. | .. | 4 | 3 | .. | .. | .. | .. | 14 |
| 9·0 | 1 | 5 | .. | .. | .. | 1 | 4 | .. | .. | .. | .. | 11 |
| 9·5 | .. | 4 | .. | .. | .. | .. | 5 | .. | .. | .. | .. | 9 |
| 10·0 | .. | 5 | .. | .. | .. | 1 | 2 | .. | .. | .. | .. | 8 |
| 10·5 | .. | 3 | .. | .. | .. | .. | 2 | .. | .. | .. | .. | 5 |
| 11·0 | .. | 1 | .. | .. | .. | .. | 3 | .. | .. | .. | .. | 4 |
| 11·5 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 |
| 12·0 | .. | 1 | .. | .. | .. | .. | 1 | .. | .. | .. | .. | 2 |
| 12·5 | .. | 5 | 3 | .. | .. | .. | .. | .. | .. | .. | .. | 8 |
| 13·0 | .. | 2 | 4 | .. | .. | .. | 2 | .. | .. | .. | .. | 8 |
| 13·5 | .. | 3 | 8 | .. | .. | .. | 4 | 4 | .. | .. | .. | 19 |
| 14·0 | .. | 3 | 15 | 1 | .. | .. | 3 | 2 | .. | .. | .. | 24 |
| 14·5 | .. | 1 | 9 | 1 | .. | .. | 4 | 8 | 1 | .. | .. | 24 |
| 15·0 | .. | .. | 3 | 3 | 1 | .. | 4 | 18 | 5 | .. | .. | 34 |
| 15·5 | .. | .. | .. | 3 | .. | .. | 2 | 9 | 1 | .. | .. | 15 |
| 16·0 | .. | .. | .. | 1 | 1 | .. | .. | 17 | 4 | .. | .. | 23 |
| 16·5 | .. | .. | .. | 2 | 1 | .. | .. | 14 | 3 | .. | .. | 20 |
| 17·0 | .. | .. | .. | .. | 1 | .. | .. | 5 | 4 | .. | .. | 10 |
| 17·5 | .. | .. | .. | .. | .. | .. | .. | 2 | 7 | 1 | .. | 10 |
| 18·0 | .. | .. | .. | .. | .. | .. | .. | 2 | 6 | .. | .. | 8 |
| 18·5 | .. | .. | .. | .. | .. | .. | .. | .. | 5 | .. | .. | 5 |
| 19·0 | .. | .. | .. | .. | .. | .. | .. | .. | 7 | 2 | .. | 9 |
| 19·5 | .. | .. | .. | .. | .. | .. | .. | .. | 4 | 3 | .. | 7 |
| 20·0 | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 2 | 1 | 4 |
| Totals | 12 | 35 | 42 | 11 | 4 | 13 | 39 | 81 | 48 | 8 | 1 | 294 |
| | 104 | | | | | 190 | | | | | | |

in the specimens examined cannot be given, but their proportion was high. There were several instances of false rings in the scales and with all these the age had to be checked by reference to the otoliths and supraoccipital.

The data of measurements of the scales are not given since they are not comparable. In Table VI are shown the various 5 mm. groups, the two sexes separately, divided up according to the number of 'closely arranged sclerite zones' or 'annual rings' in the scales that have been examined.

From Table VI it is quite evident that there is a different rate of growth in the two sexes. The majority of male *G. minutus* are more than 1 year old

when they reach a length of 9 cm., past 2 years at a length of 13 cm., past 3 years when they reach a length of 15·5 cm. and past 4 years at a length of 16·5 cm. In the same way the majority of females are past 1 year at 9 cm., past 2 years at 14·5 cm., past 3 years at 17·5 cm., and past 4 years at 20 cm. Thus at the end of the 1st, 2nd, 3rd and 4th years the fish reaches approximate lengths of 8·5–9, 12·5–13, 15–15·5, and 16·5–17 cm. in the male and 8·5–9, 14–14·5, 17–17·5 and 19·5–20 cm. in the female respectively. If we take the mean of each year's length range as the nearest approximation to the actual length, the average fish reaches the lengths shown in Table VII at the end of each year in the male and female respectively.

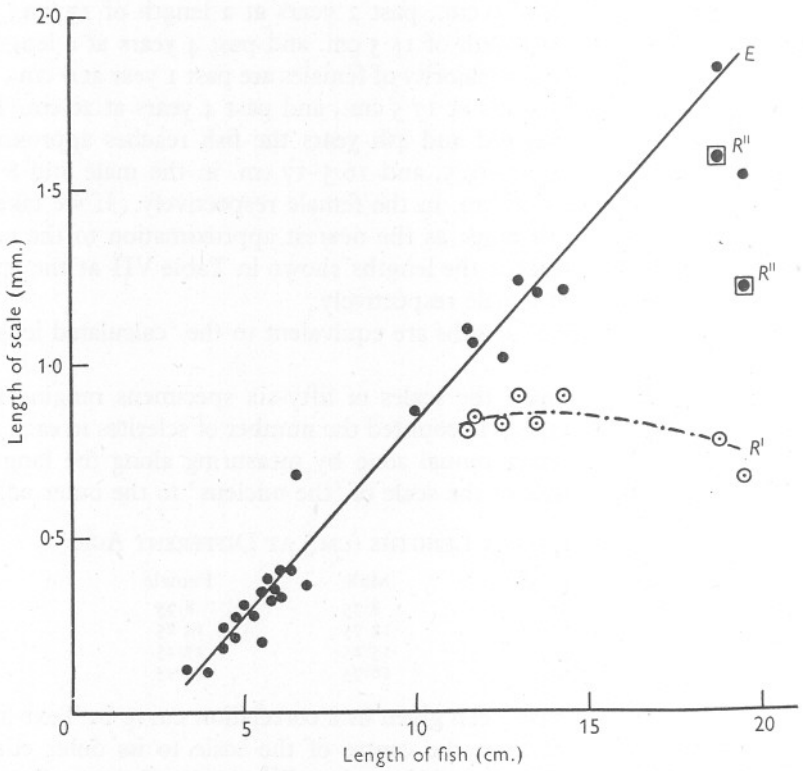
These average or 'mean' lengths are equivalent to the 'calculated lengths' given on p. 219.

Stuart Thomson examined the scales of fifty-six specimens ranging from 3·3 to 19·5 cm. (total length). He counted the number of sclerites in each zone and found the width of each annual zone by measuring along the long axis the distance from the centre of the scale of 'the nucleus' to the outer edge of

TABLE VII. AVERAGE LENGTHS (CM.) AT DIFFERENT AGES

| At the end of | Male | Female |
|---|---|---|
| 1st year | 8·75 | 8·75 |
| 2nd year | 12·75 | 14·25 |
| 3rd year | 15·25 | 17·25 |
| 4th year | 16·75 | 19·75 |

each 'ring'. The results have been given as a correlation curve in Text-fig. 3. In the graph the distance from the centre of the scale to its outer edge is plotted as curve *E*. The line $R^{I}$ and the points $R^{II}$ are the distances from the centre of the scale to the first and second rings, i.e. the annual growth of the scale in the 1st and 2nd years. Thomson did not separate the sexes, and his data cannot be analysed from that aspect. Also he measured no scales of fish between lengths of 6·8 and 10, 14·3 and 18·8 and above 19·5 cm. Yet his data reveal certain interesting details. It can be seen from the graph that *G. minutus* is past 1 year when it reaches a length of 10 cm. (total length) and just past 2 years when it is 15·87 cm. (total length). Thomson noted that a fish of 19·36 cm. (total length) is just past 3 years. Converting these lengths into standard lengths for comparing them with the writer's observations, they become 9, 14 and 17·2 cm. approximately. Thomson examined scales from the median region of the flanks slightly posterior to the pectoral fin and either slightly above or below the lateral line. His data for the fish above 19·36 cm. (total length) give very conflicting results, as all these fish are said to be above 2 and below 3 years. That fish of 23·5 and of 19·36 cm. (total length) are not of the same year class is clear—because, while the growth in the 1st, 2nd and 3rd year is 10, 5·87 and 3·49 cm. (total lengths) respectively, decreasing systematically every year, if the group 19·36–23·5 cm. belongs to the same year group, viz. the 4th year group, it means that the growth in the 4th year is greater




Text-fig. 3. The length in mm. of the scale from its 'centre' to its 'edge' at the different lengths of fish (data from J. S. Thomson, 1904). ●, measurements of the scale from the centre to the edge ($E$); ⊙ measurements of the scale from the centre to the first ring ($R^{I}$); ▣, measurements of the scale from the centre to the second ring ($R^{II}$).

## Table VIII. Thomson's Measurements of *Gadus minutus* Scales

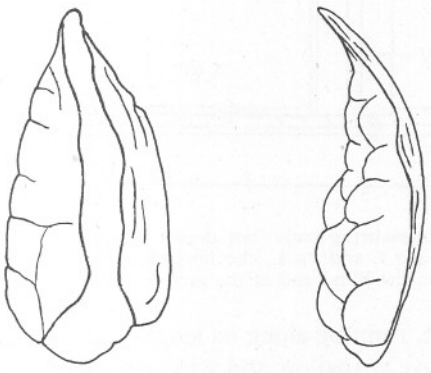
| Total length in cm. | Average length of scale in mm. from centre to growing edge | Average no. of sclerites | | | Approximate age |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | |
| 3·3 | 0·12 | 0 | .. | .. | 3 months |
| 3·9 | 0·21 | 4 | .. | .. | 3 months |
| 5·0–5·9 | 0·34 | 7 | .. | .. | 3 months |
| 6·0–6·8 | 0·47 | 8 | .. | .. | 3 months |
| 10·0 | 0·86 | 23 | .. | .. | 1 yr. 1 month |
| 11·5–11·7 | 1·07 | 30 | 9 | .. | 1 yr. 3–4 months |
| 12·5–14·3 | 1·18 | 29 | 11 | .. | 1 yr. 3–4 months |
| 15·87 | Not taken | .. | .. | .. | 2 yrs. 1 month |
| 17·14–18·09 | Not taken | .. | .. | .. | 2 yr. 7 months approx. |
| 18·80 | 1·84 | 26 | 25 | 11 | 2 yr. 3–4 months |
| 19·36 | Not taken | .. | .. | .. | 3 yr. 1 month |
| 19·50 | 1·53 | 19 | 21 | 16 | About 3 yr. |
| 19·68 | Not taken | .. | .. | .. | Under 3 yr. |
| 20·32 | Not taken | .. | .. | .. | 2 yr. 1 month |
| 22·22 | Not taken | .. | .. | .. | 1 yr. 11 months |
| 23·75 | Not taken | .. | .. | .. | 2 yr. 11 months |

than the 3rd year. This evidently suggests that the 19·36–23·5 cm. length group must have really consisted of more than one year group. This conflicting result in the data of Thomson must have arisen from the difficulty of reading the scales of older age groups. Thomson's data are summarized in Table VIII.

Thus from Thomson's data one finds that the length-groups 3·3–10 and 10–15·87 cm. belong to O- and I-groups respectively. Above 15·87 cm. the results are not very definite. As far as the O- and I-groups are concerned, Thomson's values agree quite well with the present results. In the writer's experience, above the I-group the sclerites become very close and crowded, and in the few scales that were examined there was great difficulty in identifying the rings. In most of them the rings could not be satisfactorily discerned without the previous knowledge of the probable age of the fish from the supra-occipital or the otolith. It must have been this evident overcrowding and narrowing of the sclerites that forced Thomson to overlook the rings after the first 2 years.

*Growth rate from the otolith*

The otoliths were collected by making a vertical cut in the skull behind the orbit and bending the front portion of the skull as suggested by Hickling (1933). When the heads alone were boiled they were collected after boiling and removing the supra-occipital. No change, or difficulty in reading the otoliths,



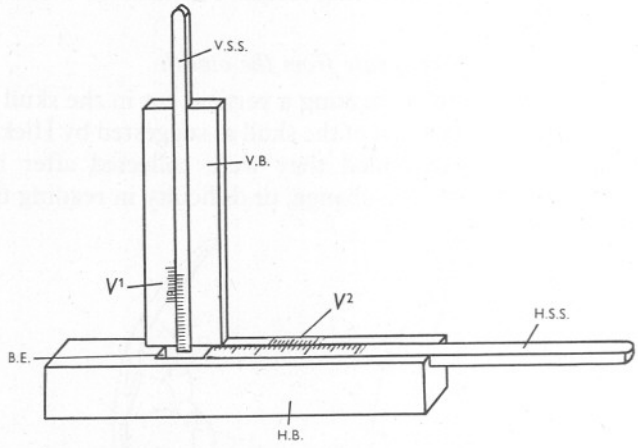

Text-fig. 4. Diagram of the otolith of *Gadus minutus* showing (A) its dorsal aspect and (B) its sagittal aspect.

of boiled specimens was found. The otolith of *G. minutus* is roughly drop-shaped with a slight concavity on its ventral side (Text-fig. 4). The posterior end of the otolith is bulbous and the anterior end tapers to a blunt point which bends downwards in the natural position.

On the dorsal surface there is a fairly broad but shallow acoustic canal. The ventral surface is rugose and has several thick and massive bulbous excrescences. These bulbous swellings are especially massive towards the middle and

posterior end of the otolith. They contribute to the thickness and mass of otolith, and make it impossible to read the otolith without cutting it. For age determination the otolith is cut transversely at about its widest and thickest region. The cut surfaces are then moistened with water, or glycerine, or even better with saliva, when they show the opaque and translucent bands clearly. With several it was found necessary to make ground sections, as in rock-sectioning, to read the zones clearly and satisfactorily (Plate II, figs. 2, 3). The method of grinding employed was much as suggested by Johnston (1938), with the only difference that the grinding was performed by hand with the aid of carborundum and a ground-glass plate.

The length and greatest thickness of the otolith were measured with a scale made for the purpose (Text-fig. 5). This consists of two small rectangular blocks of wood attached at right angles to one another. Each block has




Text-fig. 5. The otolith measuring scale (not drawn to scale). H.B. and V.B., the horizontal and vertical blocks; H.S.S. and V.S.S., the horizontal and vertical sliding scales; $V^1$ and $V^2$, the verniers; B.E., the blind end of the groove.

a groove, 7 mm. wide, running along its length up to the junction between the two blocks. The groove is shallow and wide enough to receive the widest and thickest otolith of *G. minutus*. Sliding wooden scales as wide and high as the grooves work in each. These scales may be called the 'vertical' and 'horizontal' scales. The blocks are so fixed to each other that the end of the vertical scale dips and fits into the horizontal groove at its blind end. The zero end of each scale is towards its outer end. Towards the zero end of each scale there is a vernier scale on the border of the groove. The otolith, when being measured, is placed at the blind end of the horizontal groove with its rugose side upwards. The horizontal scale is then moved towards the blind end until it holds the otolith firmly and straight. The length of the otolith can then be read on the horizontal scale and its vernier. To measure the thickness of the otolith, the

horizontal scale is released and the otolith is so adjusted, lying in the same position, as to place its thickest portion just beneath the 'dipping end' of the vertical scale. The vertical scale is then moved down to hold the otolith rigidly and the thickness is read on the vertical scale and its vernier.

The whole procedure is easy and rapid. It avoids the difficulties one encounters with an ordinary metal screw-guage or vernier, where there is the possibility of the blunt end of the otolith breaking and of not taking the measurements at the longest axis. The readings with the scale just described are as accurate as those with a screw-guage or vernier since it is possible to measure in mm. up to two decimal places.

As many as 600 otoliths were measured with this scale and the data revealed certain interesting points.

There is virtually no correlation (i) between the length of the fish and the length of the otolith, or (ii) between the length of the fish and the thickness of the otolith. There is no correlation (iii) between the length and thickness of the otolith, or (iv) between the otolith measurements and the sex or age of the fish.

There is no particular rule for the calcium accumulations of the otolith. An otolith of a 2-year-old fish may be as long and thick as that of a 3- or even 4-year-old one. Again, the otoliths of fish of the same age may show very different dimensions, the range of variation being quite big. This makes it difficult to compare the otoliths of fish of the same age or the same length or the same sex.

This fact was again revealed by the few measurements made of the width of the zones of the otolith. These are not published, because several sources of error seemed unavoidable. For example, it is not possible to cut the sections in precisely the same sagittal plane in all the otoliths, so that the measurements are not strictly comparable with one another. Instead the fish have been tabulated in 5 mm. length groups, against their age as assessed by the number of annual zones in the otoliths only, and treated in the same way as with the data relating to the scale readings (Table IX). From this it appears that the majority of male fish are past their first year when they reach a length of 10 cm., past 2 years at 13·5 cm., past 3 years at 16 cm., and past 4 years at 17·5 cm. The corresponding lengths for females were 10, 15, 18 and 19·5 cm. If the means are then calculated as with the data for scale readings, we get the 'calculated lengths' of the fish shown in Table X.

The zones in the otolith become very crowded at the periphery of the sections in the older age groups and it becomes a difficult problem to differentiate the various zones. False zones and 'doubled zones' are very prevalent. The massive nature of the otoliths and the lack of correlation in their measurements leave them useful only for direct age reading (even this is trustworthy only for the first two year-groups). Their zonations cannot be used for back-calculation.

TABLE IX. ANALYSIS OF THE OTOLITHS OF *GADUS MINUTUS* ACCORDING TO THE LENGTH AND AGE OF THE FISH

| Length of fish in cm. | Age in years: Male 1− | 1+ | 2+ | 3+ | 4+ | 5+ | Female 1− | 1+ | 2+ | 3+ | 4+ | 5+ | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7·0 | 11 | .. | .. | .. | .. | .. | 13 | .. | .. | .. | .. | .. | 24 |
| 7·5 | 15 | .. | .. | .. | .. | .. | 10 | .. | .. | .. | .. | .. | 25 |
| 8·0 | 12 | 2 | .. | .. | .. | .. | 9 | 1 | .. | .. | .. | .. | 24 |
| 8·5 | 19 | 5 | .. | .. | .. | .. | 23 | 4 | .. | .. | .. | .. | 51 |
| 9·0 | 13 | 9 | .. | .. | .. | .. | 14 | 8 | .. | .. | .. | .. | 44 |
| 9·5 | 11 | 9 | .. | .. | .. | .. | 12 | 10 | .. | .. | .. | .. | 42 |
| 10·0 | 7 | 18 | .. | .. | .. | .. | 11 | 14 | .. | .. | .. | .. | 50 |
| 10·5 | 6 | 13 | .. | .. | .. | .. | 5 | 18 | .. | .. | .. | .. | 42 |
| 11·0 | 2 | 14 | .. | .. | .. | .. | 1 | 11 | .. | .. | .. | .. | 28 |
| 11·5 | .. | 9 | .. | .. | .. | .. | 1 | 15 | .. | .. | .. | .. | 25 |
| 12·0 | 1 | 4 | 1 | .. | .. | .. | .. | 5 | .. | .. | .. | .. | 11 |
| 12·5 | .. | 4 | 1 | .. | .. | .. | .. | 9 | .. | .. | .. | .. | 14 |
| 13·0 | .. | 3 | 1 | .. | .. | .. | .. | 9 | .. | .. | .. | .. | 13 |
| 13·5 | .. | 6 | 18 | .. | .. | .. | .. | 9 | .. | .. | .. | .. | 33 |
| 14·0 | .. | 2 | 15 | .. | .. | .. | .. | 21 | 11 | .. | .. | .. | 49 |
| 14·5 | .. | 8 | 29 | .. | .. | .. | .. | 30 | 37 | .. | .. | .. | 104 |
| 15·0 | .. | 1 | 22 | 5 | .. | .. | 1 | 11 | 25 | .. | .. | .. | 65 |
| 15·5 | .. | 1 | 49 | 23 | .. | .. | .. | 10 | 23 | .. | .. | .. | 106 |
| 16·0 | .. | 2 | 7 | 19 | 1 | .. | .. | 5 | 38 | 1 | .. | .. | 73 |
| 16·5 | .. | 1 | 1 | 10 | .. | .. | .. | 6 | 41 | 5 | .. | .. | 64 |
| 17·0 | .. | .. | 2 | 9 | 4 | .. | .. | 4 | 23 | 7 | 1 | .. | 50 |
| 17·5 | .. | .. | 1 | 4 | 11 | .. | .. | .. | 11 | 6 | .. | .. | 33 |
| 18·0 | .. | .. | .. | .. | 1 | 1 | .. | .. | 1 | 7 | 1 | .. | 11 |
| 18·5 | .. | .. | .. | .. | .. | 1 | .. | .. | 2 | 15 | 2 | .. | 20 |
| 19·0 | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 11 | 9 | 1 | 22 |
| 19·5 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 7 | 23 | 15 | 45 |
| 20·0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 2 | 2 | 5 |
| 20·5 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 10 | .. | 10 |
| 21·0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 4 | 3 | 7 |
| 21·5 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | 2 | 4 |
| 22·0 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 1 |
| 22·5 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | 2 |
| Totals | 97 | 111 | 147 | 70 | 17 | 2 | 100 | 200 | 213 | 60 | 54 | 26 | 1097 |
| | 444 | | | | | | 653 | | | | | | |

TABLE X. CALCULATED LENGTHS FROM OTOLITHS

| At the end of | Calculated lengths in cm.: Male | Female |
|---|---|---|
| 1st year | 9·75 | 9·75 |
| 2nd year | 13·25 | 14·75 |
| 3rd year | 15·75 | 17·75 |
| 4th year | 17·25 | 19·25 |

*Growth rate from the Supra-Occipital Crest*

The supra-occipital crest or spine is a thin flat piece of bone projecting from the posterior part of the skull like a triangular crest in the median line. The crest is made up of two parts, a frontal portion and a supra-occipital portion. The anterior frontal portion forms only a small part in the total crest. It starts

roughly in the anterior one-third of the frontal in the median line and rises from the skull at an angle of 45° (approx.). Immediately after passing the anterior one-third of the frontal, the crest bends back at an angle of 30° (approx.) to the plane of rise of the bone, and runs back to join the supra-occipital portion of the crest. The posterior edge of the frontal portion of the crest is split mesially, and the anterior edge of the supra-occipital portion of the crest is lodged in this split like the blade of a pen-knife when closed. It is a sort of interlocking joint which is more or less in the shape of an isosceles triangle. At the apex of this triangle, at the junction of the two portions of the crest, there is a slight depression of the border.

