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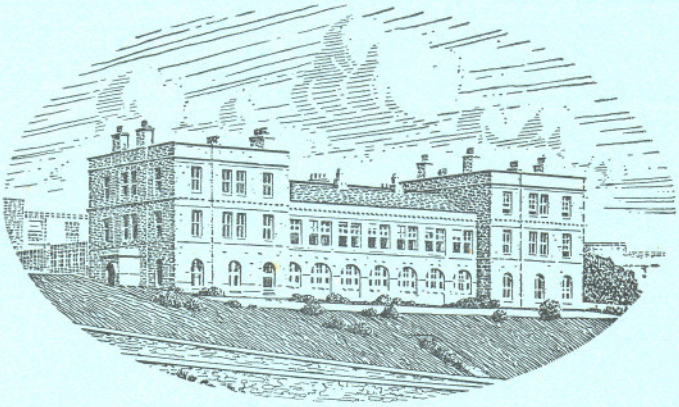

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STUDIES ON *CHAETOPTERUS VARIOPEDATUS* (RENIER). I. THE LIGHT-PRODUCING GLANDS

By J. A. Colin Nicol

Zoologist at the Plymouth Laboratory

(Plates I, II and Text-figs. 1–4)

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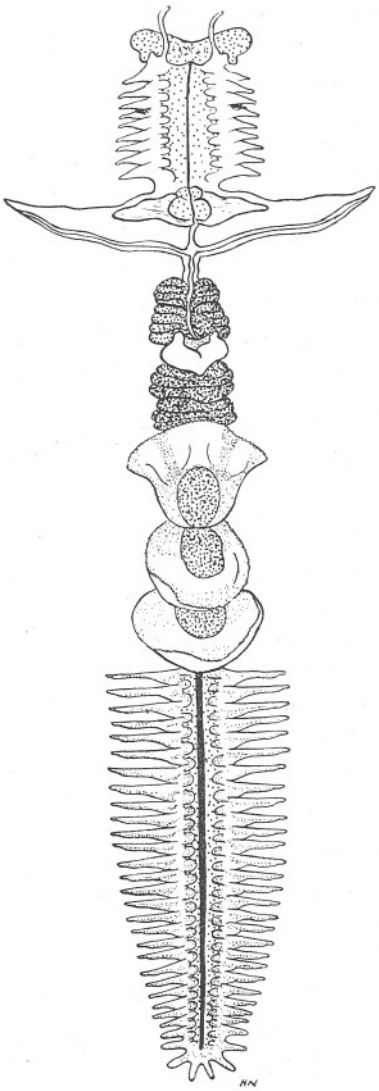
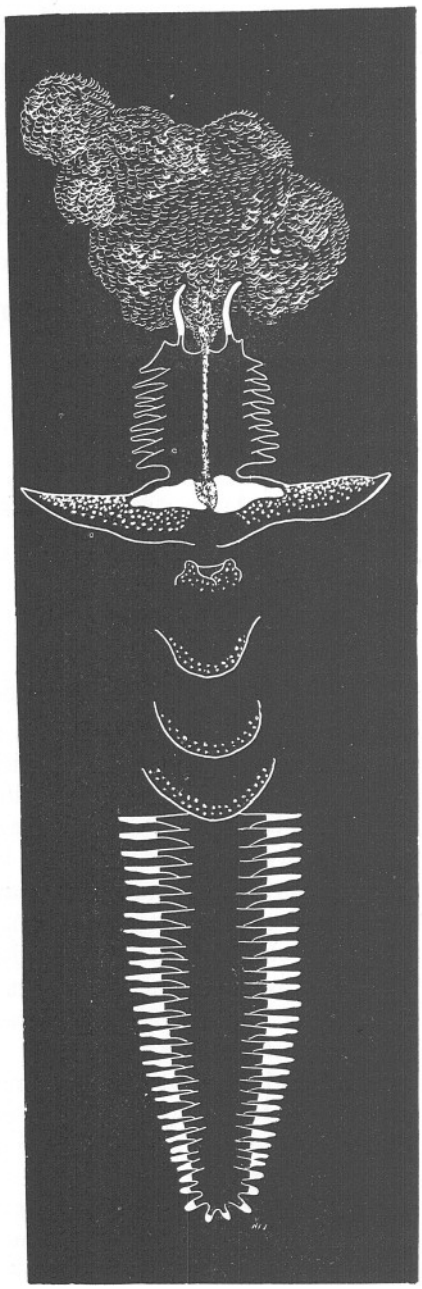
INTRODUCTION

Chaetopterus variopedatus (Renier) is a tube-dwelling worm that has noteworthy luminescent powers. Production of light is by an extracellular process resulting from the discharge of a luminescent slime into the sea water. Because of its luminescent ability, the epidermal glands of *Chaetopterus* have been repeatedly described in detail, but it is still not clear what elements produce the luminescent secretion. I have, therefore, re-examined the histology of the light-producing regions of *Chaetopterus* with a view to determining the character of the photocytes or light-producing glandular cells.

For the convenience of the reader who may be unacquainted with the morphology of *Chaetopterus*, a picture of the animal is given in Text-fig. 1. *Chaetopterus* consists of three greatly dissimilar regions. The anterior region is flattened, and includes eleven segments (nine setigers). There is a pair of peristomial tentacles on the head. The middle region begins with segment XII, which is provided with a large pair of wing-like (aliform) notopodia. There is a lateral ciliated groove on the dorsal surface of each of these notopodia; the two lateral grooves converge medially, and open into a medial dorsal ciliated groove, which extends anteriorly towards the mouth. In the succeeding segments of the middle region there is a conspicuous cup organ (dorsal tubercle) in segment XIII, and a large fan or palette in each of segments XIV–XVI. The posterior region is less differentiated, and contains a large and variable number of segments, each provided with a pair of lateral notopodia.





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Text-fig. 1. Dorsal view of a specimen of *Chaetopterus variopedatus*. About life-size.

Text-fig. 2. Dorsal view of a luminescing specimen of *Chaetopterus*, as seen in the dark. About life-size.

Histological Methods

For the examination of glandular cells, material was fixed, double-embedded in Peterfi's celloidin-paraffin, sectioned at 10 μ, and stained in various ways. Of several fixatives that were tried, Bouin's solution afforded good fixation and enhanced staining. After a trial of various stains it was concluded that a haematoxylin and eosin coloration afforded the greatest distinction between different gland cells and other epidermal elements, and most sections were stained by this means.