*Method of Preparation*

The method of collection of the supra-occipital was as follows. The fish was measured, its stomach removed and the sex determined. Then a small tape with the serial number of the fish written on it with chinese black ink or marking ink was pinned through its lower jaw and through the orbit on the opposite side. This enabled the pin to pass in between the roof of the skull and the palatine bridge and thus ensured the safety of the label in subsequent boiling. Brass safety pins were used as there was no chance of their rusting and corroding, and the same pins could be used over again for several samples. After the specimens had been labelled the heads were cut out behind the pectoral axil. These heads were then placed in a water-bath and cooked up to 80° C. The temperature at which the heads are cooked is a very important factor in the utilization of bones for age determination. If the heads are overcooked the bones assume an opaque consistency and their structure is blurred. It is always best to find out the optimum temperature for the cooking or, if that is not possible, to undercook rather than overcook. This is especially important when dealing with the heads of specimens of O- and I-year groups. After cooking, the flesh and other tissues from the skull were removed by washing the skull with a powerful jet of water. In that wet state all the bones are loose and disarticulated. The supra-occipital crest can be easily pulled out of the skull and it comes off with the supra-occipital bone attached to it like a narrow sloping base on either side of the crest. With sharp scissors this base of the supra-occipital bone was cut out from both sides of the base of the crest. The supra-occipital appears then as a clean, thin, flat piece of bone with no protuberances. The bone was then placed in a labelled envelope and exposed to the air on a wooden tray. It became dry in 24 hr. This is the best way of drying the bones. If the bones are dried in the heat of an electric bulb or over a warm plate, the zones become extraordinarily clear, but such artificial heat is apt to warp the bones in such a way as to interfere with the later measurements. When these bones are stored in the envelopes in a warm place the zones become quite clear and defined. The clarity of the zones increased with storage and drying. Rarely bones from

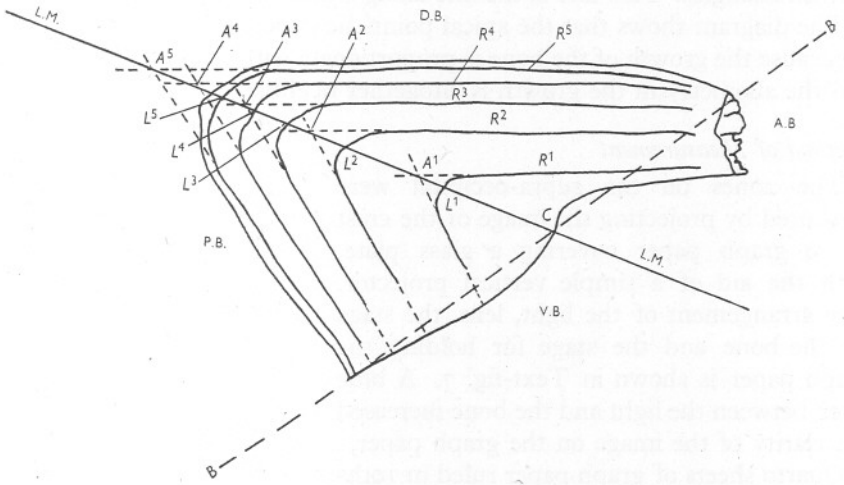
the older females contained a little fat. If this was not removed the bones took on a murky brown colour which blurred the zones to some extent during storage. The fat was removed by treatment with a mixture of equal amounts of benzene and ether, which yielded fine preparations within 24 hr. No difference was noticed in the nature and clarity of the zones due to refrigeration.

It is difficult to prepare the supra-occipital crests from formalin-preserved specimens. A few that had been collected in the early period of this work were washed in running water for 48 hr. and some of them were stained in alizarine according to the method of Tåning (1944). The other formalin-preserved heads were cut out behind the axil of the pectoral fins and boiled one by one in $2\frac{1}{2}\%$ caustic soda for about 5 min. With care and patience the supra-occipital spine could be removed from the skull, washed and air-dried. All these heads had to be cooked in boiling caustic soda or the bones of the skull never became disarticulated, and even then the results were not at all satisfactory. Usually, although the zones were quite clear, the bones showed the destructive effect of the caustic soda and were bent and curled. These bent bones did not give reliable measurements. As far as possible, therefore, a study of this type should be restricted to fresh or refrigerated specimens. If there is no choice and preserved specimens have to be dealt with, it is always best to use the alizarine-staining method. In the alizarine-stained specimens the opaque broad zones of the bone take a paler colour and rougher surface than the narrow transparent zones. Staining the bones with violet ink, indian ink and picro-carmine was tried. The inks stained the bones deeply and showed no differential shading in the staining. The picro-carmine staining was satisfactory only when the zones were clear and well defined. Dr Hart used violet ink for staining the vertebrae of *Phycis blennoides* and found it quite satisfactory (Menon, 1950). But he is of the opinion that staining is not at all necessary if the bones can be prepared from fresh material.

The supra-occipital crest of *Gadus minutus* shows on its surface broad bands of opaque, white zones alternating with thin, narrow and very transparent zones. The transparent bands appear like narrow lines to the naked eye. All these bands run more or less parallel to the edge of the crest. Each opaque zone gradually passes into the next transparent zone, but each transparent zone is very abruptly succeeded by the next opaque zone. This abrupt ending of a transparent zone and beginning of the next opaque zone is marked by a well-defined line. The innermost opaque zone of the crest is paler in colour and less opaque than the other opaque zones.

Each supra-occipital has four borders: an anterior border which enters into the interlocking joint with the frontal portion of the crest, an ascending dorsal border, a descending posterior border and a ventral border by means of which it joins with the supra-occipital bone in the skull. The ventral border is not straight but is bent at about the middle to form an anterior 'ascending half' and a 'posterior descending' half. The anterior border is comparatively very

small, so that the whole bone presents a triangular appearance with the base showing a median bend. Just behind the junction of the descending and ascending halves of the ventral border there is a point on the 'base-line' wherefrom arise several radiating lines and ridges which run towards the outer edge of the crest. In some bones these lines stand out as radiating rough ridges, but they do not interfere with the clarity of the zones or with the measurements. The posterior edge of the dorsal border is wavy or frilled in outline. This is the 'growing edge'. The point from which the radiating lines and ridges arise is the 'centre of growth' and the lines are the 'axes of growth' of the bone.




Text-fig. 6. Diagram of the theoretical projection of the rings into hypothetical triangles to fix the line of measurement on the supra-occipital crest. *B–B*, the hypothetical base-line; $R^1$ to $R^5$, the annual rings (outer limits of the transparent zones); *C*, the centre of measurements; $A^1$–$A^5$, the apical points of the hypothetical triangles; $L^1$–$L^5$, the points on the annual rings to which the measurements are made from the centre along the 'line of measurement' (L.M.). A.B., D.B., P.B., V.B., the anterior, dorsal, posterior, and ventral borders of the crest, respectively.

*Line of Measurement*

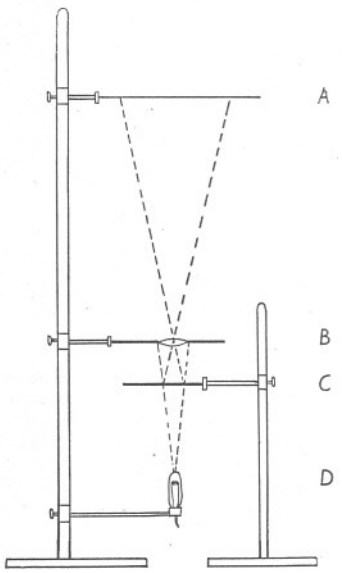
In utilizing a bone for the determination of age and rate of growth, the fixing of the line of measurement or axis of measurement is of prime importance. The line of measurement chosen for the supra-occipital crest is shown in Text-fig. 6. This axis of measurement was chosen because, apart from its convenience, (i) it is the median lying between the axis of vertical growth and the axis of horizontal growth of the fish and of the bone, and is therefore likely to give only the smallest error in calculations; and (ii) if all the zones are theoretically projected into hypothetical triangles this is the line which lies nearest to all the apical points and hence is to be regarded as the average of the sum forces of the axis of growth. In Text-fig. 6 it is shown how these

zones can be hypothetically projected into triangles. Since the anterior border of the crest is comparatively very small, the crest as a whole may be regarded as a triangle. The descending half of the ventral border is projected forward as a straight line meeting the anterior end of the dorsal border, and this forms the base-line of the triangle. Then the dorsal and posterior borders of the crest are projected in straight lines until they meet usually just behind the growing edge. This is the apex of the triangle. In the same way the dorsal and posterior borders of each of the transparent bands are projected to form hypothetical triangles. A line is drawn from the centre of growth passing along an axis which is nearest to the apical points of all the projected hypothetical triangles. This line is the line along which measurements were taken.

The diagram shows that the apical points lie almost in a straight line. This is because the growth of the bone is proportionate with the growth of the head and the allometry in the growth is altogether neglible.

*Method of Measurement*

The zones on the supra-occipital were measured by projecting the image of the crest on to graph paper covering a glass plate, with the aid of a simple vertical projector. The arrangement of the light, lens, the stage for the bone and the stage for holding the graph paper is shown in Text-fig. 7. A blue filter between the light and the bone increased the clarity of the image on the graph paper.




Text-fig. 7. Diagram of the simple vertical projector used for projecting the supra-occipital crests and for measuring them. *A*, stage for holding the graph paper and catching the image; *B*, the lens; *C*, stage for holding the bone; *D*, 6-watt lamp.

Quarto sheets of graph paper ruled in 10ths of an inch proved best for making the measurements. Each inch line is assumed as a separate ordinate and each such ordinate is used for a separate bone. The point of intersection between each such ordinate and the abscissa is taken to mark the centre of growth of the bone and the starting-point of the measurements. This point is superimposed on the centre of growth of the bone in the image. Fixing the graph paper at that point the paper is slightly rotated until the ordinate of that point lies in a line over the accepted axis of measurement of the bone in the image. The points at which each 'annual ring' (the sharp beginning of each opaque zone) in the image cuts the ordinate on the paper are then marked with a pencil. The posterior edge of the crest also is marked on the ordinate. The scale of magnification can be found by projecting a millimetre scale to the same

magnification on the graph paper. Knowing the magnification, the measurements of the zones on the graph paper can be easily converted into absolute measurements. When the various crests are all measured and marked on the graph paper, as described, it will be found that the respective annual-zone-points of the various crests lie more or less in a straight line. The crests were magnified to about eight times their normal size. With this magnification the percentage of error seems very small.

A few of the bones showed false rings—usually as 'split' or 'doubled' rings. These can be easily distinguished by the split not being continuous throughout the rings. The very few false rings where there was no 'doubling' could be distinguished by weak and incomplete formation, and by abrupt change from opaque to transparent zone, not gradual as with true rings. These were most easily detected in reflected light using a black background.

*Validity of the annual nature of the zones*

Graham (1929*b*), Sund (1927), Hickling (1933), Dannevig (1933) and Le Cren (1947) have all examined the validity of age-determination by scales, otoliths and bones respectively. Graham and Sund based their studies on the age-determination of cod on scales only, discarding the use of the skeletal parts because of the convincing evidence they got for the validity of the scale method. Hickling used only otoliths for the determination of the age of the hake and he had substantial evidence for its application and validity. The scales and otoliths of the Norwegian cod were critically studied by Dannevig (1933), and he came to the conclusion that 'the age of cod... certainly can be computed by scales and particularly by the otoliths'. The annual nature of the zones on the operculum of the Windermere perch was substantiated by Le Cren (1947).

According to Graham (1929*c*), there are five tests for deciding the validity of any method of age determination in fishes:

(i) Agreement with Petersen's method.
(ii) Seasonal record of the ring or zone formation.
(iii) Observation of a stock over a long period of years.
(iv) Marking experiments.
(v) Tank or pond experiments with fish of known age.

The present investigation of *G. minutus* covers only a period of 15 months and so it is not possible to examine the validity of the method of age determination employed from the aspect of test 3. Tests 4 and 5 were not possible for several reasons, and so it has been possible only to apply the remaining two tests to the validity of the present method.

*Seasonal record*

This test consists in the observation of the nature of the margin of the supra-occipital crest throughout the year, to find out and establish the period of formation of the opaque and transparent zones, and thus to determine

whether in the course of 1 year one opaque zone and one transparent zone only are laid. Graham (1929*a*) and Hickling (1933) remark that the seasonal record is a convincing test for the validity of the method. But neither of them found a sharp and complete turn over from one kind of marginal zone to the other at any time in the year. Hickling (1933) states: 'It is true that a sharp turn over from one margin to the other is completely lacking. No sample had 100% of its otoliths with an opaque zone at the edge and none had 0%.'

The percentages of supra-occipital crests of *G. minutus* with the opaque zones and transparent zones at the margin respectively for each month of the period of investigation are given in Table XI and in Text-fig. 8.

It can be seen from Table XI that in no month has there been a sample with 100% of the supra-occipital crests with either opaque zone or transparent zone at the margin. The maximum and minimum percentages of supra-occipital with the opaque and transparent zones have been 86 and 31, and 69 and 14 respectively. Hickling (1933) attributed the lack of complete turn over from one type of margin to the other in the otolith of the hake to the formation of 'subsidiary rings' in the growth of otolith as a normal feature. In the cod of Norwegian waters, on the other hand, Dannevig (1933) found a complete turn over from one type of margin to the other in both scales and otoliths. According to Hickling (1933) the causative factor for the ring formation in the otolith of the hake is an internal one and the nature of the zones depends on the condition of the fish and seasonal rate of growth of fish. Dannevig (1933) has suggested that the zone formation 'may be due to the variation in the quantity of organic substances'. The zones in the scales of cod, according to him, may 'originate in different ways by moderately low or very high temperature'.

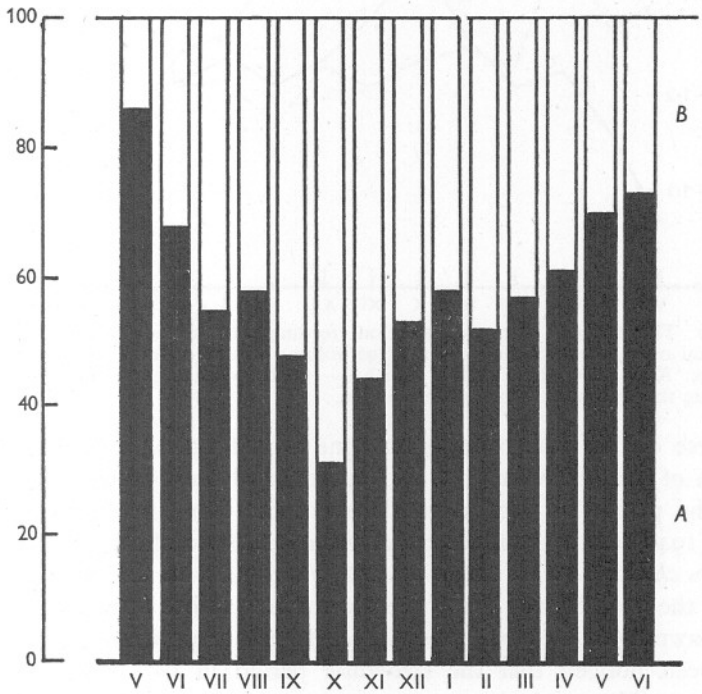
The data of the supra-occipital crests of *G. minutus* show that the percentage of these crests with an opaque zone at the margin remains fairly high from January to August. This percentage is low from September to November, the lowest being in the month of October. Hickling (1933) also got more or less identical results with the hake otolith. It was found that although there was no sharp turn over in the nature of the marginal zone at any particular period of the year, there were two distinct periods when the major emphasis was for the formation of one or the other type of zone. Thus the major period for laying the opaque zone is from January to August and that for the transparent zone is from September to November.

The results of the analysis of the margin of the supra-occipital crest are shown in Text-fig. 9. In addition two other factors, the condition factor $K$ for the fish in each month, and the average volume of food in the stomachs of ten fish in each month, have been included for comparison. The condition factor $K$ used is the average for fish of all length groups and of both sexes together. Hickling (1933), in a similar study, treated the otolith data without taking sex into consideration and then compared it to the condition factor of

## TABLE XI. PERCENTAGE OF FISH WITH OPAQUE OR TRANSPARENT ZONES AT THE MARGIN OF THE SUPRA-OCCIPITAL CREST

The figures in brackets are the actual number of crests examined having the respective type of zone at the margin.

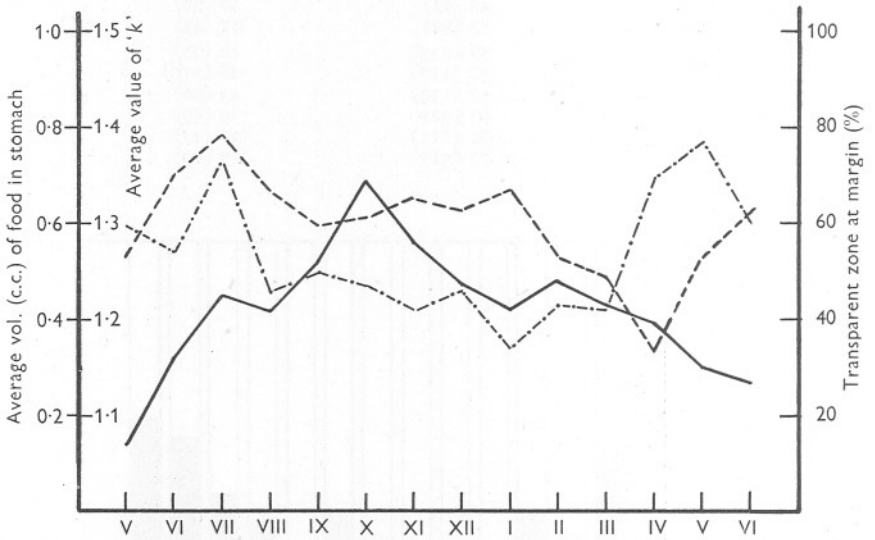
| Month | Percentage of crests with opaque zone at the margin | Percentage of crests with transparent zone at the margin |
|---|---|---|
| May 1948 | 86 (68) | 14 (11) |
| June | 68 (76) | 32 (36) |
| July | 55 (34) | 45 (28) |
| Aug. | 58 (77) | 42 (55) |
| Sept. | 48 (67) | 52 (72) |
| Oct. | 31 (32) | 69 (70) |
| Nov. | 44 (51) | 56 (66) |
| Dec. | 53 (49) | 47 (43) |
| Jan. 1949 | 58 (135) | 42 (98) |
| Feb. | 52 (117) | 48 (110) |
| Mar. | 57 (131) | 43 (96) |
| Apr. | 61 (92) | 39 (59) |
| May | 70 (111) | 30 (47) |
| June | 73 (51) | 27 (19) |




Text-fig. 8. Histogram showing the number of supra-occipitals per 100 examined exhibiting (*A*) the opaque zone, and (*B*) the transparent zone respectively at their margins in successive months.

the adolescent female hake. Although this did not lead to any conflicting results with the hake, it is better to treat such data from comparable factors and common standards when possible.

The condition factor is lowest during the spawning period February to May. This is the main period of formation of the opaque zone on the supra-occipital crests. Hickling (1933) found that 'the transluscent band is laid on the otolith of the hake at the time of the poorest condition, that is, of greatest physiological stress. In mature fish this is the exhaustion due to spawning and in immature fish to its precursor in the innate physiological rhythm which can be detected in the somatic tissues.' The observations on *G. minutus* show just




Text-fig. 9. The relation between condition, feeding, and zone formation in the supra-occipital of *G. minutus*. -·-·-·-, average volume in c.c. of food per stomach; ------, average '*K*' for the whole sample of fish; ——, the percentage of supra-occipital crests showing the transparent zone at the margin.

the reverse of this: the transparent zone is laid during a period of normal condition of fish (September to November) and the opaque zone is formed during the period of poorest condition of the fish (the spawning period). Yasuda (1940) made a similar observation on the otoliths and vertebrae of *Scombrops chilodipteroides* and *Theragra chalcogramma*. He observed that the rings on the otoliths and vertebrae are formed before spawning—3 months before spawning on the otolith and 1½ months before spawning on the vertebrae. It has been noticed that the spawning period in *Gadus minutus* is from February to May and the transparent zone (the counterpart of Yasuda's 'rings') is laid on the supra-occipital crest from September to November, i.e. the transparent zone is laid nearly 4–6 months after the spawning or, conversely, it is laid 2–4 months before the next spawning. If were are to accept

Hickling's (1933) finding that the fluctuation in the 'physiological stress' is the causative factor for the zone formation in the skeletal parts, it will have to be assumed that the effect of the physiological stress becomes apparent on the supra-occipital crest of *G. minutus* only some months after its actual occurrence.

Taking the average volume of food (Table I, p. 189) into consideration, we find that there is not much of a correlation with the zone formation. The highest percentage of supra-occipital crests with opaque zone at the margin is found during the period of 'most active feeding' and the lowest percentage of opaque-zone formation occurs during the period of 'average feeding'. But the correlation ends with this.

It appears that of these two factors—the physiological stress and feeding—the physiological stress is the more acceptable as the causative factor for the formation of the 'ring'. The effect of the physiological stress is made apparent on the bone as the transparent zone.

Without going further into the question on the causative factor, we find that the zones are annual, being laid at definite periods of the year and can be used as valid indices of age in *G. minutus*.

*Agreement with Petersen's Method*

This test is useful only if the following conditions are satisfied: (i) the sample analysed must be large; (ii) the samples must contain all the year groups in a proportion at least fairly comparable with their proportion in the population; (iii) the Petersen graph of the size analysis must show reasonably distinct modes.