Review of Previous Work

It has been pointed out by several observers that the luminescent regions of *Chaetopterus* are recognizable in the living animal because of their chalky white appearance against the yellowish ground colour of the body. These whitish areas are considered to contain the glandular luminescent cells. These were mentioned by Joyeux-Laffuie (1890), who stated that unicellular gland cells with refringent contents were scattered over the luminescent regions. According to the descriptions of later histologists, the epidermal glandular cells are divisible into categories of granular or homogeneous eosinophile cells, fibrous eosinophile cells, and basophile cells.

Granular and homogeneous eosinophile cells. These are ovoid or flask-shaped cells containing a basal flattened nucleus, and opening directly to the exterior through a secretory pore. The cytoplasm contains numerous closely packed eosinophilic granules, which are sometimes fused to form a homogeneous mass. These cells occur all about the circumference of the peristomial tentacles, but particularly on the dorsal side; in an oval glandular area on either side of the dorsal ciliated groove in segment XII; on the dorsal surface of the aliform notopodia; in a lateral intermediate zone about the dorsal tubercle; in the walls of the fans; and along the notopodia of the posterior region (Krekel, 1920; Trojan, 1913). It is these cells, apparently, that Dahlgren (1916) regarded as luminescent cells or photocytes. He described them as saccular elements, hanging down from the cuticle, and capable of secreting granules of luminescent material. The discharged cells appear empty and shrunken (Harvey, 1920).

Fibrous eosinophile cells. These cells, according to Krekel (1920) and Trojan (1913, 1914), are found in the apical half of notopodia of the posterior region. They are cylindrical or fusiform in shape, with a basal nucleus. The cytoplasm is intensely acidophilic, and contains a peculiar fibrous skein or knot in the shape of a figure-of-eight. These cells had been noticed earlier by Claparède (1870), who designated them 'follicules bacillipares'. A developmental cycle has been traced in the history of these cells in which early stages are represented by ovoid elements possessing a granular cytoplasm. As the cells mature they elongate and extend to the base of the epidermis, and the contained cellular granules aggregate to form a spiral fibrous knot.

Trojan (1914) believes that these fibrous cells secrete the material used in tube-building.

Basophile cells. These cells occur in the following regions: (i) in the tentacles, where they are concentrated as a dorsal band; (ii) in the dorsal triangular glandular areas at the bases of the aliform notopodia; (iii) in the walls of the dorsal tubercle and fans of the middle region; (iv) in a distal band on the anterior side of posterior notopodia; and (v) in special glands at the base of these structures. The cells are pyriform to high cylindrical, and extend through the whole thickness of the epidermis. They become thinner distally, and open to the exterior through a secretory pore. The cellular contents consist of large basophilic granules staining intensely with haematoxylin, thionine and methylene blue; they are also coloured by mucicarmine (Krekel, 1920; Trojan, 1913). It is these cells which have generally been regarded as the photocytes producing the luminescent secretion, although Dahlgren (1916) apparently thought they were merely mucous cells.

Bonhomme (1943) has recently re-examined the histology of *Chaetopterus* gland cells in the aliform notopodia and dorsal tubercle. He found that the luminous organ consists of a high-folded epithelium containing tall prismatic cells. These have a lateral flattened nucleus, and open distally by a secretory pore. The cellular contents consist of a thin basophilic lacework, which Bonhomme regards as the residual framework remaining after secretion induced by the action of fixatives. On the margins of these glandular areas he located premucigenous cells which are large and irregularly prismatic in shape, and are filled with gross basophilic granules.

In another form, *Mesochaetopterus japonicus*, basophilic cells have also been identified with light production. These cells occur on the tentacles, on the dorsal surface of the middle region, and on the posterior notopodia. They are club-shaped, tapering towards a distal opening, and are filled with basophilic secretory granules. Discharged cells appear filled with a spongy coagulum (Fujiwara, 1935).

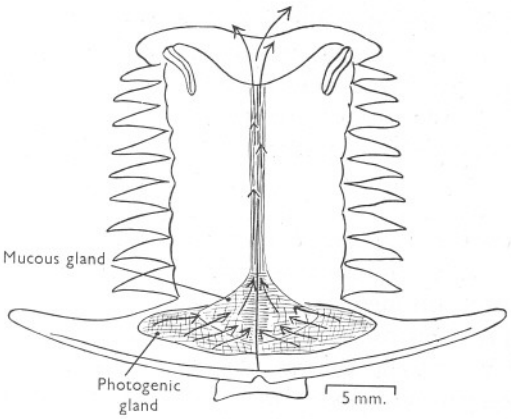
In the following account I present some new observations on the luminescent areas of *Chaetopterus*. My observations link the secretion of photogenic material with eosinophile cells. The other cell types are mucous cells, and basophilic cells which may be concerned with tube-building.

Observations

The luminescent regions have been determined by stimulating the animal to produce light in the dark. Stimuli used have been high-frequency condenser discharges, above six per second, and an isotonic solution of KCl. Both these agencies cause widespread luminescence in the worm. The following regions produce light: the peristomial tentacles; a pair of triangular areas lying on the dorsal surfaces of the aliform notopodia (segment XII), one on either side of the dorsal ciliated groove; the aliform notopodia themselves; the walls of the

dorsal tubercle; the fans in segments XIV–XVI; and all notopodia of the posterior region (Text-fig. 2).

The large glandular areas on the aliform notopodia are the regions most easily brought into luminescence by tactile stimulation. When this region is touched a luminescent secretion is discharged into the sea water; this is carried medially towards the mid-dorsal line by ciliary currents, and is then transported anteriorly towards the mouth through the activity of the dorsal ciliated groove (Text-fig. 3). Arriving in the buccal region, the luminescent secretion streams away from the animal, and illuminates the surrounding sea water. Luminescence from the secretion of this region persists for a considerable time, up to 15 min. or more. Under the binocular microscope the luminous secretion is revealed as a multitude of brightly lighted, discrete particles.



Text-fig. 3. Dorsal view of the anterior region and segment XII of *Chaetopterus*. The arrows indicate the course of luminous particles secreted by the luminescent glands at the bases of the aliform notopodia.

The other regions of the body give off a brief transitory flash, quickly dying away in a minute or two, and they do not discharge a luminescent secretion which is carried away into the surrounding medium. When segments of the posterior region are stimulated to lighten, the notopodia become coated or caked with a thick secretion which adheres for some time to the appendages. This secretion is probably the oxidized photogenic material, which luminesces and becomes exhausted very rapidly after it is released.

Bonhomme (1943) considers that the tentacles do not themselves give off light, but acquire luminescence secondarily when luminous secretion is carried forwards in the dorsal ciliated groove to a ciliated groove lying along each tentacle. This is incorrect, and the peristomial tentacles do lighten, as can be shown by the following experiment. The anterior region of an animal was transected at the level of the third or fourth segment, without inducing luminescence. The anterior fragment was then placed in isotonic KCl, upon

which both tentacles luminesced. There was no question of luminescent secretion being carried to the tentacles from other regions in this fragment, and light originated in the tentacles themselves.

Trojan (1913) and Krekel (1920) regard a whitish glandular area at the base of each posterior notopodium as a luminescent structure, and Panceri (1878) figures this region as luminous. Krekel, unfortunately, did not have living animals for observation. There is a conspicuous whitish fleck at the base of each posterior notopodium, and I find that this region is not luminescent. Distally, beyond this whitish glandular area, the notopodium is brightly luminous.

Epidermal Gland Cells

The story of epidermal secretions in *Chaetopterus* has obviously become rather complicated. In presenting an evaluation of these observations it is necessary to consider the probable functions of epidermal secretions in this species. So far as is known they involve production of mucus, tube-formation, and luminescence. One would, therefore, expect to find at least three kinds of epidermal gland cells corresponding to these functions, and such cells may or may not be visually distinguishable from one another.

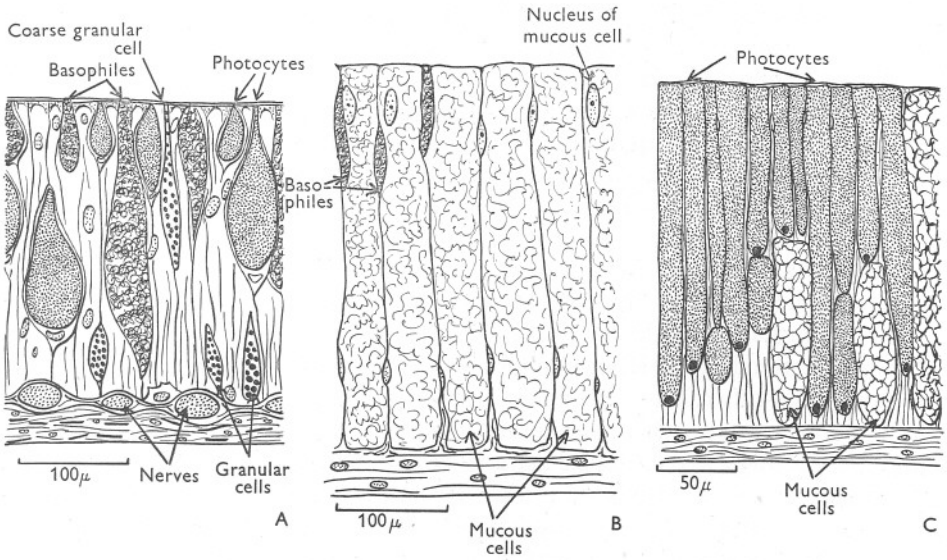
Mucous Cells

As is well known, *Chaetopterus* is a mucous filter-feeder and produces enormous quantities of mucus for trapping and entangling food particles as it pumps water through its tube (MacGinitie, 1939; MacGinitie & MacGinitie, 1949). This mucous material is poured forth from the walls of the dorsal tubercle and the aliform notopodia, and it is carried forward in the dorsal ciliated groove towards the mouth. There is little doubt that it is secreted by the abundant basophilic cells which form conspicuous whitish areas on those organs. Those cells are, accordingly, mucous cells.

The mucous glands occurring as conspicuous masses at the bases of the aliform and posterior notopodia and in the dorsal tubercle are made up of closely packed very large cells (Text-fig. 4; Pl. I, figs. 2–4 and 6). There is also a small number of mucous cells about the longitudinal ciliated groove on each peristomial tentacle. These are greatly elongated prisms about $20 \times 200\,\mu$ in the aliform notopodia, up to $350\,\mu$ long on the dorsal tubercle, and reaching the enormous length of $650\,\mu$ on the posterior notopodia. Nuclei are present at two levels in the mucous epithelium, and there is reasonable doubt as to which nuclei actually belong to the mucous cells. Towards the base of the epithelium there are small flattened nuclei squeezed between the mucous cells. These apparently belong to connective tissue cells located in a thin strand of connective tissue which extends a short distance between the bases of the mucous cells from the underlying fibrous layer. Distally toward the free surface, there are greatly elongated and faintly staining nuclei lying against the walls of the cells. These correspond to the

nuclei figured by Bonhomme, and seem to be the nuclei of the mucous cells. Cell boundaries are faint but definite. The entire cell is filled with an indistinct alveolar material, the walls of the alveoli seemingly consisting of interlacing fine fibrils. The contents stain faintly with alum haematoxylin and are basophilic. They do not stain with mucicarmine and iron haematoxylin.

The following observations should demonstrate that the mucous cells are not responsible for the luminescent secretion. The secretion of mucus from segments XII and XIII (aliform notopodia and dorsal tubercle) is a continuous



Text-fig. 4. A, section across the epidermis of the aliform notopodium. B, section through the mucous epithelium beside the dorsal ciliated groove. C, section through the light gland on the aliform notopodium.

process, whereas release of luminous material is a discontinuous process, under nervous control. It is difficult to conceive of a cellular organization by which an exocrine glandular cell produces and releases two different substances, one continuously, the other at rare intervals.

The main argument for identifying the basophilic mucous cells with light production has been the exact spatial correspondence between areas containing these cells, and luminescence. As shown above, the three regions containing large accumulations of mucous cells are the dorsal triangular regions on the aliform notopodia, the walls of the dorsal tubercle, and the bases of the posterior notopodia. Only the first of these three areas produces conspicuous light; the tubercle gives off a very weak and transitory flash; and the basal areas of the posterior notopodia do not luminesce. Consequently, there is no correspondence between aggregations of mucous cells and luminescence.