Graham (1929*c*) has pointed out that the test is applicable to the first three or four age groups, and he further asserts that even in cases of agreement it only confirms the correctness of the method of age assessment for a fair majority of the fish.

Examining these three conditions of the utility of this test one notes that the first condition has no limiting factor. The bigger the sample, the closer is the approximation to the truth. There is no absolute criterion of the probable number in the sample to satisfy the condition. With regard to the third condition, only the modes of the early years will be distinct and well defined. As the rate of growth decreases with age the differences in the lengths of older age groups become very small and the Petersen curve tends to flatten at these later age groups. In fishes which have a short span of life this flattening of the curve may occur even earlier.

The second condition is especially important. The curve is one that represents the percentage composition of the length groups in a sample of population. The sample, therefore, should contain primarily all the year groups and, secondly, should contain them in such numbers that are proportionally comparable to their numbers in the population. In actual practice it is always possible that the gear employed for the collection of the samples

introduces a certain amount of selection in the sampling. In Text-figs. 10 and 11, showing the monthly analysis of the length groups of the *G. minutus* examined, the curve shows a very disturbing character, namely the absence of the O-group and I-group in the earlier samples. This is due to the selective

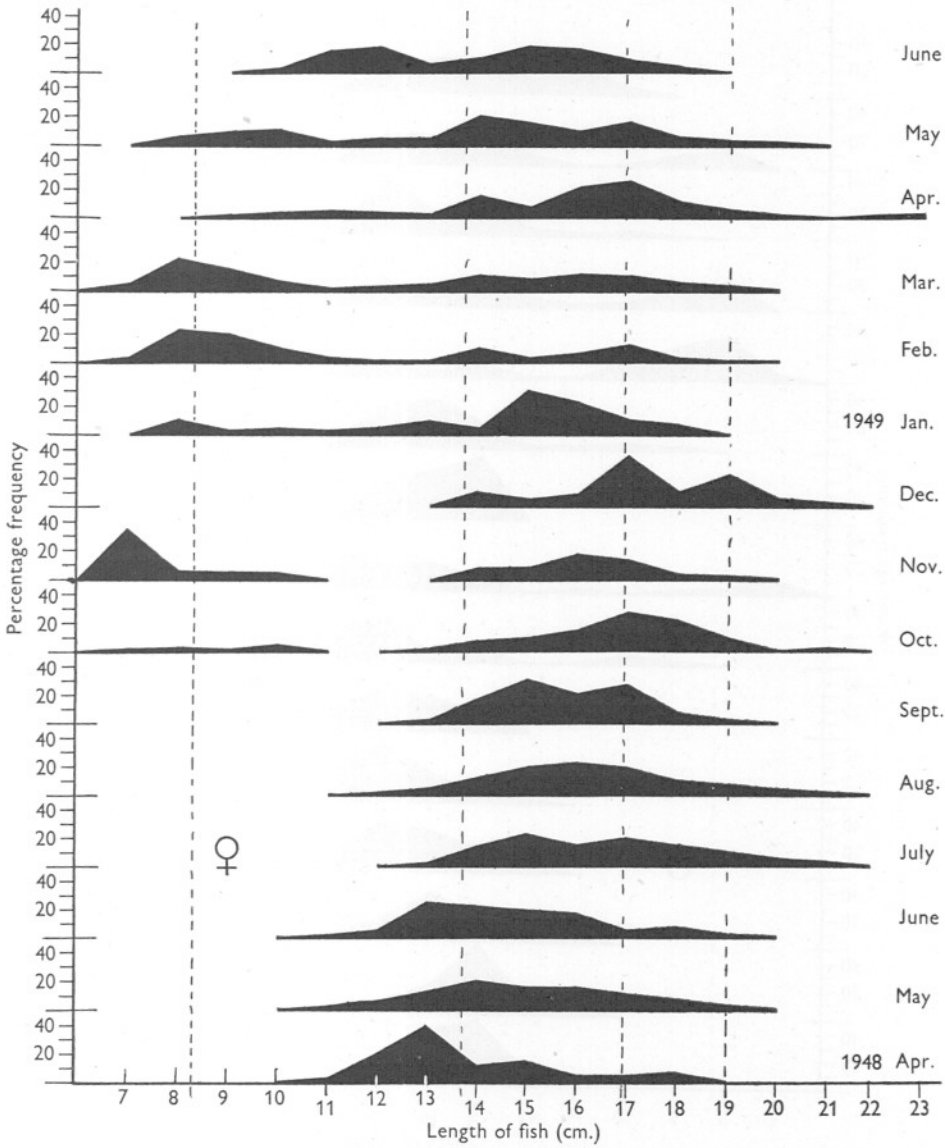
TABLE XII. TABLE SHOWING THE MONTHLY ANALYSIS OF THE SIZE OF THE SPECIMENS EXAMINED. FEMALE

| Length of fish in cm. | 1948 | | | | | | | | | 1949 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June |
| 7 | .. | .. | .. | .. | .. | .. | 1 | 96 | .. | .. | 13 | 6 | .. | .. | .. |
| 8 | .. | .. | .. | .. | .. | .. | 2 | 18 | .. | 9 | 89 | 35 | .. | 14 | .. |
| 9 | .. | .. | .. | .. | .. | .. | 1 | 15 | .. | 3 | 77 | 24 | 1 | 19 | .. |
| 10 | .. | .. | .. | .. | .. | .. | 7 | 14 | .. | 4 | 41 | 9 | 8 | 24 | 6 |
| 11 | 2 | 6 | 4 | .. | .. | .. | .. | .. | .. | 2 | 11 | 1 | 11 | 6 | 29 |
| 12 | 3 | 14 | 11 | .. | 2 | .. | .. | .. | .. | 5 | 2 | 3 | 8 | 9 | 33 |
| 13 | 21 | 29 | 74 | 6 | 13 | 2 | 4 | .. | .. | 9 | 3 | 6 | 5 | 9 | 11 |
| 14 | 45 | 47 | 70 | 30 | 34 | 34 | 14 | 22 | 14 | 4 | 38 | 14 | 33 | 49 | 17 |
| 15 | 13 | 42 | 57 | 49 | 53 | 60 | 16 | 22 | 6 | 29 | 12 | 12 | 16 | 33 | 33 |
| 16 | 15 | 43 | 51 | 32 | 59 | 42 | 25 | 47 | 11 | 23 | 28 | 18 | 48 | 19 | 30 |
| 17 | 5 | 25 | 13 | 42 | 55 | 53 | 46 | 38 | 49 | 11 | 36 | 17 | 63 | 37 | 14 |
| 18 | 4 | 17 | 20 | 29 | 31 | 13 | 39 | 9 | 15 | 7 | 11 | 8 | 25 | 12 | 8 |
| 19 | 6 | 4 | 4 | 18 | 22 | 5 | 16 | 6 | 31 | .. | 6 | 6 | 10 | 7 | .. |
| 20 | .. | .. | .. | 8 | 11 | .. | .. | .. | 6 | .. | 3 | .. | 2 | 4 | .. |
| 21 | .. | .. | .. | 3 | 3 | .. | 1 | .. | 4 | .. | .. | .. | .. | .. | .. |
| 22 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. |
| 23 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. |
| | 114 | 227 | 304 | 217 | 283 | 209 | 172 | 287 | 136 | 106 | 370 | 159 | 233 | 242 | 181 |

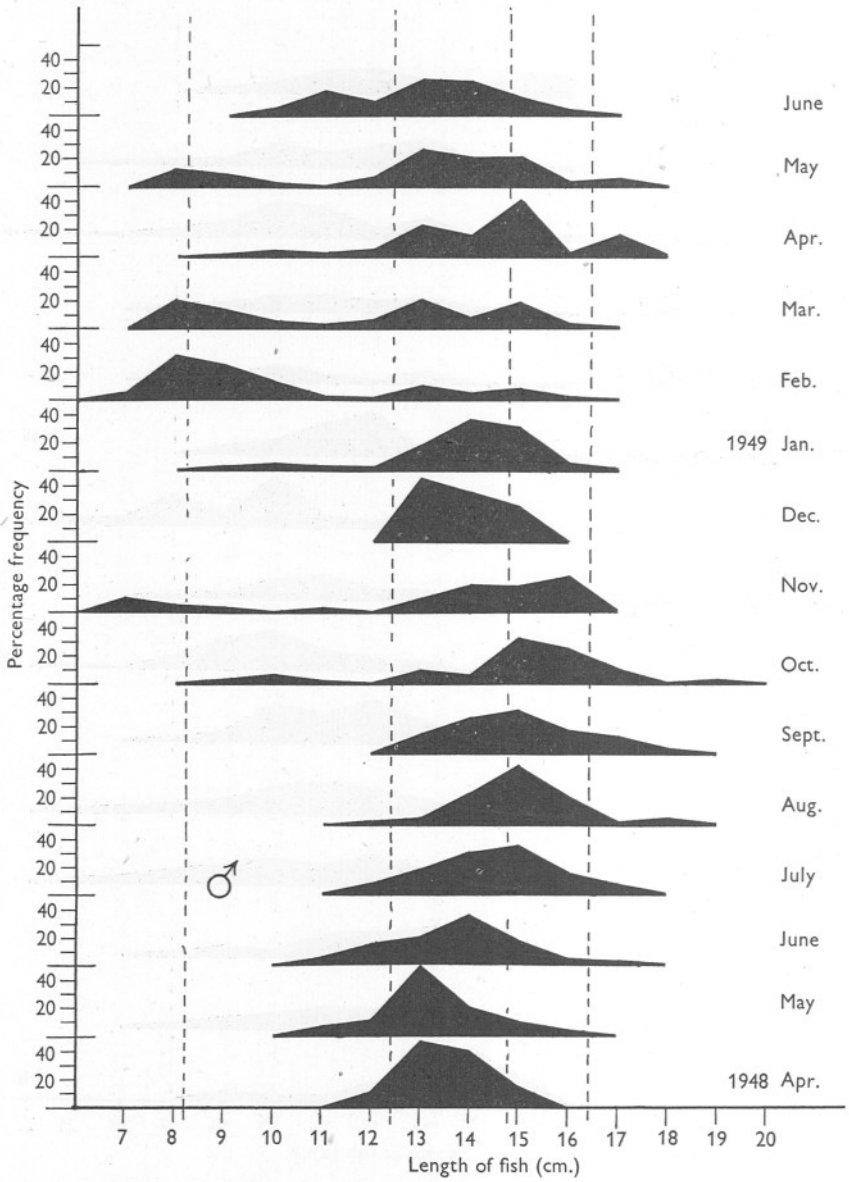
TABLE XIII. TABLE SHOWING THE MONTHLY ANALYSIS OF THE SIZE OF THE SPECIMENS EXAMINED. MALE

| Length of fish in cm. | 1948 | | | | | | | | | 1949 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June |
| 7 | .. | .. | .. | .. | .. | .. | .. | 9 | .. | .. | 14 | .. | .. | .. | .. |
| 8 | .. | .. | .. | .. | .. | .. | .. | 4 | .. | .. | 95 | 36 | .. | 12 | .. |
| 9 | .. | .. | .. | .. | .. | .. | 1 | 3 | .. | 2 | 76 | 26 | 2 | 10 | .. |
| 10 | .. | .. | .. | .. | .. | .. | 3 | .. | .. | 7 | 39 | 11 | 5 | 3 | 4 |
| 11 | .. | 18 | 9 | .. | .. | .. | 1 | 2 | .. | 2 | 5 | 6 | 3 | .. | 12 |
| 12 | 5 | 31 | 25 | 4 | 2 | .. | .. | .. | .. | 2 | 4 | 11 | 6 | 7 | 7 |
| 13 | 24 | 141 | 34 | 9 | 3 | 11 | 4 | 8 | 11 | 23 | 28 | 36 | 28 | 29 | 18 |
| 14 | 21 | 55 | 59 | 14 | 14 | 21 | 3 | 16 | 9 | 47 | 17 | 12 | 17 | 22 | 17 |
| 15 | 7 | 29 | 28 | 18 | 25 | 25 | 16 | 15 | 6 | 39 | 21 | 33 | 40 | 23 | 9 |
| 16 | .. | 11 | 7 | 8 | 11 | 13 | 12 | 21 | .. | 5 | 2 | 5 | 3 | 3 | 2 |
| 17 | .. | .. | 5 | 4 | 1 | 10 | 5 | .. | .. | .. | .. | .. | 17 | 5 | .. |
| 18 | .. | .. | .. | .. | 2 | 2 | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| 19 | .. | .. | .. | .. | 1 | .. | 1 | .. | .. | .. | .. | .. | .. | .. | .. |
| | 57 | 285 | 167 | 57 | 59 | 82 | 46 | 78 | 26 | 127 | 301 | 176 | 121 | 114 | 69 |

sampling by the gear (Tables XII and XIII). Throughout the investigation the main gear used for the collection of the samples was the otter trawl, which would be liable to select against the smaller size groups. This is clearly seen in the earlier part of the investigation in which the O-group was completely lacking. Later it was possible to collect a few of the O-group specimens from




Text-fig. 10. The size-composition (length-frequency) of the females in the samples of *G. minutus* in successive months. ------, the yearly lengths back-calculated from the supra-occipital crests.




Text-fig. 11. The size-composition (length-frequency) of the males in the samples of *G. minutus* in successive months. ------, the yearly lengths back-calculated from the supra-occipital crests.

the trawling surveys of Mr P. G. Corbin, who used the ordinary otter trawl with a sprat-net cod-end. All these have been included in the graphs. Also plotted on the graphs are the lengths that the fish reaches at the end of each year calculated from the supra-occipital. These are shown as vertical lines at the respective 'calculated lengths'. The spawning period of the fish is from February to May with its maximum in April. It can then be assumed that this period is the initial starting-point of the annual growth. It can be seen from the graphs that the first mode of the curves in the graphs for January, February and March in the female, and February, March and May in the male, lie more or less on the calculated lengths. In November 1948, another month when some specimens of O- and I-groups were obtained, the first mode lies much in front of the calculated length for the first year. The 2nd year and 3rd year modes also show more or less the same position as the calculated lengths in the months of February, March, April and May in the size-analysis graphs for both male and female. It is not possible to follow one lower-age

TABLE XIV

| | Male | | Female | |
|---|---|---|---|---|
| At the end of | Mode or observed length in cm. | Calculated length in cm. (from supra-occipital) | Mode or observed length in cm. | Calculated length in cm. (from supra-occipital) |
| 1st year | 8 | 8·2 | 8 | 8·3 |
| 2nd year | 13 | 12·4 | 14 | 13·7 |
| 3rd year | 15 | 14·8 | 17 | 16·9 |

class throughout the year in the graphs due to the influence of selective sampling by the gear. But the close approximation of the first three modes to the calculated lengths for the first 3 years in the months of February to May, in general, is a fair vindication of the test and the validity of the method (see Table XIV). Considering that the modes are given only to the nearest cm. the agreement is as exact as can be expected.

## AGE AND RATE OF GROWTH OF *GADUS MINUTUS*

The above two tests have substantially confirmed that the zones are annual and one opaque zone and its immediately succeeding transparent zone denote 1 year's growth and that they are the 'annual rings' comparable to the annual rings of the scales and otoliths of other fishes.

The mean lengths of the supra-occipital crest at each 5 mm. body-length in the male and female respectively are given in Table XV and plotted in Text-figs. 12 and 13 against the respective body-lengths as correlation curves.

The mean lengths of the 1st, 2nd, 3rd rings, etc., at each respective body-length, have been included in the graphs to represent the respective rings on the length-group of the supra-occipital. It can be seen from this that the lengths of each annual ring lie along a straight line, to quite a remarkable

degree, clearly proving that the rings once formed did not show any addition or diminution in their sizes and quality. The back-calculation was done in two ways—graphically and by the Lea-Dahl formula. The graphical back-calculation was carried out as follows.

TABLE XV. TABLE SHOWING THE LENGTH OF THE SUPRA-OCCIPITAL CREST AT THE DIFFERENT LENGTHS OF FISH

| | Length of the supra-occipital crest in mm. | | | | | |
|---|---|---|---|---|---|---|
| | Female | | | Male | | |
| Length of fish in cm. | Empirical mean lengths | S.E. of mean | Theoretical lengths $X$ | Empirical mean lengths | S.E. of mean | Theoretical lengths $Y$ |
| 7·0 | 2·81 | 0·029 | 2·69 | 2·78 | 0·033 | 2·69 |
| 7·5 | 3·07 | 0·033 | 2·97 | 2·99 | 0·024 | 2·97 |
| 8·0 | 3·38 | 0·031 | 3·24 | 3·32 | 0·028 | 3·24 |
| 8·5 | 3·60 | 0·034 | 3·52 | 3·44 | 0·017 | 3·52 |
| 9·0 | 3·83 | 0·026 | 3·71 | 3·72 | 0·033 | 3·79 |
| 9·5 | 3·99 | 0·033 | 4·03 | 3·98 | 0·038 | 4·07 |
| 10·0 | 4·41 | 0·033 | 4·34 | 4·36 | 0·037 | 4·34 |
| 10·5 | 4·79 | 0·020 | 4·66 | 4·57 | 0·035 | 4·62 |
| 11·0 | 4·96 | 0·039 | 4·98 | 5·01 | 0·026 | 4·89 |
| 11·5 | 5·21 | 0·030 | 5·30 | 5·21 | 0·025 | 5·16 |
| 12·0 | 5·58 | 0·030 | 5·62 | 5·42 | 0·035 | 5·44 |
| 12·5 | 5·92 | 0·047 | 5·94 | 5·62 | 0·038 | 5·71 |
| 13·0 | 6·32 | 0·031 | 6·25 | 6·04 | 0·032 | 5·99 |
| 13·5 | 6·60 | 0·039 | 6·57 | 6·30 | 0·035 | 6·26 |
| 14·0 | 6·81 | 0·083 | 6·89 | 6·68 | 0·042 | 6·54 |
| 14·5 | 7·12 | 0·052 | 7·21 | 6·85 | 0·035 | 6·81 |
| 15·0 | 7·56 | 0·052 | 7·53 | 7·10 | 0·038 | 7·09 |
| 15·5 | 7·85 | 0·058 | 7·85 | 7·54 | 0·039 | 7·36 |
| 16·0 | 8·16 | 0·035 | 8·17 | 7·71 | 0·045 | 7·64 |
| 16·5 | 8·66 | 0·049 | 8·48 | 8·08 | 0·052 | 7·91 |
| 17·0 | 8·86 | 0·056 | 8·80 | 8·32 | 0·029 | 8·19 |
| 17·5 | 9·07 | 0·082 | 9·12 | 8·45 | 0·039 | 8·46 |
| 18·0 | 9·45 | 0·082 | 9·44 | 8·69 | 0·021 | 8·74 |
| 18·5 | 9·87 | 0·074 | 9·76 | (8·88) | .. | 9·01 |
| 19·0 | 10·24 | 0·071 | 10·08 | .. | .. | .. |
| 19·5 | 10·37 | 0·046 | 10·39 | .. | .. | .. |
| 20·0 | 10·69 | 0·064 | 10·71 | .. | .. | .. |
| 20·5 | 11·13 | 0·048 | 11·03 | .. | .. | .. |
| 21·0 | 11·40 | 0·058 | 11·35 | .. | .. | .. |
| 21·5 | 11·60 | 0·067 | 11·67 | .. | .. | .. |
| 22·0 | (11·96) | .. | 11·99 | .. | .. | .. |
| 22·5 | (12·26) | 0·010 | 12·30 | .. | .. | .. |

*Notes.* $X$, $Y$; the theoretical lengths calculated from the formulae:

$$L = 3{\cdot}18 + 1{\cdot}57l \text{ for the females above 9·0 cm.,}$$

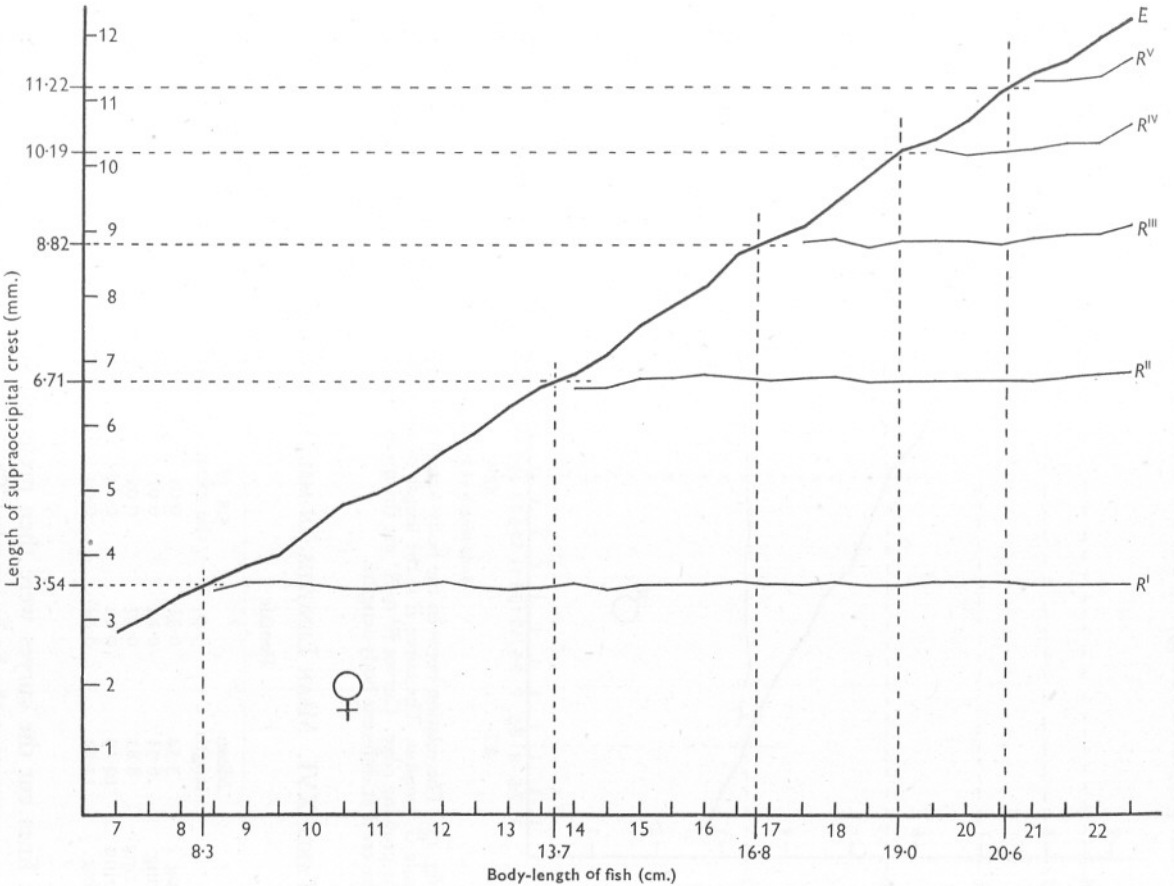
and

$$L = 2{\cdot}10 + 1{\cdot}82l, \text{ for the males.}$$

The theoretical lengths for the groups below 9·0 cm. in the females were calculated from the formulae used for the males. The empirical lengths are nearly the same in both sexes towards the lower length groups. The difference in the lengths of the supra-occipital crests in the two sexes is marked from maturity.