In order to obtain some comparative data on the relative amounts of mucus produced by various regions of the body, fragments of animals were placed in sea water and, after an interval to allow for secretion, the viscosity of the water was estimated in arbitrary units. Pieces of the animal selected were the anterior region (including segment XII); segment XIII and the dorsal tubercle; segments XIV–XVI and fans; and the posterior region. These were placed in separate dishes, an equal amount of water was added to each container and a sample of water drawn after 30 min. Relative viscosity figures were obtained by measuring the time taken for a drop to run through a length of thistle tubing. Mean relative times were: 5·3 sec. for the anterior region; 1·0 sec. for the dorsal tubercle; 0·5 sec. for the fans; and 0·2 sec. for the posterior region. The last figure was equivalent to a determination for sea water. These figures show that most mucus is secreted by the aliform notopodia, a considerable quantity by the dorsal tubercle, and none by the posterior notopodia. In contrast, it may be mentioned again that although a great deal of light is produced by the aliform notopodia, very little originates in the dorsal tubercle; the posterior notopodia, however, are brightly luminescent.

The copious mucus secreted by the aliform notopodia and the dorsal tubercle forms a vehicle for suspending and carrying away the luminous material secreted by the aliform notopodia. The luminescent material released by the dorsal tubercle is negligible. The fact that the posterior notopodia do not produce mucus when the animal is stimulated to luminesce offers an explanation why the photogenic material continues to lie on the surface of the notopodia, and is not dispersed in the surrounding medium. The function of the basal glandular areas on the posterior notopodia remains obscure. These glands are regarded as the modified terminal regions of nephridial organs (Trojan, 1913). Since they are not luminescent they cannot be concerned with luminescence of eggs and larvae, a suggestion that has occasionally been adumbrated. There is a possibility, however, that they secrete only during spawning.

Eosinophilic Light Cells (*Photocytes*)

These occur in the peristomial tentacles, basal dorsal surface of the aliform notopodia, distally on the aliform notopodia, dorsal tubercle, fans, and on the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 1–6, 7–8, 10–11).

On the tentacles the eosinophilic cells are scattered over the surface, and are more concentrated on one side opposite the longitudinal ciliated groove. The aliform notopodia contain occasional scattered eosinophile cells distributed over both dorsal and ventral surfaces away from the lateral ciliated groove. Towards the base of the aliform notopodium, on the dorsal surface, there is a dense and extensive aggregation of eosinophilic cells. These lie lateral to a more median area which consists of basophilic mucous cells, and

which borders the dorsal ciliated groove. The two kinds of cells are not mutually exclusive for there are a few eosinophilic cells dispersed through the mucous gland, and a few mucous cells scattered through the eosinophile glandular area.

In the dorsal tubercle of the middle region there is a narrow zone containing a few eosinophile cells. This lies at the transition between the dense mucous glandular layer covering the outside of the tubercle, and the ciliated epithelium leading inside the cup. Eosinophile cells are scattered over the dorsal surface of the fans. In the posterior region, the distal surface of each notopodium contains a great number of closely spaced eosinophile cells.

The eosinophile light cells have a similar appearance in all regions of the body in which they occur. On the tentacles, aliform notopodia, dorsal tubercle, fans, and posterior notopodia, they are round or oval to elongate elliptical in shape, depending on the height of the epithelium. Dimensions in these regions lie in the range $12–25 \times 30–50\,\mu$. There is a small triangular nucleus at the base of the cell. The dense aggregations of eosinophilic cells lying at the bases of the aliform notopodia are tall cylindrical in shape, and have dimensions of $6 \times 150\,\mu$. The nucleus, again basal, is relatively minute compared with the size of the cell. These cells, at the bases of the aliform notopodia, reach the basement membrane. In other regions, however, the oval or elongate cell has the appearance of hanging down from the cuticle, and a long thin tag extends from the base of the cell to the basement membrane. The contents of all these cells are closely similar. The cells are filled with a deeply staining dense mass of eosinophilic material in which there are all gradations from a coarse or fine granular to a homogeneous consistency.

Dahlgren (1916), who has briefly dealt with the photocytes of *Chaetopterus*, describes them as granular cells. His figure seems to be a composite one, based on the structure of the eosinophile light cells described above, and the coarse eosinophile cells described in the next section.

The evidence for regarding these eosinophilic cells as the light-producing cells consists of the following observations. The eosinophilic cells have the same spatial distribution as the photogenic regions. The tentacles glow quite brightly, relative to their area, and contain many eosinophilic cells. Light production is very faint and transitory in the dorsal tubercle and fans, and relatively few eosinophilic cells are present on those structures. The distal regions of all the posterior notopodia luminesce very brightly, and these appendages are abundantly provided with eosinophilic cells. Regions that do not luminesce bear no eosinophile light cells having the characteristics described above.

Three animals were stimulated into luminescence by placing them in isotonic KCl for several minutes. The brightly luminous areas on the basal dorsal surface of the aliform notopodia were dissected out under a binocular microscope. These pieces of tissue were fixed, and were examined

histologically. Two of them contained extensive patches of both basophilic mucous cells, and eosinophilic cells. The third consisted almost entirely of a dense aggregation of eosinophile cells (Pl. I, fig. 3).

An attempt was made to discriminate the photogenic cells by strongly stimulating the animal into luminescence, and then looking for secreting and exhausted cells. The results were ambiguous. Even after prolonged stimulation electrically or by treatment with KCl, it was still possible to elicit further luminescence by mechanical agitation of the glandular regions in segment XII. Histological examinations showed a certain amount of both mucous and eosinophilic material outside the cells, some exhausted eosinophilic cells, and numerous eosinophile cells still replete with secretory material. It appears to be difficult to exhaust all the luminescent cells by prolonged excitation.

It has been a common observation that dropping an animal into a fixative evokes luminescence. A bright flash is produced when an animal is dropped into fixatives like Bouin's, Zenker's, and Helly's fluids. If the animal is previously anaesthetized by immersion in isotonic $MgCl_2$ for 5–15 min., and is then placed in the fixative solution, it does not luminesce. These effects were utilized in searching for the luminescent gland cells. Animals, with and without previous treatment with $MgCl_2$, were dropped into fixative, and histological sections were prepared (Pl. II, figs. 7 and 8). Sections of animals that had been treated with $MgCl_2$ showed no secretion of eosinophile material. Sections of animals that had been dropped directly into fixative solutions showed many eosinophilic cells caught in the act of discharging a secretory mass from a distal cellular orifice, and a dense layer of eosinophilic secretion lying over the surface of the epidermis. Comparative examinations were restricted to the aliform notopodia, as being regions easiest to study.