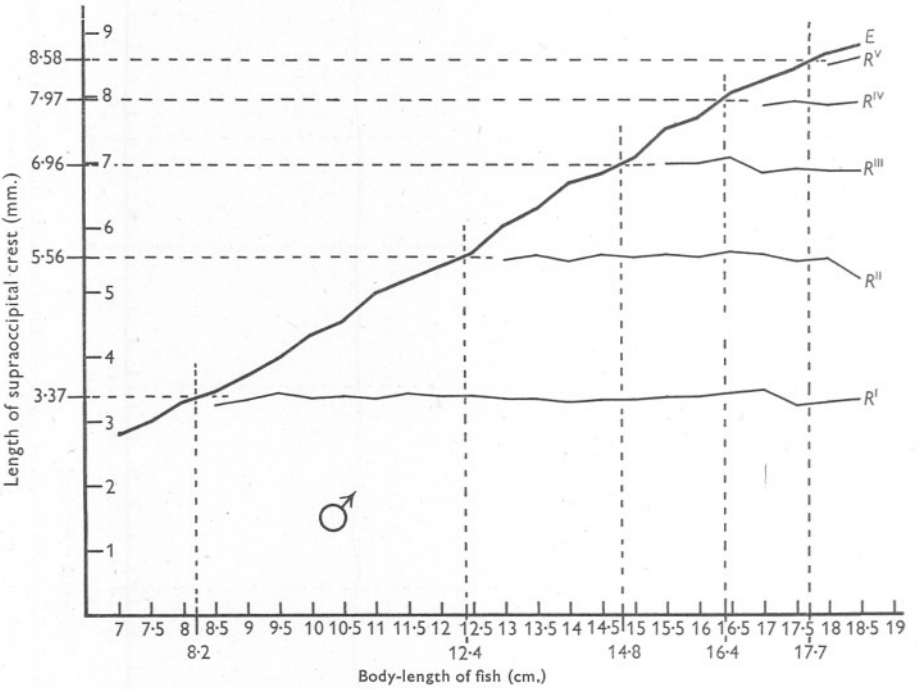
The figures in brackets denote that the number of crests examined were less than 5.

The mean lengths of the 1st, 2nd, 3rd, 4th and 5th 'rings' were worked out from all the supra-occipitals examined for either sex irrespective of the lengths of the fish (Table XVI).




Text-fig. 12. The relation between the body-length of fish and length of supra-occipital crests in the female *G. minutus*. The curve *E* is the length of crest from the centre of measurements to the growing edge. Curves $R^I$ to $R^V$ are the mean lengths of the respective annual rings on the crest at different body-lengths.

These lengths were then plotted on the abscissa of the graph of the curve of correlation of the length of fish and length of supra-occipital crests. They were then projected straight to cut the correlation curve. The points at which




Text-fig. 13. The relation between the body-length and length of supra-occipital crest in the male *G. minutus*. The curve *E* is the length of crest from the centre of measurement to the growing edge. Curves $R^I$ to $R^V$ are the mean lengths of the respective annual rings on the crest at different body-lengths.

TABLE XVI. MEAN LENGTHS (IN MM.) OF SUCCESSIVE ANNUAL RINGS

| | Female | | | Male | | |
|---|---|---|---|---|---|---|
| | Mean length | S.D. | S.E. of the mean | Mean length | S.D. | S.E. of the mean |
| I ring | 3·54 | 0·31 | 0·01 | 3·37 | 0·27 | 0·01 |
| II ring | 6·71 | 0·24 | 0·01 | 5·56 | 0·21 | 0·01 |
| III ring | 8·82 | 0·27 | 0·02 | 6·96 | 0·23 | 0·02 |
| IV ring | 10·19 | 0·29 | 0·04 | 7·97 | 0·17 | 0·03 |
| V ring | 11·22 | 0·14 | 0·04 | 8·58 | 0·21 | 0·11 |

these lines cut the curves were then projected vertically down to meet the ordinate containing the body-lengths. The points at which these vertical projections cut the ordinate denoted the 'calculated lengths' of the fish at the end of the 1st, 2nd, 3rd, 4th and 5th years respectively. The calculated lengths thus arrived at are given in Table XVII.

The actual observations from the supra-occipital crests show slightly higher values for the body-lengths. The various 5 mm. length groups of either sex are tabulated below according to the number of 'annual rings' or age discerned on their respective supra-occipital crests as with the scales and otoliths (Table XVIII).

TABLE XVII. 'CALCULATED LENGTHS', DERIVED FROM MEASUREMENTS OF THE SUPRA-OCCIPITAL CREST

| | Body-length of fish in cm. | |
|---|---|---|
| At the end of | Female | Male |
| 1st year | 8·3 | 8·2 |
| 2nd year | 13·7 | 12·4 |
| 3rd year | 16·9 | 14·8 |
| 4th year | 19·0 | 16·4 |
| 5th year | *c.* 20·6 | *c.* 17·7 |

TABLE XVIII. ANALYSIS OF THE SUPRA-OCCIPITAL CRESTS OF *GADUS MINUTUS* ACCORDING TO THE LENGTH AND AGE OF THE FISH

| | Age in years | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Length of fish | Female | | | | | | Male | | | | | | |
| in cm. | 1− | 1+ | 2+ | 3+ | 4+ | 5+ | 1− | 1+ | 2+ | 3+ | 4+ | 5+ | Total |
| 7·0 | 20 | .. | .. | .. | .. | .. | 11 | .. | .. | .. | .. | .. | 31 |
| 7·5 | 36 | .. | .. | .. | .. | .. | 10 | .. | .. | .. | .. | .. | 46 |
| 8·0 | 34 | 9 | .. | .. | .. | .. | 36 | 1 | .. | .. | .. | .. | 80 |
| 8·5 | 24 | 18 | .. | .. | .. | .. | 23 | 19 | .. | .. | .. | .. | 84 |
| 9·0 | 12 | 22 | .. | .. | .. | .. | 15 | 26 | .. | .. | .. | .. | 75 |
| 9·5 | 6 | 34 | .. | .. | .. | .. | .. | 32 | .. | .. | .. | .. | 72 |
| 10·0 | .. | 50 | .. | .. | .. | .. | .. | 20 | .. | .. | .. | .. | 70 |
| 10·5 | .. | 31 | .. | .. | .. | .. | .. | 19 | .. | .. | .. | .. | 50 |
| 11·0 | .. | 35 | .. | .. | .. | .. | .. | 32 | .. | .. | .. | .. | 67 |
| 11·5 | .. | 38 | .. | .. | .. | .. | .. | 34 | .. | .. | .. | .. | 72 |
| 12·0 | .. | 26 | .. | .. | .. | .. | .. | 30 | .. | .. | .. | .. | 56 |
| 12·5 | .. | 35 | .. | .. | .. | .. | .. | 33 | 8 | .. | .. | .. | 76 |
| 13·0 | .. | 40 | .. | .. | .. | .. | .. | 11 | 50 | .. | .. | .. | 101 |
| 13·5 | .. | 24 | 9 | .. | .. | .. | .. | 4 | 58 | .. | .. | .. | 95 |
| 14·0 | .. | 20 | 16 | .. | .. | .. | .. | .. | 65 | 2 | .. | .. | 103 |
| 14·5 | .. | 16 | 26 | .. | .. | .. | .. | .. | 65 | 9 | .. | .. | 116 |
| 15·0 | .. | 4 | 54 | .. | .. | .. | .. | .. | 42 | 19 | .. | .. | 119 |
| 15·5 | .. | 1 | 57 | .. | .. | .. | .. | .. | 3 | 56 | 2 | .. | 119 |
| 16·0 | .. | .. | 74 | 1 | .. | .. | .. | .. | .. | 14 | 7 | .. | 96 |
| 16·5 | .. | .. | 54 | 5 | .. | .. | .. | .. | .. | 9 | 9 | .. | 77 |
| 17·0 | .. | .. | 40 | 11 | .. | .. | .. | .. | .. | .. | 9 | .. | 60 |
| 17·5 | .. | .. | 14 | 22 | .. | .. | .. | .. | .. | .. | 2 | 2 | 40 |
| 18·0 | .. | .. | 4 | 29 | .. | .. | .. | .. | .. | .. | 1 | 1 | 35 |
| 18·5 | .. | .. | .. | 22 | 4 | .. | .. | .. | .. | .. | .. | 1 | 27 |
| 19·0 | .. | .. | .. | 14 | 5 | .. | .. | .. | .. | .. | .. | .. | 19 |
| 19·5 | .. | .. | .. | 7 | 11 | .. | .. | .. | .. | .. | .. | .. | 18 |
| 20·0 | .. | .. | .. | .. | 11 | .. | .. | .. | .. | .. | .. | .. | 11 |
| 20·5 | .. | .. | .. | .. | 10 | .. | .. | .. | .. | .. | .. | .. | 10 |
| 21·0 | .. | .. | .. | .. | 2 | 5 | .. | .. | .. | .. | .. | .. | 7 |
| 21·5 | .. | .. | .. | .. | 1 | 3 | .. | .. | .. | .. | .. | .. | 4 |
| 22·0 | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | 1 |
| 22·5 | .. | .. | .. | .. | .. | 2 | .. | .. | .. | .. | .. | .. | 2 |
| Total | 132 | 403 | 348 | 111 | 44 | 11 | 95 | 261 | 291 | 109 | 30 | 4 | 1839 |

From this table the means of lengths arrived at the end of each year were calculated as with the data of scales and otoliths. These mean lengths are the 'observed lengths' (Table XIX).

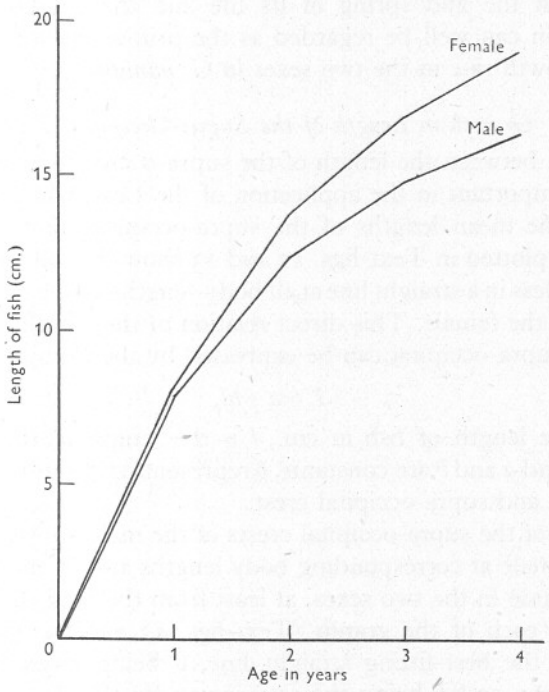
TABLE XIX. 'OBSERVED LENGTHS', DERIVED FROM GROUPING THE FISH ACCORDING TO THE NUMBER OF ANNUAL RINGS IN THE CREST

| At the end of year | Length of fish in cm. | | | |
|---|---|---|---|---|
| | Female | | Male | |
| | Range | Mean | Range | Mean |
| 1st | 8·5–9·0 | 8·75 | 8·5–9·0 | 8·75 |
| 2nd | 14·0–14·5 | 14·25 | 12·5–13·0 | 12·75 |
| 3rd | 17·0–17·5 | 17·25 | 15·0–15·5 | 15·25 |
| 4th | 19·0–19·5 | 19·25 | 16·0–16·5 | 16·25 |

Working out these means as with otoliths and scales, it is found that the differences between the graphically calculated lengths and the 'observed mean lengths' diminish with age.

The growth of *G. minutus* diminishes with age. The maximum size to which the fish usually grows is about 22·5 cm. in the female and 19·0 cm. in the male. The maximum age to which the fish generally lives is found to be 5 years. Only four males and eleven females of over 5 years' age have been seen, and so the measurements of their supra-occipital crests give only rough and approximate averages. Because of this the length that the fish reaches at the end of its 5th year, calculated from the measurements of the crest, is not included in Table XXI. The calculated lengths of the fish at the end of each year have been plotted in Text-fig. 14. It is seen from this that the rate of growth is extremely rapid in the first year. In the 2nd and 3rd years the growth diminishes, and it is very little from the 4th year onwards. The sexes grow at different rates. This is a well known feature in several other fishes, the males growing more slowly than the females. Comparing the growth rate of males with that of the females it is seen that both grow at the same rate and pace in the first year reaching almost the same lengths, viz. 8·2 and 8·3 cm. respectively. Maturity is reached at the beginning of the 2nd year and spawning occurs for the first time in the 2nd year of life. The males grow slower than the females in this 2nd year but the difference in growth is not very marked, the final lengths at the end of the 2nd year being 13·7 cm. in the female and 12·4 cm. in the male. After the spawning the differential growth between the male and the female becomes very marked. Hickling (1933), in *Merluccius merluccius*, and Hart (1946), in *Merluccius hubbsi*, have pointed out that the metabolic strain of spawning is greater in mature males than in females. Greater energy is spent in building up the reserves of the reproductive elements than in linear growth in a spent male. This is a very likely cause for the difference in growth rate between the males and females of *Gadus minutus* after the first spawning in the 2nd year. The diminution in the rate of growth of females

after the first spawning is also marked, but not to the same extent as in the males. With every succeeding year the growth rate diminishes at such a rate that the males reach the same length in 4 years as the females reach in 3 years.




Text-fig. 14. Average growth rate of the male and female *G. minutus*.

The respective annual increments for each of the first 4 years of life in the male and the female are shown in Table XX.

It is significant that while the growth of females in each year is approximately two-thirds that of the preceding year, the growth in the male is approximately only half that of the preceding year.

TABLE XX. ANNUAL GROWTH INCREMENTS (CM.) DERIVED FROM 'CALCULATED LENGTHS'

| Year | Female | Male |
|---|---|---|
| 1st | 8·3 | 8·2 |
| 2nd | 5·4 | 4·2 |
| 3rd | 3·2 | 2·4 |
| 4th | 2·0 | 1·6 |

The comparatively much smaller number of males over 5 year's age in the population analysed can only be due to the reason suggested by Hickling (1933) for the hake. 'In the male hake, it is certainly true that the metabolic strain of the reproduction cycle increases at a very high rate with increase of length and there is no evidence that the male can prolong its life by a slackening off

of sexual activity.' The facts point rather towards a condition when 'reproduction may eventually overbalance normal metabolism and result in death' (Orton, 1929). The maturity at the beginning of the 2nd year, the occurrence of spawning in the 2nd spring of its life and the consequent differential metabolic strain can well be regarded as the primary factors influencing the differential growth rate in the two sexes in *G. minutus*.

*Growth in Length of the Supra-Occipital Crest*

The relation between the length of the supra-occipital crest and the length of the fish is important in the application of the Lea-Dahl formula for back-calculation. The mean lengths of the supra-occipital crests at the different lengths of fish plotted in Text-figs. 12 and 13 show that all the points in each sex lie more or less in a straight line at all body-lengths above 7·0 cm. in the male and 9·0 cm. in the female. This direct relation of the length of the fish to the length of the supra-occipital can be expressed by the formula

$$L = a + bl,$$

where $L$ is the length of fish in cm., $l$ is the length of the supra-occipital crest in mm., and $a$ and $b$ are constants, $b$ representing the ratio of increments of length of body and supra-occipital crest.

The lengths of the supra-occipital crests of the male are slightly lower than those of the female at corresponding body lengths and so the constants $a$ and $b$ are not the same in the two sexes, at least from the time they are beginning to mature. In each of the graphs (Text-figs. 12 and 13) the constants are obtained from the best-fitting straight line, $a$ being given by the value of $L$ when $l$ is zero, and $b$ being the ratio given by the slope of the line (the tangent of its angle to the vertical).

Interpolating the values of the constants in the formula for *G. minutus*, it becomes

$L = 3{\cdot}18 + 1{\cdot}57l$ for the female above 9·0 cm.,
and $L = 2{\cdot}10 + 1{\cdot}82l$ for the male (and probably all immatures).

Using these formulae it is possible to back-calculate the lengths of fish at any particular length of the supra-occipital crest. Conversely the theoretical lengths of the supra-occipital crests at any particular body-length also can be calculated. The theoretical lengths of the supra-occipital crests calculated by means of these formulae are given in Table XV (p. 220).

It is found that the back-calculated lengths of fish estimated by these formulae differ from the actual observed lengths only by 0·1–0·5 cm.

It would appear from the formula $L = a + bl$ that the value of '$a$' is the length of fish at which the supra-occipital crest begins to develop. If so the crest ought to develop at 2·1 cm. But actually the supra-occipital crest is first observed when the fish is 1·1 cm. long (it appears as a very narrow and small streak on the dorsal aspect of the neurocranium). If this 'presupraoccipital

fish length' of 1·1 cm. is applied to the orthodox Lea-Dahl formula it is possible to back-calculate body-lengths from the formula

$$L_r = \frac{L_R}{l_R} l_r + 1{\cdot}1,$$

where $L_r$ and $L_R$ are two different body-lengths, with $l_r$ and $l_R$ their corresponding crest-lengths. The ratio $L_R/l_R$ has been found empirically, $l_r$ is any chosen crest-length, and $L_r$ the body-length which is to be calculated. The modified Lea-Dahl formula differs from that used above (viz. $L = a + bl$) in having a smaller value for '$a$' and in using an empirical ratio which tends to be greater than '$b$'. The lengths back-calculated by the modified Lea-Dahl formula usually differ from the actual observed lengths by 0·1 to 0·9 cm., and, except for the smallest immature fish, the formula seems to have no particular merit.

### *Comparison between the Growth Rate Determined by Supra-Occipital Crest, Scales, Otoliths and Petersen Method*

The length of the fish at the end of the respective years of its life history arrived at by examination of the scales, otoliths, supra-occipital crests and the size analysis are now compared (Table XXI). The data of the lengths calculated from the supra-occipital crests are given in two ways—one showing the lengths calculated by the graphical method, and the other calculated by the Lea-Dahl formula.

TABLE XXI. CALCULATED LENGTHS IN CM. OF *GADUS MINUTUS*

| Age (years) | From scales | From otoliths | From supra-occipital | | From size analysis |
|---|---|---|---|---|---|
| | | | Graphical | L–D formula | |
| | | Female | | | |
| 1 | 8·75 | 9·75 | 8·3 | 7·7 | 8·0 |
| 2 | 14·25 | 14·75 | 13·7 | 13·5 | 14·0 |
| 3 | 17·25 | 17·75 | 16·9 | 17·4 | 17·0 |
| 4 | 19·75 | 19·25 | 19·0 | 19·0 | .. |
| | | Male | | | |
| 1 | 8·75 | 9·75 | 8·2 | 8·0 | 8·0 |
| 2 | 12·75 | 13·25 | 12·4 | 12·5 | 13·0 |
| 3 | 15·25 | 15·75 | 14·8 | 15·4 | 15·0 |
| 4 | 16·75 | 17·25 | 16·4 | 16·4 | .. |

In the back-calculation by the Lea-Dahl formula all the lengths have been calculated from the fish length and supra-occipital length of the fish at the end of the 4th year. All these lengths are standard lengths. The values arrived at by using the supra-occipital measurements are nearest to the actual observed lengths found in the size analysis. The lengths derived by examination of the otoliths and scales are higher than the empirical lengths. The differences between the lengths calculated by the graphical method and those by the Lea-Dahl formula are only 0·2–0·6 cm., which are unimportant in adults.

These calculated lengths and the age and growth rate of female *G. minutus* calculated from supra-occipital crests compare quite well with the findings of Stuart Thomson (1904), allowing for certain personal errors. Cunningham (1891) made some interesting observations on the growth rate of *G. minutus* by size analysis. The measurements and other details given by him are quoted in Table XXII.

Cunningham states that the more than 200 specimens less than 3 in. in length collected from Whitsand Bay 'are undoubtedly from the ova shed the preceding spring.... It is also clear that the specimens of 4·5–6·4 in. obtained on 9 July 1891 near the Eddystone were in their second year.' As growth rate decreases gradually, he regarded specimens of April 1891 to be 2 years of age.

TABLE XXII. SUMMARY OF CUNNINGHAM'S OBSERVATIONS ON *GADUS MINUTUS*

| Date | Length in cm. | Length in in. | Calculated age | Place of capture |
|---|---|---|---|---|
| May 1890 | 2·8–4·3 | 1·1–1·7 | 8–12 weeks | Cattewater |
| June 1891 | 4·2–7·2 | 1·6–2·9 | About 3 months | Whitsand Bay |
| July 1891 | 11·5–16·2 | 4·5–6·4 | 1 year and 3 months | North of Eddystone |
| April 1891 | 14·3–19·0 | 5·6–7·5 | 2 years | East of Eddystone |
| June 1889 | 13·7–15·0 | 5·4–5·8 | 1 year and 2 months | Whitsand Bay |
| | 20·0 | 7·8 | 2 years and 2 months | Whitsand Bay |

Cunningham's estimation of the length reached in the 1st year coincides fairly well with the present findings. His consideration of the 14·3–20 cm. length-group as belonging to one and the same age group, viz. past 2 years, is incorrect. That length group is really composed of two or even three age classes. The treatment of the data irrespective of sex also has contributed to the mixing of the different year classes.

## THE RELATION BETWEEN THE LENGTH AND WEIGHT OF *GADUS MINUTUS* AND ITS VALUE AS AN INDEX OF THE SPAWNING SEASON

Hickling (1930, 1940) and Hart (1946) have shown how the analysis of the weights of fish may yield interesting results from which important conclusions can be drawn. All the *G. minutus* were weighed in a Salter spring balance to the nearest gram. These weights were treated separately for each cm. length group and month in either sex. From the weights of several specimens of a cm. length group, the average weight for that particular length group was worked for each month. These average weights were used for computing the ponderal index for separate cm. length-groups of either sex. The ponderal index was worked out from the formula used both by Hickling (1930) and Hart (1946), viz.:

$$K = \frac{W}{L^3} \times 100,$$

where $W$ is the average weight of fish in gm., $L$ is the mean length of fish in cm. and $K$ is the ponderal index to be calculated. With suitable precautions

the ponderal index can often be taken as a measure of the fish's condition, and in these circumstances can appropriately be termed 'condition factor'.

Ponderal indices have been computed in three ways:

(i) Ponderal index for each mean cm. length group for each month in either sex.

(ii) The average ponderal index for each cm. length group of either sex for the whole year.

(iii) The average ponderal index of the whole sample of fish of either sex in every month.

Hart (1946) has stated that the *K* values may give a very good idea of the broad outline of the seasonal cycle for the species. He observed that 'apart from the seasonal variation in condition there is a secondary variation related to the length of the fish'. With increase in age 'there is a lower level of condition throughout the seasonal cycle consequent upon the increased metabolic strain of spawning. The point of inflexion on a curve showing this diminution of *K* with increasing length is thus a good indication of the length at which sexual maturity is attained.' In a growing organism a progressive variation of the ponderal index can be due to allometric growth. This point has been borne in mind when using the ponderal index variation of the *G. minutus* as an indicator of the spawning period.

The average values of *K* in relation to the length of the fish of either sex are given below (Table XXIII).

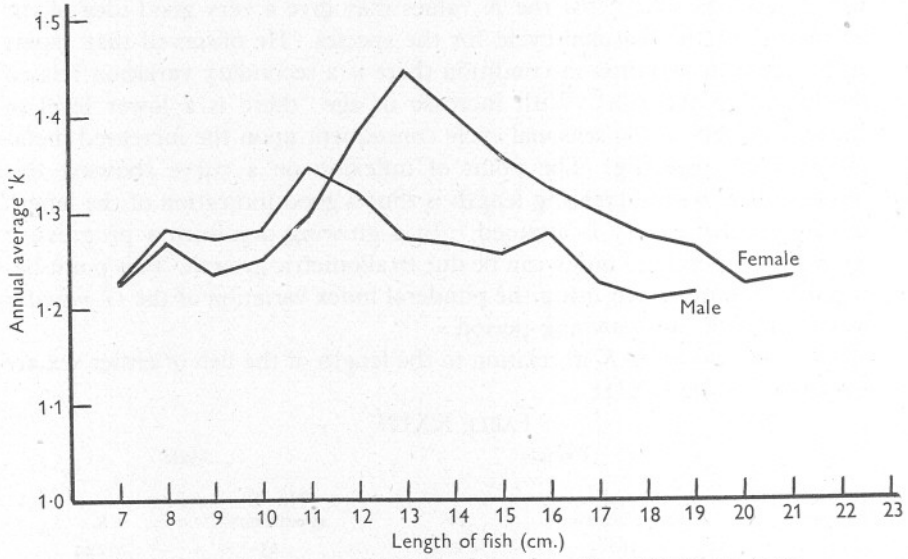
TABLE XXIII

| | Female | | Male | |
|---|---|---|---|---|
| Mean length of fish in cm. | No. of specimens | *K* | No. of specimens | *K* |
| 7 | 116 | 1·224 | 23 | 1·224 |
| 8 | 167 | 1·270 | 147 | 1·282 |
| 9 | 140 | 1·235 | 120 | 1·271 |
| 10 | 113 | 1·250 | 72 | 1·280 |
| 11 | 72 | 1·297 | 58 | 1·347 |
| 12 | 90 | 1·383 | 104 | 1·320 |
| 13 | 192 | 1·448 | 407 | 1·272 |
| 14 | 465 | 1·402 | 344 | 1·266 |
| 15 | 453 | 1·356 | 334 | 1·253 |
| 16 | 491 | 1·322 | 103 | 1·275 |
| 17 | 504 | 1·299 | 47 | 1·225 |
| 18 | 248 | 1·273 | 4 | 1·209 |
| 19 | 141 | 1·263 | 2 | 1·214 |
| 20 | 34 | 1·224 | .. | .. |
| 21 | 11 | 1·231 | .. | .. |
| 22 | 1 | 1·018 | .. | .. |
| 23 | 2 | 0·789 | .. | .. |

These average values of *K* in relation to the length of fish of either sex have been plotted as two curves in Text-fig. 15.

From the above graph it is seen that the *K* value is low in the very small length groups and gradually builds up until it falls in the greater length groups. If the point of inflexion of these curves is to be taken as an index of the length

at first spawning, it is found that the males mature at an average length of 11 cm. and the females at an average length of 13 cm. The *K* values of males are higher than those of the females of corresponding lengths before maturity. The *K* values of mature and post-mature males are lower than those of the females of corresponding lengths. This agrees with the observations of Hickling (1930) on the European hake and Hart (1946) on the Patagonian hake. These low values of *K* for the mature and post-mature males have been explained by Hickling (1930) as due to 'the very rapidly increasing metabolic strain of spawning in the older males'. From direct observation it has been




Text-fig. 15. The average *K* at the different lengths of fish in the male and female *G. minutus*.

noticed that the majority of males below 11 cm. and the majority of females below 13 cm. are immature; but observations on the actual gonadial changes could not be carried out in detail. In general, however, the deduction seems fairly substantiated that the average male matures at 11 cm. and the average female at 13 cm. Maturity is thus attained when the fish is in its 2nd year of life. The early maturity in contrast to the long adolescence of so many other larger gadoids is presumably due to the shorter span of life of *G. minutus*.

The length at which the fish matures now having been fixed, data from the *K* values have been selected to examine the seasonal variation of the ponderal index of each length group of either sex. These monthly variations of *K* are given in Table XXIV.

The variation of *K* values indicates the spawning period of the fish. The decline in the values denotes the beginning of the spawning in the species, since this downward trend is assumed to be consequent upon the lower level

TABLE XXIV. TABLE SHOWING THE PONDERAL INDEX *K* FOR THE INDIVIDUAL LENGTH GROUPS IN THE DIFFERENT MONTHS

| Year | Month | Length in cm. 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Female | | | | | | | | | | |
| 1948 | May | .. | .. | .. | .. | 1·248 | 1·393 | 1·488 | 1·185 | 1·233 | 1·221 | 1·079 | 1·235 | 1·283 | .. | .. | .. | .. |
| | June | .. | .. | .. | .. | 1·254 | 1·410 | 1·639 | 1·294 | 1·252 | 1·367 | 1·303 | 1·235 | 1·370 | .. | .. | .. | .. |
| | July | .. | .. | .. | .. | .. | .. | 1·684 | 1·603 | 1·511 | 1·489 | 1·434 | 1·285 | 1·312 | 1·188 | (1·296) | .. | .. |
| | Aug. | .. | .. | .. | .. | .. | (1·447) | 1·442 | 1·567 | 1·481 | 1·318 | 1·425 | 1·344 | 1·283 | 1·338 | (1·339) | .. | .. |
| | Sept. | .. | .. | .. | .. | .. | .. | (1·431) | 1·385 | 1·363 | 1·294 | 1·303 | 1·372 | 1·312 | .. | .. | .. | .. |
| | Oct. | (1·268) | (1·290) | (1·235) | 1·264 | .. | .. | 1·468 | 1·585 | 1·463 | 1·416 | 1·343 | 1·269 | 1·327 | .. | (1·080) | .. | .. |
| | Nov. | 1·215 | 1·272 | 1·255 | 1·281 | .. | .. | .. | 1·603 | 1·523 | 1·440 | 1·323 | 1·235 | 1·356 | .. | .. | .. | .. |
| | Dec. | .. | .. | .. | .. | .. | .. | .. | 1·541 | 1·492 | 1·416 | 1·364 | 1·252 | 1·254 | 1·188 | 1·209 | .. | .. |
| 1949 | Jan. | .. | 1·276 | (1·246) | 1·241 | (1·325) | 1·331 | 1·488 | 1·505 | 1·514 | 1·392 | 1·364 | 1·372 | .. | .. | .. | .. | .. |
| | Feb. | 1·189 | 1·260 | 1·221 | 1·231 | 1·254 | (1·403) | (1·332) | 1·348 | 1·314 | 1·270 | 1·312 | 1·303 | 1·196 | (1·325) | .. | .. | .. |
| | Mar. | .. | 1·242 | 1·214 | 1·224 | (1·251) | (1·331) | 1·304 | 1·276 | 1·185 | 1·270 | 1·282 | 1·303 | 1·166 | .. | .. | .. | .. |
| | Apr. | .. | .. | (1·239) | 1·259 | 1·251 | 1·373 | 1·304 | 1·130 | 1·126 | 1·118 | 1·229 | 1·143 | 1·101 | (1·125) | .. | (1·018) | (0·789) |
| | May | .. | 1·246 | 1·224 | 1·234 | 1·387 | 1·366 | 1·370 | 1·228 | 1·252 | 1·200 | 1·131 | 1·212 | 1·196 | 1·180 | .. | .. | .. |
| | June | .. | 1·294 | 1·246 | 1·266 | 1·341 | 1·392 | 1·424 | 1·284 | 1·272 | 1·298 | 1·222 | 1·262 | .. | .. | .. | .. | .. |
| | | | | | | | | Male | | | | | | | | | | |
| 1948 | May | .. | .. | .. | .. | 1·297 | 1·331 | 1·286 | 1·276 | 1·221 | 1·221 | .. | .. | .. | | | | |
| | June | .. | .. | .. | .. | 1·317 | 1·465 | 1·350 | 1·309 | 1·294 | 1·468 | 1·291 | .. | .. | | | | |
| | July | .. | .. | .. | .. | .. | 1·401 | 1·314 | 1·312 | 1·310 | 1·492 | 1·253 | .. | .. | | | | |
| | Aug. | .. | .. | .. | .. | .. | (1·331) | (1·261) | 1·290 | 1·271 | 1·221 | (1·221) | (1·217) | (1·218) | | | | |
| | Sept. | .. | .. | .. | .. | .. | .. | 1·257 | 1·265 | 1·256 | 1·231 | 1·214 | (1·200) | .. | | | | |
| | Oct. | .. | .. | (1·254) | (1·270) | (1·372) | .. | 1·268 | (1·276) | 1·268 | 1·251 | 1·221 | .. | (1·210) | | | | |
| | Nov. | 1·332 | 1·291 | (1·282) | .. | (1·380) | .. | 1·261 | 1·285 | 1·276 | 1·258 | .. | .. | .. | | | | |
| | Dec. | .. | .. | .. | .. | .. | .. | 1·272 | 1·271 | 1·288 | .. | .. | .. | .. | | | | |
| 1949 | Jan. | .. | .. | (1·242) | 1·290 | (1·325) | (1·242) | 1·264 | 1·284 | 1·299 | 1·371 | .. | .. | .. | | | | |
| | Feb. | 1·116 | 1·242 | 1·235 | 1·280 | 1·360 | 1·231 | 1·239 | 1·221 | 1·215 | (1·201) | .. | .. | .. | | | | |
| | Mar. | .. | 1·264 | 1·228 | 1·290 | 1·346 | 1·209 | 1·214 | 1·203 | 1·165 | 1·170 | .. | .. | .. | | | | |
| | Apr. | .. | .. | (1·212) | 1·224 | (1·209) | 1·199 | 1·163 | 1·186 | 1·156 | (1·147) | 1·118 | .. | .. | | | | |
| | May | .. | 1·329 | 1·317 | (1·292) | .. | 1·339 | 1·292 | 1·260 | 1·240 | (1·228) | 1·261 | .. | .. | | | | |
| | June | .. | .. | .. | 1·302 | 1·368 | 1·435 | 1·312 | 1·286 | 1·283 | (1·314) | .. | .. | .. | | | | |

The numbers of individuals on which the above figures are based may be ascertained from Tables XII and XIII.
The figures in brackets are based on 3 or less than 3 individuals.

of condition 'due to the increased metabolic strain'. The decline occurs after January and the mean $K$ values remain low till May. This indicates that the spawning period of the fish is between February and May. The lowest level of condition is in March–April when the spawning is at its height. This observation agrees well with Cunningham's (1891) assumption, in his computation of the growth rate of the fish, that the annual life cycle of *G. minutus* begins in April. In June and July there is a rapid recovery and increase of $K$ in both sexes. There is a minor drop in August and September, but this drop is much smaller than that observed during the spawning months. In the analysis of the food of *G. minutus* three periods had been distinguished in the annual life cycle of the fish according to their feeding activity; viz. a period of low feeding synchronizing with the months of spawning, a period of active feeding during the months immediately following the spawning, when the fish is recuperating from the strain of spawning, and a period of 'average feeding' when the fish is growing. During the period of low feeding the $K$ value is very low, and during the period of active feeding there is a sudden increase in the $K$ values. The $K$ values show a fluctuation during the period of average feeding when the fish is growing. At the beginning of this period, i.e. in August and September, there is a minor drop in the condition factor. It is possible that the metabolic changes in the fish at this period tend more towards an increase in linear dimensions than the building up of weight, a process which would automatically reduce the condition factor.

There is a differential seasonal variation of $K$ values between the various year-groups which is quite suggestive. The males and females of the length-group 12–16 cm. show a bigger seasonal variation than the others. Hart (1946) also observed a similar differential variation in *Merluccius hubbsi*. He explained the anomaly as due to inadequate sampling. Selective sampling may have contributed to the differential variation in *Gadus minutus* also to some extent, but the length-group 12–16 cm. consists of I, II and III groups of males and I and II groups of females, and are mostly spawners for the first and second time. It is probable that the earliest spawnings in the life history of such a short-lived fish are the most important in contributing to a potential increase and stabilization of the population (i.e. contribute a relatively larger bulk of reproductive products), and this may be one of the major causes for the differential variation of $K$ values between particular length-groups.

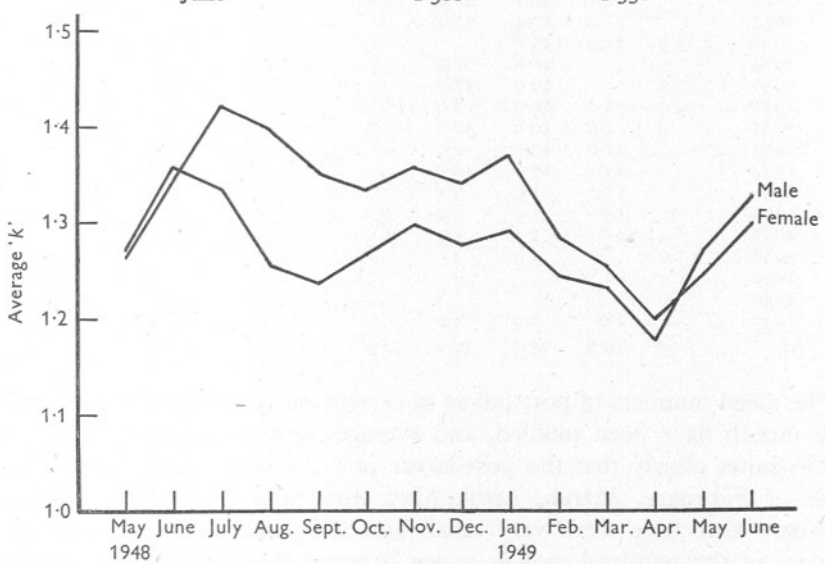
There is no evidence from ponderal index variation or direct observation to suggest that the older age-groups spawn earlier than the younger. The spawning periods in all the groups synchronize. There is no shoreward movement of the older and larger groups occurring earlier than the smaller ones similar to the movements observed by Hickling (1930) in *Merluccius merluccius* and Hart (1946) in *M. hubbsi*. Unlike the long-lived hake, the poor-cod is not an off-shore fish and its total span of life is small. Its distribution is limited within the 200 m. contour, and the population here studied was sampled only

within some 15 miles of the coast, so that any possible migration towards shallower regions is scarcely apparent.

The males in general show a lower $K$ value throughout the spawning and growing periods than do the females. This agrees with Hickling's (1930)

TABLE XXV. PONDERAL INDEX $K$ FOR THE WHOLE SAMPLE IN EACH MONTH

| Month | Female | Male |
|---|---|---|
| May 1948 | 1·263 | 1·265 |
| June | 1·347 | 1·356 |
| July | 1·422 | 1·347 |
| Aug. | 1·398 | 1·254 |
| Sept. | 1·351 | 1·237 |
| Oct. | 1·334 | 1·266 |
| Nov. | 1·350 | 1·296 |
| Dec. | 1·327 | 1·277 |
| Jan. 1949 | 1·369 | 1·290 |
| Feb. | 1·283 | 1·234 |
| Mar. | 1·254 | 1·232 |
| Apr. | 1·158 | 1·179 |
| May | 1·248 | 1·283 |
| June | 1·300 | 1·330 |




Text-fig. 16. The mean $K$ values for the whole sample of fish in successive months.

observation that the metabolic strain of spawning is greater in males than in females; but the recovery from the metabolic stress appears to be more rapid in the male than in the female when spawning is over.

The average ponderal index has also been calculated for the whole sample of fish of either sex in each month to examine whether by treating the data from bulk sample there is any marked departure from the observations on individual length groups. These monthly averages are given in Table XXV.

These values have been plotted as two curves in Text-fig 16, which indicates

the same trend of events as deduced from the variations in condition of individual length-groups. The spawning period is clearly defined as between February and May and the recovery of males after spawning is more rapid than that of the females.

That the main spawning period of *Gadus minutus* is from February to May is further shown by analysis of the data on the seasonal occurrence of the post-larvae in the Plymouth region. The data are given in the records of Russell (1930–47) and Corbin (1948) from their routine sampling of the young of teleostean fishes in the Plymouth area, covering the periods 1924–39, and 1946 onwards. These data have been abstracted in Table XXVI.

TABLE XXVI. AVERAGE MONTHLY CATCHES OF POST-LARVAE OF *GADUS MINUTUS* PER HALF-HOUR OBLIQUE HAUL WITH THE 2 M. RING TRAWL

| Year | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1924 | | | | | 33·9 | 24·9 | 4·2 | | | | | |
| 1925 | | | | 42·9 | 49·8 | 4·8 | .. | .. | | | | |
| 1926 | | | | 56·1 | 40·2 | 12·9 | .. | .. | .. | | | |
| 1927 | | | | 17·4 | 43·2 | .. | .. | .. | .. | .. | .. | .. |
| 1928 | .. | 3·9 | 24·0 | 135·6 | | | | | | | | |
| 1929 | | | | 10·5 | 0·9 | 1·2 | 0·3 | .. | .. | .. | | |
| 1930 | | .. | .. | 19·0 | 37·0 | + | .. | .. | .. | .. | .. | .. |
| 1931 | .. | 9·0 | 175·0 | 80·0 | 18·0 | .. | .. | .. | .. | .. | .. | .. |
| 1932 | .. | .. | 1·0 | 10·0 | 52·0 | 1·0 | .. | .. | .. | .. | .. | .. |
| 1933 | .. | .. | 21·0 | 12·0 | 1·0 | .. | .. | .. | .. | .. | .. | .. |
| 1934 | .. | .. | 2·0 | 17·0 | 19·0 | .. | .. | .. | .. | .. | .. | .. |
| 1935 | .. | .. | 1·0 | 1·0 | 5·0 | .. | .. | .. | .. | .. | .. | .. |
| 1936 | .. | + | 1·0 | 1·0 | 1·0 | 4·0 | .. | .. | .. | .. | .. | .. |
| 1937 | .. | .. | 10·0 | 2·0 | 1·0 | 1·0 | + | .. | .. | .. | .. | .. |
| 1938 | .. | 7·0 | .. | 5·0 | + | .. | .. | .. | .. | .. | .. | .. |
| 1939 | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. |
| 1946 | | | | | | .. | 2·0 | .. | .. | .. | .. | .. |
| 1947 | .. | .. | 2·0 | 1·0 | 2·0 | .. | .. | .. | .. | .. | .. | .. |
| Av. | .. | 1·7 | 19·8 | 25·7 | 19·1 | 2·9 | 0·4 | .. | .. | .. | .. | .. |

The mean numbers of post-larvae of *G. minutus* (per ½ hr. oblique haul) for each month have been totalled, and averages derived for each month. The result shows clearly that the post-larvae of *G. minutus* occurred only in the hauls of February, March, April, May, June and July. The numbers in February and June were very small and still smaller in July. From the analysis of the ponderal indices it was inferred that the spawning period is from February to May, the height of spawning being in March and April. The number of post-larvae is greatest in April and May. The occurrence of a few post-larvae in June and July may be due to a few late spawners as well as to a few post-larvae being carried over to these months, for there are no data regarding the size of the post-larvae recorded. Thus the post-larvae recorded in the months of June and July may include the slower-growing individuals from earlier spawnings.

When the individual years are considered there is a certain amount of fluctuation in the general picture, the post-larvae occurring earlier in some years

and later in others. The maximum number of post-larvae occurred in March or April in some years and in May in others. Table XXVII gives the number of times the post-larvae have occurred in the hauls (*not* numbers of larvae) in individual months during the period under survey.