Finally, dried smears were made of secretions from non-luminous and luminous animals. To do this some of the mucous slime from the dorsal surface of the anterior region was sucked up in a pipette and smeared on a slide. After drying, the smears were fixed in Bouin's fluid, and stained with haematoxylin and eosin. Smears from non-luminous animals showed only a small amount of dispersed basophilic mucous material. Smears from luminous animals showed, in addition, many particles of eosinophilic material scattered in the mucus, or aggregated into lumps. These particles were often in packets closely resembling the contents of eosinophilic cells (Pl. II, fig. 9).

Other Gland Cells

Two additional types of epidermal gland cells must be mentioned. These are densely staining basophilic cells, and coarsely granular eosinophilic cells.

The dense basophilic cells were found scattered singly in the tentacles, on the aliform notopodia, in the walls of the fans, in the dorsal tubercle at the

transition between mucous cells and the internal ciliated layer, and about the circumference of the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 4, 7–8 and 10). They are scattered infrequently between the mucous cells at the bases of the aliform notopodia and on the dorsal tubercle. To a greater or lesser degree they are dispersed over the ventral surface of segment XII, and in the epidermis of the anterior region.

These cells tend to be thin, elongated, and fusiform where the epithelium is high, and irregularly pyriform where the epithelium is low. Dimensions are 3–12 μ wide $\times$ 30–120 μ high. The nucleus is small and oval in shape, and lies at the base of the cell. The cell contents are basophilic and stain heavily with alum haematoxylin. They also selectively stain with mucicarmine. After Bouin fixation they have the appearance of a deeply staining alveolar meshwork of fine fibrils, with darkly stained points in the interstices of the meshes. The cells were sometimes seen in the act of secreting, when a slender tongue of secretory material projected through a narrow distal orifice. These darkly staining basophilic cells apparently have a widespread and general distribution over the epidermis. There is no evidence to show that they are in any way concerned with light production.

The coarse granular eosinophilic cells were noted about the circumference of the aliform notopodia, in the posterior notopodia, in the dorsal walls of the fans, and mixed with photocytes in the wall of the dorsal tubercle (Text-fig. 4; Pls. I and II, figs. 4–8, 10 and 11). They are also dispersed over the ventral surface of segment XII and in the epidermis of the anterior region. In shape they are frequently pyriform: the proximal portion is swollen and lies in the basal epidermal region, and a long neck extends up to the free surface. When not compressed by neighbouring glandular cells they are often elongate and cylindrical. Dimensions reach 15 $\times$ 180 μ. There is a small, elliptical basal nucleus. The cell contains a number of scattered and discrete coarse granules up to 3 μ in size which are weakly eosinophilic. There is no evidence that these cells are related to the photocytes or that they are concerned in light production.

Epidermal Gland Cells and Tube-formation

It has not been possible to confirm the existence of fibrous eosinophilic cells, concerned with tube-formation, in the posterior notopodia (Dahlgren, 1916; Trojan, 1914). It is suggested that the fibrous knots and skeins seen in the eosinophilic cells of the posterior notopodia by earlier observers were fixation artifacts resulting from localized condensations and swirls in the secretory contents of the eosinophilic photocytes. In addition, as previously mentioned, coarse eosinophile cells are also scattered over these appendages.

The functions of the dense basophilic and coarse eosinophilic cells lie outside the scope of this investigation since they are not involved in light

production. It is suggested, however, that it would be of interest to investigate whether they are involved in tube-building. For comparison with the various gland cells, the staining reactions of the tube were investigated by peeling off thin strips and fixing in Bouin's fluid, so as to subject them to the same initial treatment as gland cells of the body wall. They were then stained with eosin, haematoxylin or mucicarmine. The preparations so obtained were found to have little affinity for eosin, but to stain deeply with haematoxylin; they were also coloured by mucicarmine. This provides suggestive evidence that the original secretion involved in tube-formation is basophilic, and implicates the dense basophilic cells, although it is not maintained that a correlation in staining affinities of this kind itself affords any conclusive proof. Presumably the material forming the tube is secreted in a fluid, or soft condition, and is moulded and hardened after release. Enders (1907) has studied the tube-building activities of *Chaetopterus*, and he describes how a worm enlarges its tube by splitting it longitudinally, and then produces a new strip of hardened 'mucus' to fill the gap. During this process the ventral lip is used to fashion and shape the new wall of the tube. The possibility should be considered that the coarse eosinophilic cells may also play some role in tube-formation, by hardening the material secreted for the formation of the tube, such as takes place during the secretion of the byssus in *Mytilus* (Brown, 1949).

Conclusions

It has been shown in this investigation that four recognizably different kinds of gland cells can be seen in the epidermis of *Chaetopterus variopedatus*. These cells are all epicrine in nature in that they discharge their secretion to the external surface. They occur scattered individually over the surface, but are often aggregated into multicellular glands. These consist of groups of a few similar cells, or dense aggregations of cells which form massive glandular surfaces, as in the basal regions of the aliform notopodia. In the latter regions, also, the glandular surfaces are increased by folding of the epithelium.

The four kinds of glandular cells are readily distinguishable by their morphological appearance and staining characteristics. The photocytes, containing a densely staining eosinophilic mass, are confined to the luminescent regions. Mucous cells, containing a loose alveolar mucigen material, are aggregated into multicellular glands at the bases of the aliform notopodia, in the walls of the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell types, coarse granular eosinophilic and densely staining basophilic cells, are scattered singly through the epidermis and have a widespread distribution. Both these latter kinds of cells may be concerned with fabrication of the tube.

Only one kind of cell is implicated in light production in *Chaetopterus*,

and this is of interest when compared with *Cypridina*. In the latter two separate cellular types are involved, one of which contains large yellow granules of luciferin, the other small colourless granules of luciferase. On release the granules dissolve in the water and interact to produce light. Corresponding to the absence of two recognizably different kinds of photogenic particles in *Chaetopterus* is the reported failure to isolate extracts of luciferin and luciferase from this worm (Harvey, 1926, 1940).