It is seen from Table XXVI that there has been a gradual decline in the occurrence of post-larvae of *G. minutus* in Plymouth waters in recent

TABLE XXVII. OCCURRENCES OF POST-LARVAE IN PARTICULAR MONTHS

| Month | No. of Occurrence | No. of years covered |
|---|---|---|
| Jan. | 0 | 11 |
| Feb. | 4 | 12 |
| Mar. | 9 | 12 |
| Apr. | 15 | 16 |
| May | 16 | 16 |
| June | 8 | 17 |
| July | 4 | 17 |
| Aug.–Dec. | 0 | 13–16 |

years. In the collections from the Young Fish Trawl for 1948–49 only three post-larvae have been found of *G. minutus* in forty-eight hauls and of these, two post-larvae occurred in April 1949 and one in June 1948. This decline in the occurrence of post-larvae of *G. minutus* may be only a part of the general decline of post-larvae of all teleostean fishes in Plymouth waters observed by Russell. This decline is thought to be due to a decrease in the amount of rich Atlantic surface water entering the western channel, so that the more localized stocks of fish have spawned under adverse conditions, resulting from an increased proportion of comparatively impoverished coastal water.

## SUMMARY

The volumetric and qualitative analysis of the food of *Gadus minutus* has been discussed. The post-larvae feed entirely on copepods, mostly *Pseudocalanus elongatus*. The O-group feeds on copepods, small decapods, amphipods, polychaetes and isopods. The adolescent and adult groups feed on larger decapods like *Processa canaliculata*, *Galathea* spp. and *Portunus* spp., fish, polychaetes and amphipods.

The age and rate of growth of *G. minutus* have been computed from a study of the supra-occipital crest. These age determinations have been correlated with the age determined by scales, otoliths and size-analysis. Back-calculations have been made by graphical method and by using the Lea-Dahl formula. The differences between the back-calculated lengths and actual observed lengths are negligible.

The spawning period has been determined by analysis of the seasonal fluctuation of the condition factor of the fish. This has been verified by examination of the data on the seasonal abundance of the post-larvae in the Plymouth area. The spawning period is from February to May and the height of spawning is in March and April.

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[1] I am grateful to Mr Michael Graham for sending me this paper.

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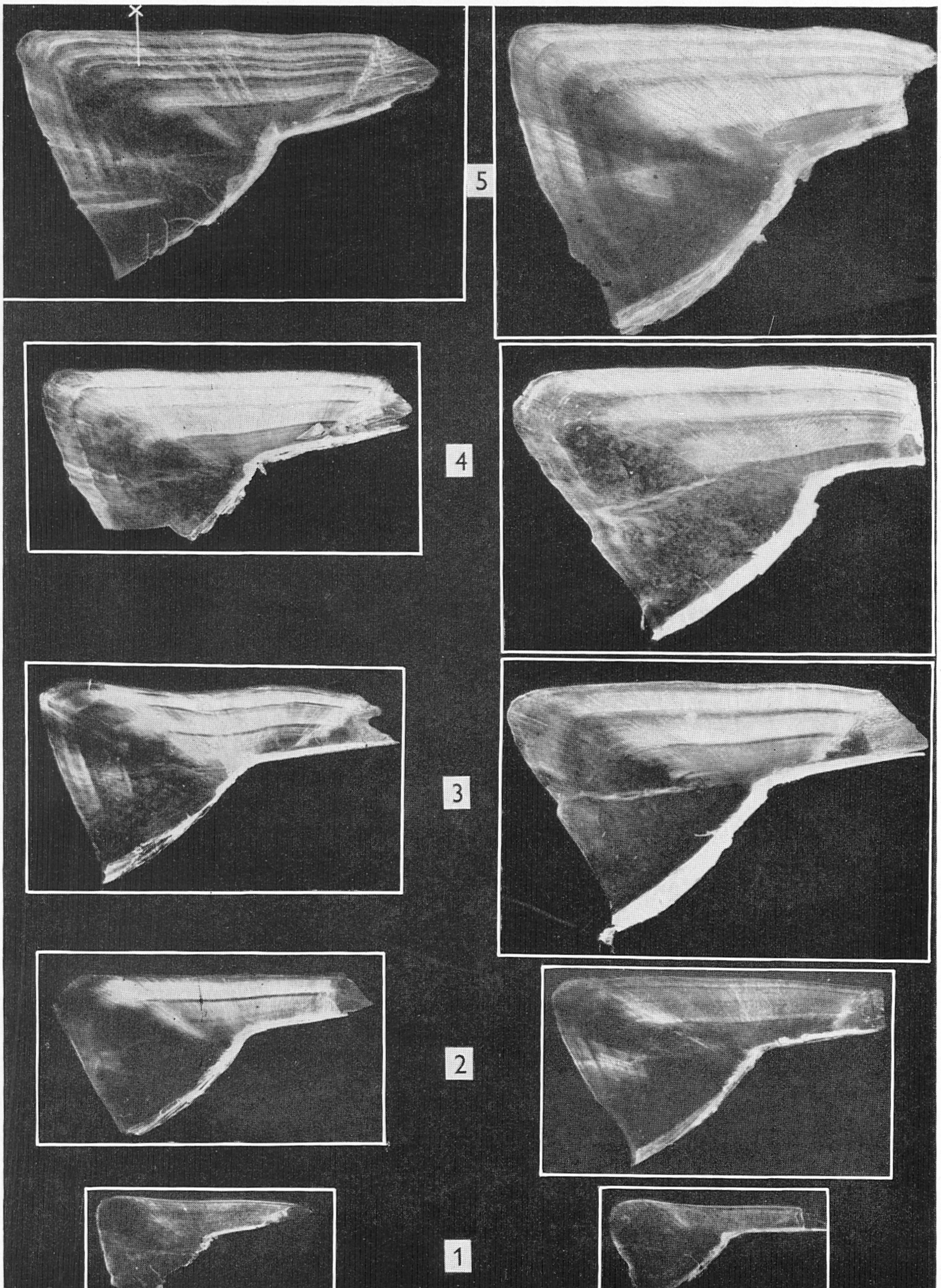
## Appendix. List of Organisms Found in the Stomach Contents of *Gadus minutus*

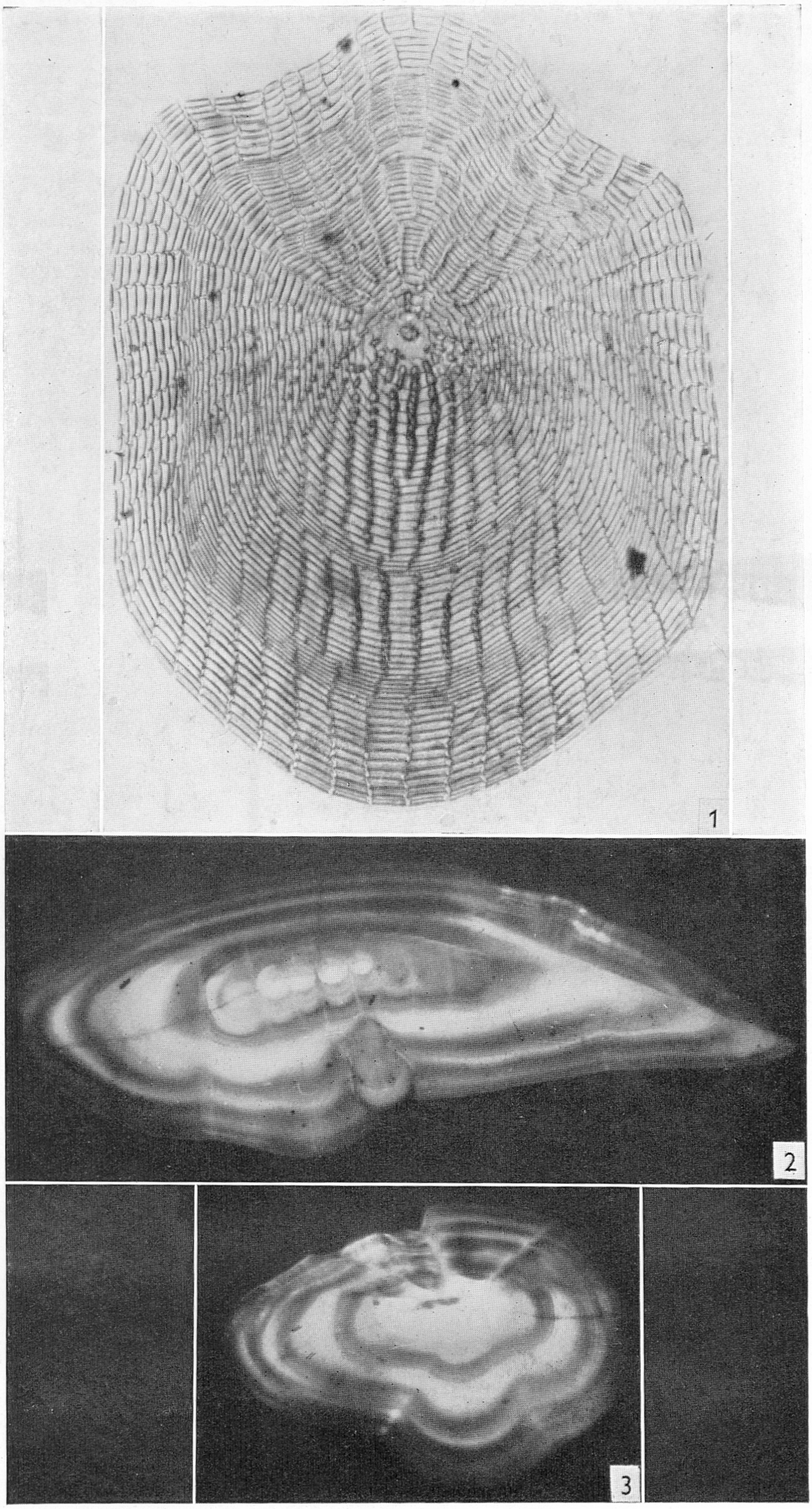
*Food of I- to V-Year Groups of* Gadus minutus

| | |
|---|---|
| Polychaeta | *Goniada* sp. |
| | *Pallasia murata* |
| | *Amphitrite* sp. |
| Crustacea | |
| Copepoda | *Calanus finmarchicus* |
| | *Labidocera wollastoni* |
| Cumacea | *Diastylis* sp. |
| Leptrostraca | *Nebalia bipes*[1] |
| Isopoda | *Rocinela danmoniensis* |
| | *Conilera cylindracea* |
| Amphipoda | *Orchomenella nana* |
| | *Ampelisca brevicornis* |
| | *A. spinipes* |
| | *A. tenuicornis* |
| | *A. diadema* |
| | *Leucothoë* sp. |
| | *Panoploea minuta* |
| | *Iphimedia obesa* |
| | *Urothoë elegans* |
| | *Monoculodes carinatus* |
| | *Monoculodes* sp. |
| | *Apherusa ovalipes* |
| | *Apherusa henneguyi* |
| | *Nototropis falcatus* |
| | *Cheirocratus assimilis* |
| | *Maera othonis* |
| | *Erichthonius brasiliensis* |
| | *Eurystheus maculatus* |
| | *Phtisica marina* |
| | *Pseudoprotella phasma* |
| Mysidacea | *Leptomysis gracilis* |
| | *Anchialina agilis* |
| Euphausiacea | *Nyctiphanes couchi* |
| Decapoda | *Pandalina brevirostris* |
| | *Hippolyte varians* |
| | *Spirontocaris cranchi*[1] |
| | *Processa canaliculata* |
| | *Crangon vulgaris* |
| | *Philocheras bispinosus* |
| | *Galathea intermedia* |
| | *G. dispersa* |
| | *G. strigosa*[2] |
| | *Munida bamffica*[1] |
| | *Porcellana longicornis* |
| | *P. platycheles* |
| | *Upogebia* sp. |
| | *Eupagurus bernhardus* |
| | *E. prideauxi* |
| | *Portunus pusillus* |
| | *P. holsatus* |
| | *P. depurator* |
| | *Corystes cassivelaunus*[3] |
| | *Inachus dorsettensis* |
| | *Macropodia longirostris* |
| Mollusca | *Nucula nitida* |
| | *Natica catena* |
| | *Turritella communis* |
| | *Philine aperta*[4] |
| | *Heterosepiola atlantica*[3] |
| Echinodermata | *Ophiura texturata* |
| | *Cucumaria* sp.[3] |
| Fish | *Gadus minutus*?[1] |
| | *Callionymus* spp. |
| | *Crystallogobius nilssoni* |
| | *Trigla* spp. |
| | *Ctenolabrus* sp. |

[1] Occurred only twice.
[2] Occurred only in twelve stomachs.
[3] Occurred only once.
[4] Occurred only thrice.




A B




Figs. 1–3.

*Food of the O-Group of* Gadus minutus

| | | | |
|---|---|---|---|
| Polychaetes | *Goniada* sp. | Decapoda | *Pandalina brevirostris* |
| Crustacea | | | *Hippolyte varians* |
| Copepoda | *Calanus finmarchicus* | | Small *Processa canaliculata* |
| | *Pseudocalanus elongatus* | | *Crangon vulgaris* |
| | *Centropages typicus* | | *Philocheras bispinosus* |
| | *Temora longicornis* | | *Galathea intermedia* |
| | *Acartia clausi* | | Small *Porcellana longicornis* |
| Isopoda | *Conilera cylindracea* | | *Eupagurus bernhardus* |
| Amphipoda | Small *Ampelisca spinipes* and *A. diadema* | | Small *Portunus* spp. |
| | *Apherusa ovalipes* | Mollusca | *Nucula nitida* |
| | *A. henneguyi* | | *Natica catena* |
| | *Phtisica marina* | | Small *Turritella communis* |
| Mysidacea | *Leptomysis gracilis* | | |
| Euphausiacea | *Nyctiphanes couchi* | | |

## EXPLANATION OF PLATES

### PLATE I

Ten supra-occipital crests of *Gadus minutus* photographed against a black background by reflected light. ×3·8.

A, five supra-occipital crests belonging to male *Gadus minutus* measuring (1) 8·0 cm.—age 1; (2) 12·4 cm.—age 2, just completing the 2nd transparent zone; (3) 14·6 cm.—age 3; (4) 16·5 cm.—age 4, just completing the 4th transparent zone; (5) 18·1 cm.—age 5 (the ring marked *X* is a false one caused by 'doubling': it can be seen that this ring is not complete and becomes continuous with the succeeding transparent zone in the vertical portion of the crest). B, five supra-occipital crests belonging to female *Gadus minutus* measuring (1) 8·4 cm.—age 1; (2) 13·4 cm.—age 2; (3) 16·4 cm.—age 3; (4) 18·8 cm.—age 4; (5) 21·1 cm.—age 5.

### PLATE II

Fig. 1. A scale from a male *Gadus minutus* measuring 14·9 cm. The photograph is of an alizarine-stained scale. ×42.

Fig. 2. Longitudinal section of the otolith of a female *Gadus minutus* measuring 18·8 cm. Four opaque zones and four transparent zones are clearly visible. The 4th transparent zone is at the margin. This is one of the very few of the older fishes in which the 'age rings' could be so clearly discerned in the otolith. ×11·5.

Fig. 3. The transverse section of the above same otolith. ×11·5.

# ADVANCES IN THE PHYSIOLOGY OF PERIPHERAL NERVE

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The last 20 years have seen many advances in our knowledge of the mechanisms responsible for the transmission of impulses in peripheral nerve fibres. This has come about largely through researches on the nerves of marine invertebrates. Much of the work has been done at Plymouth. The purpose of this article is to give some of the reasons why certain features of these nerves, which distinguish them from the nerves of vertebrates, should make them so desirable for experimental work.

The giant nerve fibre of the squid did not come into the limelight until the middle nineteen-thirties, nor did the other smaller single fibres which can be dissected out of the nerve trunks of cuttlefish, crabs and lobsters. Before describing the work with single fibres, we will go further back to about 1926 when, as the result of work by A. Levin at Plymouth, it was realized that the multi-fibred limb nerves of Crustacea were highly suitable for studies of the effect of activity on nerve metabolism.

## Multi-fibred Invertebrate Nerves

For many years it had been believed that in the transmission of nerve impulses no heat is evolved. Until the end of the last century practically all views attributed to nerve a completely passive role in the conduction of an impulse. As recently as 25 years ago the impulse was pictured, in Sir William Bayliss's words, as a 'reversible physico-chemical process, not associated with loss of material on account of metabolic reactions'. However, this was wrong. Heat is set free, but its amount was too small to detect. A. V. Hill finally demonstrated this phenomenon in frog's nerve: but, as he said (in 1932): 'physiological laboratories ought to be built near the sea, or at least within reach of aquaria where delicate marine animals could be stored. The heat production of crab's nerve could have been measured 20 years ago: actually 14 years were wasted before it was measured in frog's nerve.' Whereas, by 1930, it had become possible to measure the heat production following a single impulse in the crab's nerve, in frog's nerve, where much less is produced, 100 impulses are required.

Heat production is only one sign of metabolism. In every aspect the extra metabolism due to stimulation of a crustacean nerve is much greater than it is in the frog's nerve. This superior efficiency of the frog's nerve is evident in

its comparative resistance to fatigue: it can continue to pass impulses at a high frequency for a long time, while the crab's nerve fatigues rapidly. We now understand the reason for this difference. The fibre of a vertebrate nerve possesses a myelin sheath, composed of lipoid material, which in effect 'insulates' the fibre except at the nodes of Ranvier, where the sheath is absent. It has recently been shown that the nervous impulse progresses by 'jumping' from node to node. This means that the active process, which spreads over the whole membrane in the invertebrate non-myelinated fibre, affects only that part of the frog fibre which is free from the myelin covering, so it is only in the region of the nodes that any extra metabolism occurs when the fibre becomes active. The whole of the inter-nodal part of the fibre is a purely passive bridge with quite simple electrical properties, doing no more than enable one node to excite the next. The frog fibre is only 10 $\mu$ across, but the nodes may be 2 mm. apart, so the area of membrane involved in activity is very small. Apart from the greater economy which goes with this ingenious mechanism, there is the added advantage that considerably faster transmission is possible with a given size of fibre.

The two features of invertebrate nerve which the physiologist finds so much to his advantage, namely the high rate of metabolism and the occasional appearance of large fibres, might neither have been found if the myelin sheath had been developed in this type of nerve. One can think of only two possible reasons why the large fibre evolved: first, because a large fibre conducts faster than a small one, and at a higher frequency; secondly, because a large fibre is more resistant to fatigue than a small one, for the surface activity is supported by a relatively larger volume of axoplasm (the name given to the interior substance of a nerve fibre). One advantage of fast transmission is plain enough, reaction times are reduced; but there is another, more subtle, reason which may be suggested. A large muscle mass as, for instance, the mantle muscle of the jet-propelled squid, may have to be synchronously activated in all its parts from one ganglion. Low-velocity fibres would produce a *wave* of contraction, inefficient for propulsion, while high-velocity fibres can be sufficiently graded in size (the larger, faster fibres going to the more distant part of the muscle) to provide a synchronous burst of impulses at all nerve endings in the muscle.

Turning to the question of resistance to fatigue, we now know enough about the actual quantities of ions traversing the active membrane to be able to calculate the extent to which a nerve fibre is 'run down' when an impulse passes along it. The fibre loses some of its internal potassium and gains sodium from the outside when it is stimulated, and it takes many minutes for the original balance to be restored. The nerve can pass 100 impulses per sec. (the giant fibres up to 500 per sec.), but the axoplasm of the smallest fibres does not constitute a sufficient reserve for prolonged activity at high frequency; even after 10–20 sec. perhaps as much as a half of the internal potassium would

be lost from a 1 $\mu$ fibre. However, the very small fibres probably have a sensory function, or at any rate a function which normally requires them to pass but few impulses in a minute, so the axoplasm may well provide an adequate reserve. On the other hand, the muscles of the leg require innervation by nerve fibres which are less prone to fatigue, for they must be capable of passing impulses at high frequency, and bursts of activity may be required in quick succession.

It is not possible to be sure which of these factors has been predominant in the evolution of the larger motor fibres. Both the resistance to fatigue and the higher velocity of transmission could have been achieved by the myelin sheath, but luckily for the physiologist, another and more clumsy solution was found for the invertebrate!

Within the last 15 years advances have been made in our knowledge of the ionic equilibrium which determines the electrical potential across the membrane, and in connexion with the passage of ions across this membrane when the nerve is stimulated. It has been possible, for instance, to measure the amount of potassium which escapes from the fibres of a crustacean nerve when it is stimulated. It is improbable that this could have been done with a frog's nerve, for the ionic currents, being presumably confined to the small areas of membrane around the nodes of Ranvier, would be too small to measure.

There is another sign of activity, easily measured in a non-myelinated nerve trunk, which is so small as to be quite undetectable in a frog's nerve: this is the change in the intensity of light scattered by the nerve when it is stimulated; it is thought to be caused by a minute swelling of the individual nerve fibres.