In a treatment of luminescence it is usual to make some reference to its function in the economy of the organism. The function of luminescence in *Chaetopterus* is still unknown. Dahlgren (1916) has reproduced a painting by Horsfall in which an eel is depicted as attacking a brightly luminescent worm in its tube. The inference seems to be that the light has biological value in repelling the predator. Harvey (1920), however, has noted that light production by *Chaetopterus* would be of no avail, since an extracted worm cannot build a new tube. In presenting his theory that luminescence may sometimes have survival value to a species in attracting a predator of a predator, Burkenhead (1943) has utilized *Chaetopterus* as a theoretical example, in which luminescence excited as the result of an attack by an eel would attract, secondarily, an attack upon the eel by a dogfish. It may be significant that the anterior region of *Chaetopterus* is easily autotomized under stress and is readily regenerated, and it is this region of the worm which pours forth such an abundant luminous secretion. This suggests the idea of a sacrifice lure. Speculations of this kind obviously need to be checked by experiment and by observation of the living animal.

Summary

The luminescent regions of *Chaetopterus variopedatus* are shown to be: the peristomial tentacles, the aliform notopodia, the dorsal tubercle, fans, and notopodia of the posterior region. The brightest areas are glandular masses on the dorsal basal surfaces of the aliform notopodia and the distal surfaces of the posterior notopodia.

The photogenic glands on the aliform notopodia give off a luminescent secretion that is suspended in mucus and is dispersed into the surrounding sea water. Light from other regions is much more transitory, and the luminescent secretion is not dispersed.

Four kinds of gland cells occur in the epidermis. The photocytes have been identified as eosinophile cells containing a dense secretory mass. These cells are confined to the luminescent regions, and they are most abundant on the two most brightly luminescent areas, namely, distally on the posterior notopodia, and at the base of aliform notopodia. Mucous cells are slightly basophilic cells occurring beside the dorsal ciliated groove in segment XII, on the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell

types are coarse granular eosinophile cells, and darkly staining basophile cells. The latter two kinds of cells may be involved in tube-building.

Earlier work dealing with the epidermal glands of *Chaetopterus* is reviewed, and some comparisons are made with other forms.

REFERENCES

BONHOMME, C., 1943. L'appareil lumineux de *Chaetopterus variopedatus* Clap. Recherches histologiques. *Bull. Inst. Océanogr. Monaco*, T. 40, No. 843, 7 pp.

BROWN, C. H., 1949. Protein skeletal materials in the invertebrates. *Exp. Cell Research, Suppl.*, Vol. 1, pp. 351–5.

BURKENHEAD, M. D., 1943. A possible function of bioluminescence. *Journ. Mar. Res.*, Vol. 5, pp. 161–4.

CLAPARÈDE, E., 1870. *Les Annélides Chétopodes du Golfe de Naples*. Suppl. Geneva and Basle.

DAHLGREN, U., 1916. The production of light by animals. *Journ. Frank. Inst.*, Vol. 181, pp. 659–96.

ENDERS, H. E., 1907. Observations on the formation and enlargement of the tubes of the marine annelid (*Chaetopterus variopedatus*). *Proc. Ind. Acad. Sci.*, 1906–7, pp. 128–35.

FUJIWARA, T., 1935. On the light production and the luminous organs in a Japanese chaetopterid, *Mesochaetopterus japonicus* Fujiwara. *Journ. Sci. Hiroshima Univ.*, Ser. B, Div. 1, Zool., Vol. 3, pp. 185–92.

HARVEY, E. N., 1920. *The Nature of Animal Light*. Philadelphia and London.

—— 1926. Additional data on the specificity of luciferin and luciferase, together with a general survey of this reaction. *Amer. Journ. Physiol.*, Vol. 77, pp. 548–54.

—— 1940. *Living Light*. Princeton, N. J.

JOYEUX-LAFFUIE, J., 1890. Étude monographique du Chétoptère (*Chaetopterus variopedatus*, Renier) suivie d'une revision des espèces du genre *Chaetopterus*. *Arch. Zool. Exp. Gén.*, 2e. ser., T. 8, pp. 245–360.

KREKEL, A., 1920. Die Leuchtorgane von *Chaetopterus variopedatus* Clap. *Zeit. wiss. Zool.*, Bd. 118, pp. 480–509.

MACGINITIE, G. E., 1939. The method of feeding of *Chaetopterus*. *Biol. Bull. Woods Hole*, Bd. 77, pp. 115–18.

MACGINITIE, G. E. & MACGINITIE, N., 1949. *Natural History of Marine Animals*. New York, London and Toronto.

PANCERI, P., 1878. La luce e gli organi luminosi di alcuni anellidi. *Atti R. Accad. Napoli*, Vol. 7, No. 1, 20 pp.

TROJAN, E., 1913. Über Hautdrüsen des *Chaetopterus variopedatus* Clap. *S.B. Akad. Wiss. Wien*, Bd. 122, pp. 565–96.

—— 1914. Ueber die Bedeutung der 'follicules bacillipares' Claparède's bei *Chaetopterus variopedatus*. *Proc. IX Inter. Zool. Congr. Monaco*, 1913, pp. 390–5.

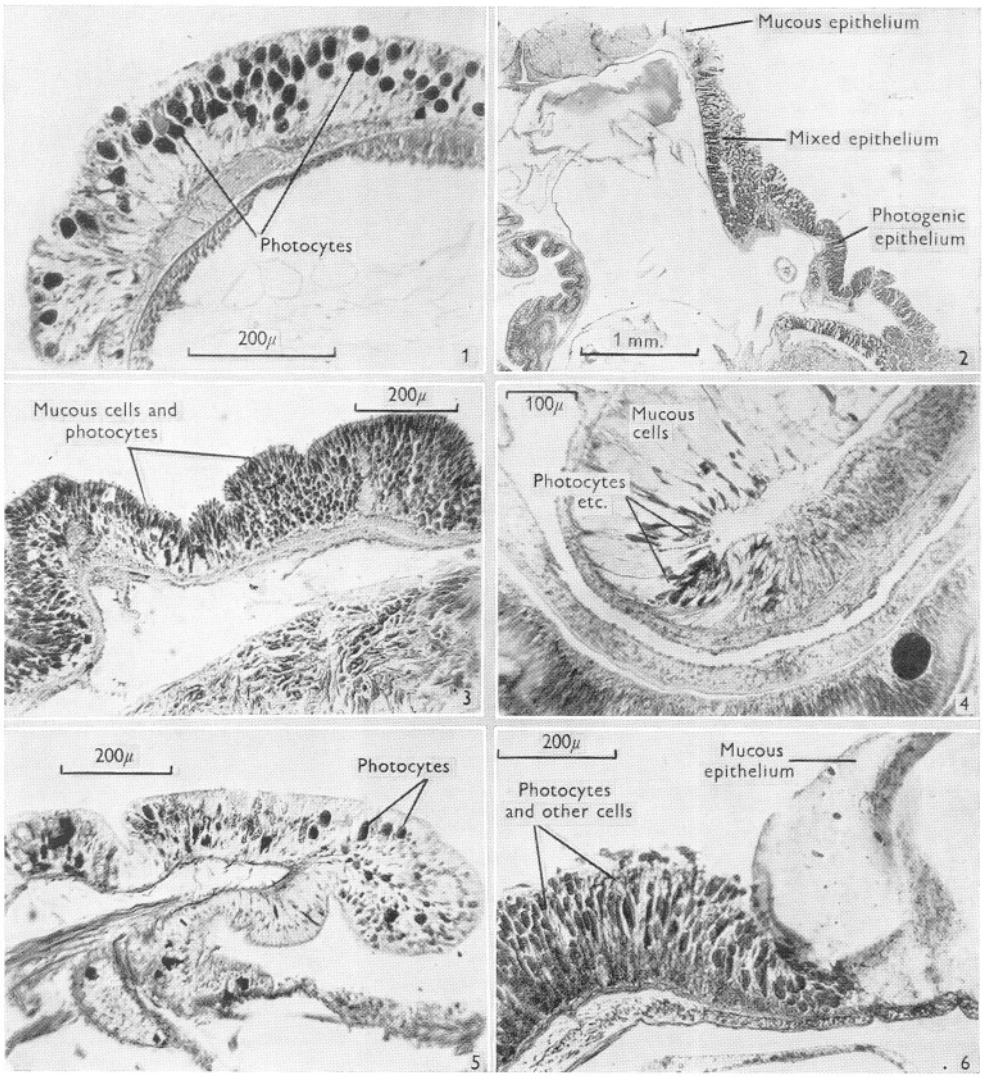
EXPLANATION OF PLATES

PLATE I

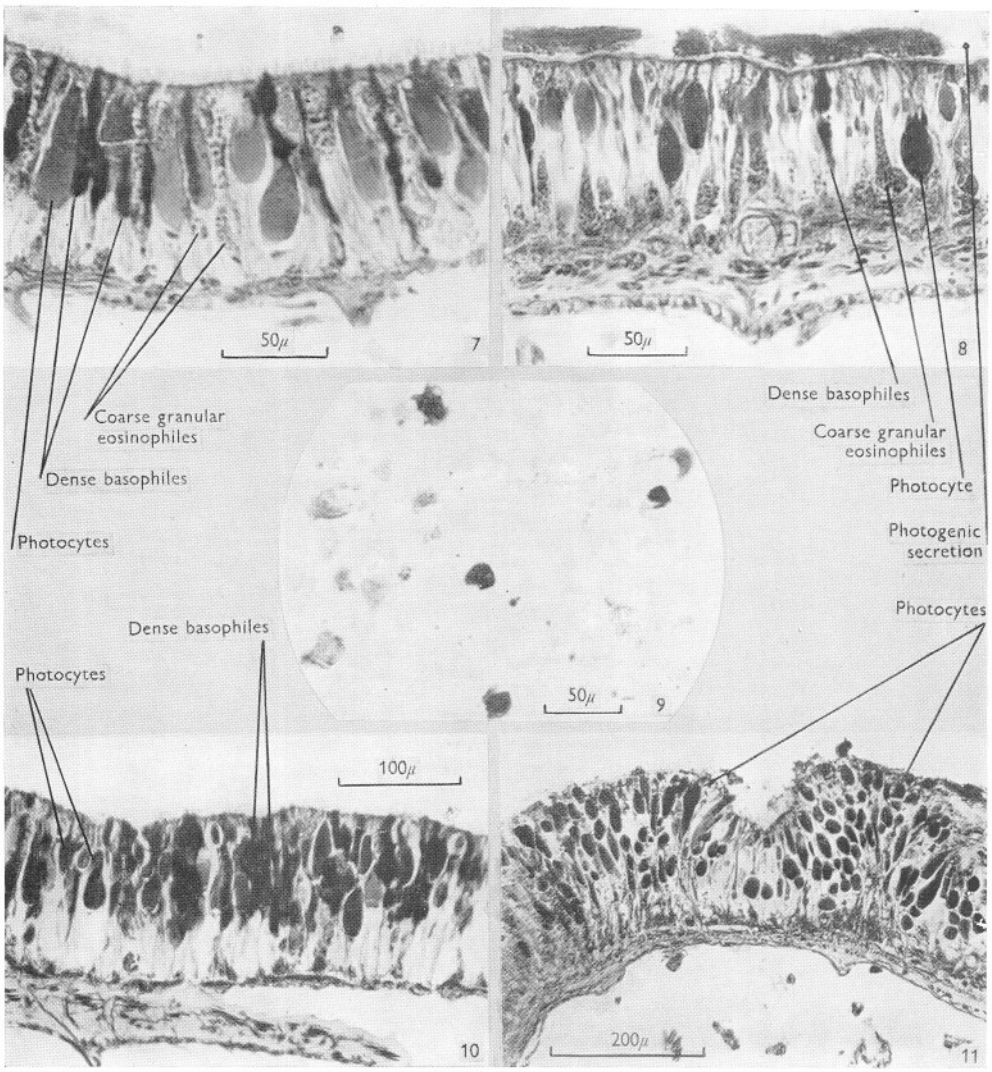
All histological sections shown in these photographs were stained with alum haematoxylin and eosin.

Fig. 1. Part of the wall of the peristomial tentacle in transverse section. Mucous cells and photocytes are interspersed in the epithelium.

Fig. 2. Transverse section through the dorsal body wall in segment XII. Lateral to the dorsal ciliated groove is a thick layer of mucous cells, which is replaced more laterally by a dense aggregation of photocytes.


Photocytes
200μ
1
Mucous epithelium
Mixed epithelium
Photogenic epithelium
1 mm.
2
Mucous cells and photocytes
200μ
3
100μ
Mucous cells
Photocytes etc.
4
200μ
Photocytes
5
200μ
Mucous epithelium
Photocytes and other cells
6

Figs. 1–6.