## Isolated Nerve Fibres

Research with single fibres started about 1935, following J. Z. Young's histological studies of the nerves of Crustacea and Cephalopods. Before describing some of the things which can be done with the giant fibre of the squid, reference will be made to the work with isolated crustacean nerve fibres. The great majority of the fibres of a crustacean nerve trunk, tens of thousands of them, are very small, having diameters between 0·5 and 5 $\mu$; the function of these fibres is not certain, but they are probably mostly connected with sensory endings. In addition to the very small fibres there are larger ones supplying the muscles. These motor fibres are relatively very few, being numbered in tens rather than in thousands, and the largest are 25–80 $\mu$ in diameter. By skilful dissection these large fibres can be isolated singly, they can be manipulated without much difficulty, and will survive and respond to stimulation for many hours in artificial saline solution. A fibre of this sort is not large enough for insertion of a micro-electrode, nor is it suitable for the other purposes which make the squid fibre so useful, such as the chemical analysis of the constituents of the axoplasm. In other words, the single

crustacean fibres can only be operated on by techniques generally used for multi-fibred bundles of nerves. What, then, is gained by using the single fibre? Why would not bundles of smaller fibres—much more easily prepared—serve just as well? Briefly, the answer can be given as follows. The physiology of peripheral nerves has reached a stage where really accurate quantitative facts and figures are required. These cannot be obtained from the multi-fibred preparation, as some examples will show. (i) Inorganic ions cross the membrane of a nerve fibre when it is stimulated: we want to know, accurately, the quantities of ions which pass a unit area of membrane per impulse. These can be measured by radio-active tracers and other methods. The difficulties of doing this accurately with a bundle of fibres are obvious enough. The fibres are of different sizes, one cannot be certain that they are all excitable, and complicated (and approximate) corrections have to be made for diffusion between the inter-fibre spaces and the exterior bulk of the solution. (ii) The electrical resistance and capacity of the nerve membrane must be measured. This can be done accurately only with a single fibre, where all the quantities involved can be determined precisely. (iii) We wish to be able to make a rapid change in the composition of the fluid surrounding the fibre. With fibres in a bundle this is not possible, for diffusion is too slow; the ions or other chemical substances would not enter or leave the inter-fibre spaces sufficiently rapidly. (iv) For certain purposes it is necessary to work with a fibre which is surrounded by only a very small volume of electrolyte solution: to do this the fibre is transferred into paraffin oil. Under such conditions it still conducts, even though the external solution occupies a layer only a few microns thick.

## The Giant Fibre

The mantle muscles of the squid and cuttlefish are supplied by nerve fibres which radiate out from the stellate ganglia. These are the so-called giant fibres. The largest are found in the squid: they may be 500–800 $\mu$ in diameter. By virtue of their large size they allow certain procedures which are not applicable to smaller fibres. An isolated fibre can be cannulated at its cut end, and a thin rod-like electrode (or even a double electrode, consisting of two independent wires wound helically around a fine glass rod) can be inserted through the cannula, and pushed down so far into the interior of the fibre that the active part of the electrode may be some centimetres from the cut end. Surprisingly enough, this operation does not destroy the excitability of the fibre, and it may conduct impulses, and to all intents and purposes be in perfect condition, for many hours after the electrode has been inserted.

The reason for wanting an internal electrode can be explained as follows. In the unstimulated fibre there is a potential difference across the membrane amounting to about 50 mV. This is known as the 'resting potential' and is in the sense of the interior of the fibre being negative with respect to the outside.

In a multi-fibred nerve trunk, or in a small fibre, the resting potential cannot be measured accurately, because it is difficult to make electrical connexion with the axoplasm in the intact part of the fibre which is conducting the impulse. The best that can be done is to make connexion with the axoplasm at the ends of the fibre: this is achieved by some form of chemical or mechanical injury to the ends, which has the effect of breaking down the electrical resistance of the membrane, thus allowing more or less direct connexion with the inside. But, owing to short circuits, one can only tap off a rather unknown fraction of the true membrane potential in this way. The insertion of an electrode into the inside of a giant fibre is a means of overcoming the difficulty; one can then record the full potential, either at rest or during the passage of an impulse. Leading off from the *outside* of the fibre is easily achieved; all that is needed is an electrode in the conducting electrolyte solution in which the active part of the fibre is bathed. An amplifier and cathode-ray tube are used for recording the membrane potential.

The earliest experiments with the internal electrode led to a rather surprising discovery. It had always been tacitly assumed that activity simply involved a transitory disappearance of the resting potential. Recordings made with external electrodes were not sufficiently reliable for this assumption to be seriously challenged. Experiments with the internal electrode showed that the membrane potential actually *reverses* its sign as the impulse passes. Further experiments have suggested that the reversal is caused by a large increase in the permeability of the membrane to sodium ions. The concentration of sodium ions in the axoplasm is very low, so there is a gradient tending to drive them in from the outside, and the negatively charged interior of the resting fibre also tends to draw in the positively charged sodium ions. A sudden breakdown in the barrier will allow sodium ions to rush in, the membrane potential will fall as the negative charge inside is satisfied by the positive sodium ions, and if the permeability becomes high enough, and the increase is preferentially in favour of sodium, the potential will actually reverse—but one gets into rather deep water here in attempting to explain it. At all events, there is now good support for the view that the action potential is primarily due to a sudden inrush of sodium. To elucidate this matter further, A. L. Hodgkin, A. F. Huxley and B. Katz have used a double internal electrode, one wire of which forces the membrane potential to change in a prescribed manner—it constrains the membrane, as it were, to pass through an abnormal action potential cycle—and the other wire records the current which flows across the membrane as the result of this. The problem, both from the technical and theoretical aspects, has become rather complicated; the findings have not yet been published.

Another facility is afforded by the large size of the squid fibre. The volume of the axoplasm is sufficient to allow analysis of its constituents. The quantities of the various inorganic ions can be estimated, the identities and amounts of the internal amino-acids, which play a part in maintaining the ionic balance,

can also be determined. The axoplasm is squeezed out of the fibre for such analyses. It is found to be of a jelly-like consistency, and other than straight chemical tests can be made: for instance, it is found that the addition of a small quantity of calcium to the solution into which the axoplasm is extruded will cause rapid solution of the jelly. Electron microscopy of the axoplasm has revealed elongated filaments showing fine striations.

A major problem which has to be faced by anyone who embarks on research with the giant squid fibre is that of obtaining living squid. With all the resources of the laboratory at Plymouth, and although squid are plentiful in the sea at most seasons of the year, the conditions are such that a specimen which is capable of living for more than 12 hr. in the laboratory tanks is a rarity. The cuttlefish is a hardier animal and will live for a long period in captivity. Unfortunately, its nerve fibres are not so large as those of the squid, being only about 150$\mu$ in diameter, and no one has attempted to insert an internal electrode through the cut end of such a fibre. However, they are large enough to possess one advantage over the crustacean fibres because the volume of a single fibre, perhaps 4 cm. long, is just great enough to allow quantitative analysis of its constituents, and an attempt has recently been made to measure the amount of sodium which enters the fibre as the result of activity. Radioactive tracers can be used to follow movements of ions through the membrane, both at rest and when it is stimulated: it is true that this is possible also with the smaller crustacean fibres, but the improvement in accuracy which goes with the use of a larger fibre makes the cuttlefish especially valuable for such purposes.

## Conclusion

It should be clear why the nerves of marine animals are much sought after. There is no reason to suppose that, in essential details, the changes in the membrane of the non-myelinated fibre which occur in activity do not also take place at the nodes of Ranvier in a myelinated nerve. The saltatory progression of the impulse in the myelinated nerve is due to a mechanism which should probably be considered as an added, and not very mysterious, refinement. The electrical excitation of one node by another is thought to involve essentially the same process as is found in non-myelinated nerve, by which one part of the membrane is excited by an adjacent one. The vital 'explosive' change at the membrane forms the subject of the most intriguing current research on peripheral nerve, and as it may be predicted that this change, if it is ultimately sufficiently understood, will be found to be fundamentally the same in both types of nerve, one may conclude that much has been learned about vertebrate nerves by studying those of invertebrates.

# NOTES ON THE PLYMOUTH MARINE FAUNA

## AMPHIPODA

By G. M. Spooner

The marine Amphipoda of the Plymouth area, as a group, were last given attention in the middle 1930's by Crawford (1936, 1937). Renewed investigation after the lapse of 15 years has indicated that knowledge of species present was by no means complete, or that some changes have occurred in the interval, or both. In a recent survey of the amphipod fauna of the Isle of Man, Jones (1948) found no indication of the existence of undescribed species, nor even of known species previously unrecorded from Britain. The experience at Plymouth has been quite the reverse.

I am grateful to Mr M. D. Menon and to Dr H. W. Chang for giving me the chance of examining amphipods from the stomachs of *Gadus minutus* L.* and *Callionymus lyra* L. respectively. The use of bottom-living fish as a method of collecting amphipods has much to commend it, as records will testify.

The genera *Gammarus*, *Marinogammarus*, and *Corophium* are not included, being reserved for separate treatment. An asterisk indicates that the species have not hitherto appeared in a list of the Plymouth marine fauna (Marine Biol. Assoc., 1931, supplemented by Crawford, 1936).

Additions to the fauna show a notable balance of species which occur to the southward or in warmer waters. Taken together the evidence provided for a certain northward spread of the fauna cannot be ignored.

### Family **Lysianassidae**

PERRIERELLA AUDOUINIANA (Bate)

Plymouth; dredgings from Asia Shoal, 2. vi. 49, ♀♀.

LYSIANASSA CERATINA (A. Walker)

Wembury Point, L.W. sievings.

*SOCARNOPSIS CRENULATA Chevreux [Chevreux, 1910, pp. 165–9, fig. 2; Chevreux & Fage, 1925, pp. 48–50, figs. 31, 32]

One ♀ amongst small sample of bottom fauna of L4, 3. vi. 49; length 9 mm., as against maximum of 7 mm. given by Chevreux & Fage. Genus and species new for Britain: previous northerly limit was Brittany.

TRYPHOSA SARSI Bonnier

Salcombe; Castle Rocks, L.W. sievings, 12. v. 49, ♀♀.

* See Menon, 1950: this *Journal* pp. 186–198.

ORCHOMENE HUMILIS (A. Costa) (=*batei* Sars)
Salcombe; Castle Rocks, L.W. sievings, 12. v. 49, ♀.

ORCHOMENELLA NANA (Kröyer)
Wembury Point, L.W. sievings. Stomachs of *Gadus minutus*, June 1948, ♂♀♀.

### Family **Ampeliscidae**

AMPELISCA SPINIPES Boeck
Regularly in stomachs of *Gadus minutus* from the trawling grounds, including large specimens up to 18 mm. long. Present at station L4 and in the Mewstone shell gravel.

AMPELISCA DIADEMA (A. Costa)
Frequent in stomachs of *Gadus minutus*, 1948.

AMPELISCA TENUICORNIS Lillj.
A few in stomachs of *Gadus minutus* 1948, more freely in *Callionymus lyra* 1949.

AMPELISCA BREVICORNIS (A. Costa) (=*laevigata* Sars)
Two adults from stomachs of *Gadus minutus*, 1948.

*AMPELISCA sp. (allied to *brevicornis*)
Stomachs of *Gadus minutus*, 2♂♂, 1 juv., June 1948.
An apparently undescribed species, most closely related to *A. brevicornis*, which it resembles in the form of pp. 7, in the form of pp. 3, and in the shape of the head. It differs notably in the more feeble invagination at the posterior corner of epimeron 3, in the presence of a raised hump dorsally on the anterior half of urosome segment 1, in the ciliation of uropod 3, and small differences in antenna 1.

### Family **Haustoriidae**

HAUSTORIUS ARENARIUS (Slabber)
Salcombe; Mill Bay, several in the sand in the lower part of the tidal zone, 17. iii. 49. Formerly not found in the Salcombe Estuary, and its presence at Mill Bay doubtless the result of the accumulation here of sand described by Wilson (1949). Otherwise recorded only from Whitsand Bay.

UROTHOË ELEGANS Bate
One in stomach of *Gadus minutus*.

### Family **Phoxocephalidae**

HARPINIA ANTENNARIA Meinert
Rame Mud, 12. vii. 39 (M. Mare), three from a grab haul.

### Family **Amphilochidae**

AMPHILOCHUS NEAPOLITANUS Della Valle
Salcombe, Castle Rocks, 12. v. 49, 3♀♀ breeding.

## Family **Leucothoidae**

LEUCOTHOË SPINICARPA (Abildg.)

From cavities in the sponge *Desmacidon*, Mewstone grounds; from amongst hydroids and sponges from Plymouth Sound; etc. One in a stomach of *Gadus minutus*.

*LEUCOTHOË sp. (allied to *L. richiardi* Lessona)

From stomachs of *Gadus minutus*, two in June 1948, one in Nov. 1948. Two of the specimens are undamaged. This species differs from *L. spinicarpa* in its posteriorly incised epimeron 3, and in its weaker gnathopod 1 dactyl which is only one third the length of the propod. It is possibly identical with the Mediterranean species *L. richiardi*, of which Della Valle (1893) gives a description and figures. Alternatively, it may be the undescribed species discovered by Crawford in *Chaetopterus* tubes (Crawford, 1936, p. 102).

LEUCOTHOË LILLJEBORGI Boeck

Rame Mud; 12. vii. 39 (M. Mare), four specimens in grab sample.

## Family **Stenothoidae**

STENOTHOË MONOCULOIDES (Mont.)

From sievings of stones and rocks near L.W. below the Laboratory, at Rum Bay, Wembury Point and at Salcombe Castle Rocks, ♀♀.

*STENOTHOË sp. (allied to *monoculoides* and *spinimana*)

A number of ♀♀, many breeding, from among hydroids collected in Mill Bay Docks, 7. vi. 49. Others from hydroids on raft near Breakwater, end March 1950.

This is apparently a distinct species, somewhat intermediate between *S. monoculoides* and the south-european *S. spinimana* Chevreux (Chevreux & Fage, 1925, pp. 134–5, fig. 133), but reaching a slightly larger size than either. The gnathopods I and II agree with those described for *S. spinimana*, and so provide a good distinction from *S. monoculoides*. There are four spines laterally on uropod 3 peduncle, and the number of antennal segments is intermediate between the two species mentioned. The telson, however, is unarmed, and in certain other respects the resemblance is to *monoculoides* rather than to *spinimana*.

The colour pattern was noted as follows: body translucent, especially the urosome; middle of body with broken dark lines between the segments round which orange patches develop; other irregular orange patches on side plates; eye carmine.

*STENOTHOË VALIDA Dana [Chevreux & Fage, 1925, pp. 137–8, fig. 137]

♂ and ♀ (with eggs) from hydroids collected in Mill Bay Docks, 7. vi. 49, in company with the foregoing. Further ♂♂♀♀ from hydroids on raft near

Breakwater, end March 1950. A large species for a *Stenothoë*, with distinctive characters. Wide-spread in warm waters and known from the south of France. The colour pattern was noted as follows: body translucent, with scattered reddish orange and orange marks; a large red-orange mark on the urosome providing a striking feature.

### Family **Phliasidae**

PEREIONOTUS TESTUDO (Mont.)

Wembury Point, from sievings of stones and weeds near L.W., 12. iv. 49, five specimens. Again 18. iii. 50, four specimens from pools above L.W.N. In the laboratory they were observed to browse on living fucoid fronds, scraping small patches off the surface. A curious species, seldom encountered: formerly taken at Salcombe by Norman.

### Family **Acanthonozomidae**

PANOPLOEA MINUTA (G. O. Sars)

Two in stomachs of *Gadus minutus*, 1948.

PANOPLOEA EBLANAE (Bate)

Rame grounds, ♀ from side of trawl, 8. iv. 49.

IPHIMEDIA OBESA Rathke

A few in stomachs of *Gadus minutus*, 1948.

### Family **Oedicerosidae**

*MONOCULODES sp. (? TESSALATUS Schneider)

From stomach of *Gadus minutus*, July 1948, one. Differs from other European species, except *M. tessalatus*, in the proportions of the gnathopod segments. If indeed this be *tessalatus*, which is a northern species, it has not previously been found so far south.

### Family **Calliopiidae**

APHERUSA BISPINOSA (Bate)

Salcombe, Castle Rocks, L.W. sievings, 12. v. 49, abundant, ♀♀ greatly in excess of ♂♂.

APHERUSA OVALIPES Norman & Scott

One of the principal species in stomachs of *Gadus minutus*, particularly in June and July.

*APHERUSA HENNEGUYI Chev. & Fage [Chevreux & Fage, 1925, pp. 180–1, figs. 185, 186]

Regularly in the stomachs of *Gadus minutus*, 1948, though less numerous than the above (about sixty-five specimens seen). Present also in a small sample of the ground fauna at station L4 on 3. vi. 49.

Known originally to Chevreux & Fage from only one locality (160 m., S.W. of Belle-Isle), this species has not previously been recognised in British waters. In view of Crawford's investigation (1937) on bottom-living amphipods, it is difficult to escape the conclusion that the species has spread into the Plymouth area but recently.

APHERUSA CIRRUS (Bate) (=*borealis* Sars)

A few in L.W. sievings among rocks at Wembury Point and Salcombe Castle. A uniform rose-pink colour seems distinctive.

*CALLIOPIUS LAEVIUSCULUS (Kröyer)

Salcombe, Castle Rocks, L.W. sievings, 12. v. 49, one. Known from localities in Cornwall, N. Devon, and occurrence in the Plymouth area to be anticipated (Crawford, 1936, p. 101).

The characters agree with Sars's figures of *C. rathkei*, which is assumed to be synonymous (following Stephensen).

## Family **Melphidippidae**

MELPHIDIPPELLA MACRA (Norman)

From stomach of *Gadus minutus*, 3. vi. 49, ♀.

## Family **Gammaridae**

*CHEIROCRATUS ASSIMILIS Lillj. [Chevreux & Fage, 1925, p. 225, fig. 235]

One ♂ from stomach of *Gadus minutus*, July 1948.

PHERUSA FUCICOLA Leach

Freely under stones, etc., near L.W., Plymouth (Rum Bay), Wembury Point, and Salcombe. Salstone, one ♂.

*MELITA HERGENSIS Reid

A characteristic species on the shore under stones, etc., in L.W. region, where it replaces *M. palmata* (Montagu). At once recognized in the field by its blue-grey colouring, broken only by white bands on the limbs which show up on closer inspection.

First taken at the mouth of the Yealm, near L.W., 3. viii. 38, when recognized as a distinct species. Independently Reid (1939) described the species, having taken it from Wembury Bay.

Amongst specimens from various parts of the coast identified by Reid in the British Museum were some from Salcombe and Polperro (Norman collection).

It has since been found freely at Rum Bay, Mt. Edgcumbe, Wembury Point, and Salcombe Castle Rocks.

Some former records of *M. palmata*, especially from the sub-littoral zones, may be expected to belong to *M. hergensis*.

MELITA GLADIOSA Bate

Salcombe, Castle Rocks, 12. v. 49, adult ♂.

MELITA PELLUCIDA G. O. Sars

Tamar Estuary, in reed bed near Cotehele, 10. iii. 48, about forty. Also obtained in the Helford River, W. Cornwall, at the head of Frenchman's Creek, Sept. 1949.

## Family **Dexaminidae**

DEXAMINE THEA Boeck

Salcombe estuary, at Castle Rocks and the Salstone, May 1949, ♀♀ and juv., accompanying *D. spinosa* (Mont.), amongst weeds.

## Family **Aoridae**

AORA TYPICA Kröyer

Salstone, 13. v. 49, both sexes freely, sieved from weeds near L.W.

MICRODEUTOPUS CHELIFER (Bate)

Wembury Point, 12. iv. 49, sieved from weeds, breeding.
Salcombe, Castle Rocks, 12. v. 49, ♀.

MICRODEUTOPUS DAMNONIENSIS (Bate) [=*propinquus* Sars]

Salstone, sieved from weeds at L.W., ♂♂♀♀.

From examining ♂♂ of different sizes it is clear that the species recognized by Chevreux & Fage (1925) as Bate's *damnoniensis* is identical with the species figured and described by Sars (originally as *propinquus*). Chevreux & Fage, however, cannot have seen fully mature specimens in which the secondary tooth on the carpus of gnathopod 1 had developed. The gnathopod 1 figured by them (fig. 308) is correct for younger ♂♂, while the form shown in Sars's (1895) pl. 192, fig. 1 refers to the larger and older. The species key given in Chevreux & Fage (pp. 294–5) therefore requires modification.

## Family **Photidae**

MICROPROTOPUS MACULATUS Norman

Salstone 13. v. 49, ♂♂♀♀ breeding.

EURYSTHEUS MACULATUS (Johnston)

Stomachs of *Gadus minutus* in June 1948. Salcombe, Castle Rocks, 12. v. 49, 2♀♀.

PODOCEROPSIS SOPHIAE Boeck

Bottom fauna of L 4, 3. vi. 49, ♂. Stomachs of *Gadus minutus*, in June 1948.

LEPTOCHEIRUS PILOSUS Zaddach

River Tamar, Cothele Ferry, 28. ii. 48, a number of juv. amongst stolons at *Cordylophora lacustris*. Also obtained in the Helford River, W. Cornwall, at head of Frenchman's Creek, Sept. 1949.

### Family **Amphithoidae**

AMPHITHOË VAILLANTI Lucas

Plymouth Sound: dredgings from Asia Shoal, 2. vi. 49, ♂♂♀♀.

### Family **Podoceridae**

PODOCERUS VARIEGATUS Leach

Salcombe, Castle Rocks, sievings at L.W., 12. v. 49, several ♂♂♀♀.

### Family **Caprellidae**

PHTISICA MARINA Slabber

In plenty in stomachs of *Gadus minutus*, 1948, especially in July. Also in stomachs of *Callionymus lyra*, 1949.

Salcombe, Castle Rocks, L.W., one; Salstone, L.W., a few, 13. v. 49.

PSEUDOPROTELLA PHASMA (Mont.)

A few in stomachs of *Gadus minutus* with the above.

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## PISCES

By G. A. Steven

Some records are given of fishes, occasional or rare in the area, recently caught in the western part of the English Channel. The nomenclature is that used in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931) based on Duncker, Ehrenbaum, Kyle, Mohr and Schnakenbeck's list in *Die Tierwelt der Nord- und Ostsee* (1925–29). An asterisk indicates species that do not appear in the *Plymouth Marine Fauna*.

### Family **Trygonidae**

TRYGON PASTINACA (L.)

One female in trawl on 18. xi. 49 in position Start Point bearing 270°, distant 8 miles.

### Family **Myliobatidae**

MYLIOBATIS AQUILA (L.)

One female in trawl on 6. xii. 49 in position Eddystone bearing 115°, distant 6 miles.

### Family **Balistidae**

BALISTES CAPRISCUS Gmelin

One caught in lobster store-pot in Fowey Harbour on 8. ix. 49. The pot had been emptied of lobsters the day before and put back in the water with the door open.

### Family **Tetrodontidae**

*TETRODON LAGOCEPHALUS L.

One specimen caught by hand in shallow water in Mousehole Harbour (Cornwall) on 21. x. 49. The fish was alive but swimming very feebly and was being attacked by seagulls.

### Family **Gadidae**

RANICEPS RANINUS (L.)

One in Agassiz trawl off Plymouth 26. x. 49.

### Family **Carangidae**

NAUCRATES DUCTOR (L.)

One in mackerel drift net in position Carn Dhu Point (Cornwall) bearing 010°, distant 24 miles, on 1. vi. 49.

### Family **Serranidae**

SERRANUS CABRILLA L.

Five specimens in trawl in position Eddystone bearing 315°, distant 40 miles, on 6. x. 49. One was brought back alive and is still living in the laboratory aquarium.

### Family **Sparidae**

CANTHARUS LINEATUS (Montagu)

One in otter trawl off Plymouth on 1. xii. 49. This fish, though rare in the Plymouth area, is not infrequently landed at Newlyn in trawled catches from deeper water on the western fishing grounds.

### Family **Scombridae**

EUTHYNNUS PELAMYS (L.)

One specimen, 17 in. long and $2\frac{3}{4}$ lb. weight, caught on 15. ix. 49 in a fixed net in Plymouth Sound.

*SARDA PELAMYS Brünnich

One specimen 20·5 cm. in length caught in Whitsand Bay on 30. ix. 49; another (31·5 cm.) in a pilchard drift net off Rame Head on 23. xi. 49; a third, off Plymouth, also in a pilchard drift net, on 6. xii. 49.

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# NOTES ON THE PLYMOUTH MARINE FLORA

## ALGAL RECORDS FOR THE PLYMOUTH REGION

By Mary Parke

The greater number of the species given in this list are new records for the Plymouth region. Recent records for some rare species have also been included.

### MYXOPHYCEAE

#### Family **Chamaesiphonaceae**

XENOCOCCUS SCHOUSBOEI Thuret

Wembury, Plymouth; on *Enteromorpha* at M.H.W.N.T.; gonidia in March.

#### Family **Oscillatoriaceae**

PLECTONEMA BATTERSII Gomont

Plymouth; M.H.W.N.T. zone on rock; March.

### CHLOROPHYCEAE

#### Family **Chlamydomonadaceae**

BRACHIOMONAS SUBMARINA Bohlin

Rame Head; in small pool above E.H.W.S.T.; July.

#### Family **Polyblepharidaceae**

PYRAMIMONAS GROSSII Parke

In inshore waters off Plymouth during all months of the year.

#### Family **Chlorodendraceae**

PRASINOCLADUS LUBRICUS Kuckuck

Salcombe, Yealm, Wembury, Plymouth, Looe: M.H.W.N.T. downwards; frequent on stones in pools and on the edges of pools or holes in the rock, also found on shells dredged from 4 m. below M.L.W.S.T.; most frequent in winter and spring but can be found throughout the year; zoosporangia at all times of the year. Recorded from Plymouth (Batters, 1900), Isle of Man (Parke, 1933), Blackpool and Millport (Fritsch, 1949).

#### Family **Chaetophoraceae**

BOLBOCOLEON PILIFERUM Pringsheim

Wembury: growing on the frond of *Laminaria digitata*; zoosporangia in March.

EPICLADIA FLUSTRAE Reinke

Salcombe, Wembury, Plymouth, Looe: in *Dynamena pumila* growing on *Fucus serratus*; zoosporangia in spring and summer; the form with longer, more slender filaments (var. *phillipsii* of Batters) is usually found in *Alcyonidium hirsutum* growing on *Chondrus crispus* at E.L.W.S.T.; zoosporangia in March.

## PHAEOPHYCEAE

### Family **Ectocarpaceae**

GIFFORDIA SANDRIANA (Zanard.) Hamel

Plymouth; on raft near breakwater and in tanks at the Plymouth laboratory; unilocular and plurilocular sporangia in spring and summer.

### Family **Acinetosporaceae**

HAPLOSPORA GLOBOSA Kjellman

Plymouth; growing on ropes hanging down from raft near the breakwater; monosporangia in May.

### Family **Myrionemataceae**

ENDODICTYON INFESTANS Gran

Wembury; in *Alcyonidium hirsutum* growing on *Chondrus crispus* at E.L.W.S.T.; plurilocular sporangia in March.

ASCOCYCLUS SPHAEROPHORUS Sauvageau

Wembury; on the fronds of *Laminaria saccharina* growing at M.L.W.S.T.; unilocular sporangia in August. Recorded previously from Sidmouth.

### Family **Corynophlaeaceae**

CORYNOPHLAEA CRISPA (Harv.) Kuckuck

Looe; on *Chondrus crispus* at M.L.W.N.T.; unilocular sporangia in June and July.

### Family **Chordariaceae**

CASTAGNEA ZOSTERAE Thuret

Looe; on *Zostera* at M.L.W.S.T.; unilocular sporangia in July.

MESOGLOIA LANOSA Crouan

River Yealm; on sandy ground 1–2 m. below M.L.W.S.T.; unilocular sporangia in July.

MYRIOCLADIA LOVENII J. Agardh. (?)

Plymouth; on shells and small stones at a depth of 8–10 m. below M.L.W.S.T.; found only from late June to August; unilocular sporangia July and August. The material from Plymouth Sound agrees very closely with the description of

Agardh's Swedish material, but according to Kylin (1933) the plant found on the British coast is not the same as that found on the west coast of Sweden. The British plant may, therefore, have to be placed in a new species.

### Family **Stictyosiphonaceae**

STICTYOSIPHON SORIFERUS (Reinke) Rosenvinge

Plymouth; on shells 6–10 m. below M.L.W.S.T.; plurilocular sporangia in July.

### Family **Striariaceae**

MYRIOTRICHIA REPENS (Hauck) Karsakoff

Looe: on *Stilophora rhizodes* and *Scytosiphon lomentaria* at M.L.W.S.T.; plurilocular sporangia in July. Recorded previously from Wembury.

MYRIOTRICHIA DENSA Batters

Looe; on *Zostera* at M.L.W.S.T.; unilocular and plurilocular sporangia in July and August. Recorded for River Yealm in 1896.

### Family **Sphacelariaceae**

SPHACELARIA FURCIGERA Kützing

Looe: on *Cystoseira ericoides* at M.L.W.S.T.; propagules in July.

### Family **Sporochnaceae**

CARPOMITRA COSTATA (Stackhouse) Batters

Eddystone; trawled within 3-mile radius from a depth of 40–50 m. growing with *Dictyopteris membranacea*; unilocular sporangia in August and September. Recorded as growing in Plymouth Sound from 1870–1900, but it has not been obtained from this locality in recent years.

### Family **Desmarestiaceae**

DESMARESTIA DUDRESNAYI Lamouroux

Eddystone; one young plant trawled within three-mile radius from a depth of 40–50 m. Previous records from this locality 1894–96.

### Family **Laminariaceae**

LAMINARIA OCHROLEUCA De la Pylaie

Plymouth; on rock from M.L.W.S.T. down to depth of 8 m.; fertile from April to November–December. See Spooner, p. 261, for further records.

## RHODOPHYCEAE

### *Protoflorideae*

### Family **Erythropeltidaceae**

ERYTHROPELTIS DISCIGERA (Berth.) Schmitz var. FLUSTRAE Batters

Lannacombe, Wembury, Plymouth; on *Plumularia*, *Flustra* and *Alcyonidium* from M.L.W.S.T. downwards; gonidia in February and March.

### *Florideae*

### Family **Chantransiaceae**

ACROCHAETIUM ENDOZOICUM (Darbyshire) Batters

Wembury; in *Alcyonidium hirsutum* growing on *Chondrus crispus* at M.L.W.S.T.; monosporangia in March.

### Family **Naccariaceae**

ATRACTOPHORA HYPNOIDES Crouan

Plymouth; on shells at a depth of 8–12 m. below M.L.W.S.T. growing with *Dudresnaya verticillata*, *Stenogramma interruptum* and *Spondylothamnion multifidum*; cystocarpia in July. Recorded previously from Exmouth.

### Family **Grateloupiaceae**

GRATELOUPIA MINIMA Crouan

Dr M. A. Westbrook (Mrs D. P. Wilson) supplies the following. Only previous records Ilfracombe and Torquay (Batters, 1900). Wembury, Church reefs, February 1932; Mewstone reefs, September 1932. Gregarious on the edges of flat stones in shallow pools at L.W.S.T. The tiny plants resembled a mat of sporelings, in colour reddish brown rather than the violet-purple described by Newton (1931); they were unbranched excepting for an occasional dichotomizing tip. The internal structure resembled that of *G. filicina*. Most of the older parts of the February plants were covered with young tetrasporangia.

### Family **Squamariaceae**

PEYSSONNELIA ATROPURPUREA Crouan

Wembury; on rock under ledges at E.L.W.S.T.; tetrasporangia in May.

### Family **Corallinaceae**

LITHOPHYLLUM HAPALIDIOIDES (Crouan) Heydr. var. *confinis* Foslie

Wembury; M.T.–L.W.N.T. on rock.

### Family **Gigartinaceae**

GIGARTINA TEEDII Lamouroux

Salcombe; on mud-covered rocks at E.L.W.S.T. Recorded from Torbay area 1811–88.

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## ADDITIONAL RECORDS OF *LAMINARIA OCHROLEUCA* DE LA PYLAIE

By G. M. Spooner

(Plate I)

*Laminaria ochroleuca* De la Pylaie was recently added to the British flora by Dr Mary Parke (1948), who found it to occur freely in the sheltered parts of Plymouth Sound. It had first come to notice in 1946 and is possibly quite a recent introduction to the country, though it may have escaped notice for some years. The species can now be recorded from two other localities: Salcombe Estuary (South Devon), and Helford River (West Cornwall).

> Salcombe, west side of the estuary, first observed 13 April 1949, a few plants round Woodville Rocks, in an area where all four *Laminaria* species and *Sacchoriza bulbosa* De la Pylaie occurred together in the L.W.S. region. Later, on 12 May, a continuous bed observed, exposed at extreme low water, on the north side of Fort Charles Rocks.
>
> Helford River, north shore at level of E. Calamansack, a few single stunted *Laminaria* plants below E.L.W.S., amongst which was one *L. ochroleuca* (the remainder *L. saccharina* Lamour.) 25 September 1949.

Both the new localities happen to be in estuaries, but in neither of the habitats in which the weeds were found can the influence of fresh water be regarded as appreciable. The fauna of each habitat includes echinoderms (at the Helford River site, large examples of *Marthasterias glacialis* (L.) occurred). It is possibly the relative shelter obtainable in these narrow inlets of the sea that is advantageous to this *Laminaria*.

In the early spring of 1949, after an unusually mild winter, there was a rich growth of various littoral brown algae. An extensive bed of *L. ochroleuca* in Rum Bay, Plymouth Sound, was well exposed by the −2 ft. tide of 16 March, and the zonation relative to *L. digitata* Lamour. well demonstrated. The two zones could be seen mixing and the populations overlapping at about M.L.W.S.

level. On the other hand, not a trace of the species could be detected on the reefs off Wembury Point, where *L. cloustoni* Edm. occupies a long stretch of shore in the region of E.L.W.S. and below. Wembury Bay is decidedly more exposed to wave action than is much of the shore inside Plymouth Sound, and a particular instance of extensive destruction of brown algae occurred during a southerly gale on 3 April 1949, as a result of which, many tons of weed were deposited in the upper tidal zone.

Further evidence was thus obtained that *L. ochroleuca* occupies the same bathymetric levels as *L. cloustoni*, which, on the south coast of Devon and Cornwall, it may tend to replace in sheltered habitats. That these two species are in active competition for the same ground where there is moderate shelter seems a fair deduction, and continued observation is desirable to show how far equilibrium between the two species has been reached.

The photograph in Pl. I, taken by Dr D. P. Wilson at Salcombe, serves to show the main features by which *L. ochroleuca* is distinguished in the field from its nearest ally, *L. digitata*.

## REFERENCE

PARKE, MARY, 1948. *Laminaria ochroleuca* De la Pylaie growing on the coast of Britain. *Nature*, Vol. 162, p. 295.

## EXPLANATION OF PLATE I

A plant of *Laminaria ochroleuca* (centre) growing amongst other oar-weeds, Salcombe, May 1949. A plant of *L. digitata* lies behind it with its stipe on the left side, showing the characteristic prostrate habit when left exposed on the shore. Several fronds of *L. saccharina* also lie prostrate. In the *L. ochroleuca* plant the stiffer stipe is semi-erect and the pronounced pale colouring of the base of the frond is well indicated.

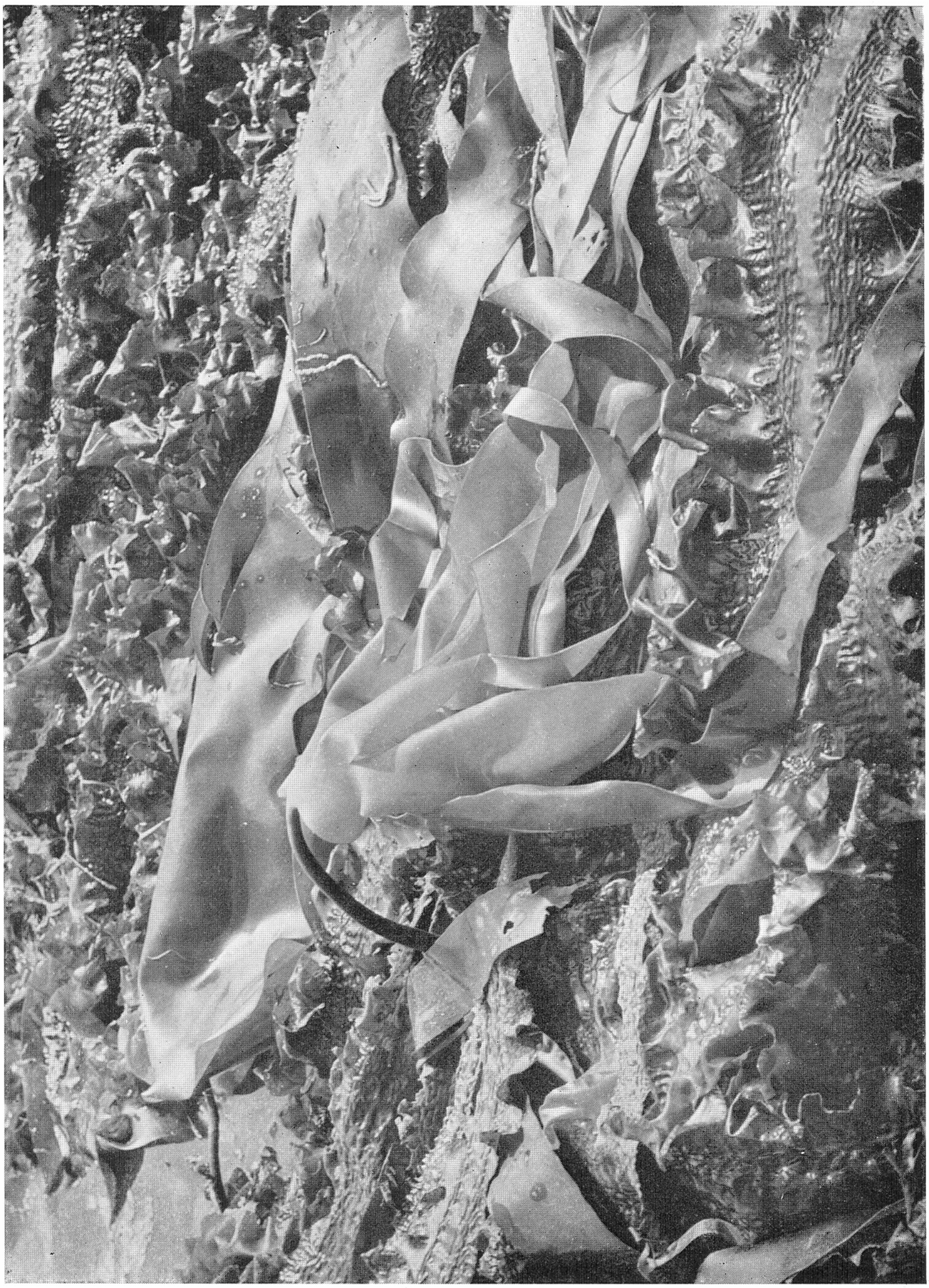

*Photo by D. P. Wilson*

# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### RICERCHE SU *ASTERINA GIBBOSA* (PENN.). I. LA MIGRAZIONE DELLE GONADI. II. L'ERMAFRODITISMO IN UNO POPOLAZIONE DI PLYMOUTH

By Guido Bacci

*Arch. Zool. Ital.*, Vol. XXXIV, 1949, pp. 23–29, 47–74.

The gonads of *Asterina gibbosa*, in individuals with an arm length of 3 mm., the smallest sizes examined, are still found in the aboral region. During subsequent growth, they turn along the internal walls of the interradial zones until they reach the vicinity of the mouth in the oral position. When this definitive position is reached (in individuals with an arm length of 9 mm. in the Plymouth *Asterina*) the genital pores open.

The great difference in the embryological processes by which analogous conditions are reached in ophiuroids is emphasized.

*A. gibbosa* is represented by an Atlantic race which has only hermaphrodite individuals and a Mediterranean race which has partly hermaphrodite and partly gonochoristic individuals (Cuenot). In the present work the problems of sex-differentiation and of sex-determination in a wholly hermaphrodite population occurring in the waters of Plymouth Sound are examined both by morphological and statistical methods.

Morphological study of the gonad development has given the following results: (i) the gonads appear ambisexual from a very early stage; (ii) the maturation of the male always precedes that of the female elements which continue their growth during the male phase; (iii) individual differences can be observed in this relative rate of maturation of the male and female elements; (iv) ripe sexual elements left in the gonad after spawning are destroyed by amoebocytes; (v) vesicular tissue formations appear in the gonad both of the male and of the female after spawning; (vi) germinal elements of the ripe gonads in the female phase are represented by female germ cells only; (vii) the absence, during the reproductive period, of transition stages between gonads in the male and in female phases shows that the change from the male to the female phase takes place between successive spawning periods.

A statistical analysis of the sexual phases in the population gives the following results: (i) all the individuals of the population are protandric hermaphrodites; (ii) sex reversal takes place in individuals having an arm length between 9 and 16 mm.; (iii) the maximum rate of change is found to occur in individuals having a size which more or less corresponds to that attained when the males and females are in equal numbers.

The necessity of dividing the study of sex in its morphophysiological (differentiation) and genetical (determination) aspects is emphasized; the existence among Metazoa of species with totally phenotypical sex-determination is considered doubtful.

On the ground of preceding statistical research (Bacci, 1947) and of the results on *Asterina* two main categories in the sex determination of hermaphrodites may be defined. In the first one (*Patella* type) the action of sex factors is exercised with an unequal intensity among the different individuals of a population. In the second (Plymouth *Asterina* type), sexual factors are in a condition of approximate balance among the different individuals of the population. While in the first category sex determination is probably due to multiple factors, in the second, sex determination is certainly due to a gene mechanism. As far as sex differentiation is concerned three principal conditions are considered in hermaphrodite animals. In the first (false gonochorists) each sexual phase contains elements of only one type. In the second, heterologous elements coexist in the same phase but never reach maturation at the same time. In the third, the heterologous elements reach maturity in the same period so that even autofecundity is made possible. For the species of the first two categories of differentiation the following principle is considered to be general. In hermaphrodite animals with distinct sexual phases sex change takes place during the period of sexual rest. G.B.

## Some New Myxosporidia from Plymouth with a Proposed New Classification of the Order

Yogendra R. Tripathi

*Parasitology*, Vol. 39, 1948, pp. 110–18

Four new species of Myxosporidia are described from fishes at Plymouth, *Sinuolinea rebae* n.sp. from the urinary bladder of *Solea solea*, *Leptotheca vikrami* n.sp. from the gall bladder of *Zeus faber*, *Zschokkella russelli* n.sp. from the gall bladder of *Gaidropsarus tricirratus*, and *Ciliata mustela* and *Zschokkella sturionis* from the gall bladder of *Acipenser sturio*. This is the first record of amyxosporidian from a chondrostean. An attempt has been made to standardize the terminology used in describing the spores. The terms as used by Kudo (1920) are adopted because they are well defined and used by many other authors. A new classification is proposed, based on the form of the spores, and an emended definition of the genus *Leptotheca* is given. Y.R.T.

## The Function of the Giant Axon of *Myxicola infundibulum* Montagu

By J. A. C. Nicol

*Can. Journ. Research*, D, Vol. 26, pp. 212–22.

The giant axon of *Myxicola infundibulum* runs throughout the nerve cord and gives off peripheral branches to the longitudinal muscles. Movements of the animal are quick synergic contractions of the whole body and slower metachronous locomotory movements. Injury to the giant axon without interrupting the rest of the nerve cord blocks the passage of the quick contraction but not of slower locomotory waves. It is concluded that the quick end-to-end shortening is intermediated by the giant axon and that slow waves of locomotion depend upon transmission through short segmentally linked neurones. Traction of one segment on another is not effective in transmitting either type of movement. The giant fibre response is of an all-or-none nature. Repetitive stimuli lead to summation of muscular contractions. The axon conducts in either direction during the natural life of the animal. The nature of the effective stimuli, the simplicity of the neuronal arrangement involved, and the character of the synergic response are discussed in terms of their survival value to the species. J.A.C.N.

## Conduction Velocity in Relation to Axon Diameter in *Myxicola infundibulum*

By J. A. C. Nicol, C. N. Smyth and D. Whitteridge

*XVII Int. Physiol. Congr.* Oxford, 1947, pp. 243–4.

Some characteristics of conduction in the giant axon of *Myxicola infundibulum* are presented. The axon tapers from 0·5–1 mm. at one end to 0·1 mm. at the other. A single electrical stimulus leads to a nerve action potential which is all or none. Sharp mechanical stimuli give rise to single nervous impulses resulting in separate muscular contractions. The axon conducts equally well in both directions, when the stimulation is electrical or mechanical. J.A.C.N.

# THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. XV (p. 735) and Vol. XXVII (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

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Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

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

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