50μ
7
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8
Dense basophiles
Coarse granular eosinophiles
Photocyte
Photogenic secretion
Coarse granular eosinophiles
Dense basophiles
Photocytes
Photocytes
50μ
9
Dense basophiles
Photocytes
100μ
10
200μ
11

Figs. 7–11.

Fig. 3. Dissected and isolated luminescent glandular epithelium from segment XII. The epidermis consists mostly of photocytes, with a few mucous cells.
Fig. 4. Transverse section of the dorsal tubercle at the junction of the mucous layer, and the ciliated surface. Mixed together at the junctional zones are photocytes, coarse granular eosinophile cells, and dense basophile cells.
Fig. 5. Transverse section of a fan. The epidermis contains a few photocytes, coarse granular eosinophile cells, and dense basophile cells.
Fig. 6. Longitudinal section of a posterior notopodium. Junction between the basal mucous gland (right) and the brightly luminescent epithelium (left). The light-producing epithelium to the left contains predominantly photocytes mixed with some coarse eosinophiles and a few basophiles.

PLATE II

Fig. 7. Section of the aliform notopodium from a specimen anaesthetized with $MgCl_2$ before fixation. Surface secretion is lacking. Photocytes, coarse eosinophiles, and dense basophiles are interspersed together.
Fig. 8. Section of the aliform notopodium from a specimen fixed without preliminary anaesthetization. A layer of eosinophilic secretion lies over the surface of the epidermis. Photocytes, coarse eosinophiles, and a few dense basophiles lie interspersed together in the epithelium. A nerve is shown in section at the base of the epithelium.
Fig. 9. Dry smear of luminescent secretion produced by segment XII. Eosinophile secretory particles are shown.
Fig. 10. Section across the aliform notopodium to show dense aggregation of photocytes and dense basophilic cells.
Fig. 11. Section across the distal region of a posterior notopodium. The epidermis contains a dense aggregation of photocytes, together with a few coarse eosinophiles and dense basophiles.

STUDIES ON *CHAETOPTERUS VARIOPEDATUS* (RENIER).
II. NERVOUS CONTROL OF LIGHT PRODUCTION

By J. A. Colin Nicol

Zoologist at the Plymouth Laboratory

(Text-figs. 1–9)

CONTENTS

The production or emission of light is under nervous control in many marine animals that have a differentiated nervous system. The nature of this control is a field of neuro-effector physiology that has been little explored, but one which could advance considerably our knowledge of the behaviour and functioning of luminescent marine animals. Nervous control of luminescence is achieved in diverse ways in different animals, namely, by squeezing forth a pre-formed secretion through muscular contraction, as appears to take place in *Cypridina*; by exposing a continuously luminescent organ through rotation or by movement of shutters, as in the teleosts *Photoblepharon* and *Anomalops*; by initiating cellular changes that lead to intracellular luminescence, for example in the photophores of the shrimp *Acanthephyra debilis*; and by directly activating light gland cells to secrete. The last method is a special example of nervous regulation of glandular secretion, and is the process occurring in the polychaete *Chaetopterus* (Dahlgren, 1916; Harvey, 1920, 1940).

Chaetopterus has long been known as one of the more brilliantly luminescent marine invertebrates, and several previous workers have investigated this animal and reported on certain features of light production. This work is summarized to form a background for the original observations that follow.

Review of Previous Work

The luminous areas have been described and figured in a previous paper (Nicol, 1952). These are the peristomial tentacles, the surfaces of the aliform notopodia, a pair of photogenic glands on the dorsal basal surfaces of the aliform notopodia, the dorsal tubercle, fans, and notopodia of the posterior region. The luminous secretion produced by the photogenic glands on the aliform notopodia is suspended in mucus, and is carried away by ciliary currents to be distributed in the surrounding sea water. Luminescence in other regions is more transitory and localized (Bonhomme, 1943; Dahlgren, 1916; Fauvel, 1927; Joyeux-Laffuie, 1890; Lespès, 1872; McIntosh, 1915; Mangold, 1910–14; Panceri, 1878; Trojan, 1913, 1914; Will, 1844).

The light is blue in colour and has been shown by Lankester (1868) to have a continuous spectrum from about 440 to 530 mμ.

Light is produced in *C. variopedatus* only as the result of stimulation. The stimuli used to excite this worm, and indeed most other marine animals investigated experimentally, seem to have been selected randomly, in order to determine whether or not they were effective, rather than to reveal the mechanism of the response. It was observed that mechanical stimulation, such as results from disturbing the animal on removing it from its tube, or pinching or tapping it, causes the production of light. Effective chemical stimuli which have been used include the application of fresh water and strong reagents such as sublimate, formol and other fixing fluids. Raising the temperature of the sea water and applying electrical currents have also been employed to induce luminescence (Dahlgren, 1916; Joyeux-Laffuie, 1890; Panceri, 1878; Trojan, 1913).

There is a general belief that light production in *C. variopedatus* is under nervous control, but a curious absence of agreement about the details of the process. Panceri (1878) observed that the production of light was confined to the region of stimulation, and that there was no transmission of excitation, and this has been confirmed by Trojan (1913). According to Hempelmann (1934), increasing the strength of the stimulus (kind ?) causes the light to spread to other parts of the body and to become more widely distributed, but Dahlgren (1916) ascribes this effect to the spread of secretion through the water. Again, Stephenson (1946) has stated that stroking the animal causes waves of light to pass over the body. Finally, Harvey has noted that the light cells are probably under nervous control 'as a strong stimulus in one part of the body causes luminescence which spreads over the whole surface of the worm' (1920), and 'a wave of light when the head end is stimulated' (1940). The luminous secretion remains bright for about a minute after stimulation ceases, and then gradually diminishes in intensity. It has also been noted that the luminescent cells fatigue rather readily, and after a period of mechanical stimulation a rest of some hours is required

before the animal can be brought to luminesce again (Harvey, 1920; Panceri, 1878; Trojan, 1913).

There is agreement that luminescence is not inhibited by previous exposure to strong light. Panceri (1878) exposed specimens of *Chaetopterus* to sunlight, and then stimulated them in the dark, and he found that the ability to produce light was not suspended, in contrast to *Beroe* and other ctenophores in which such inhibition is quite pronounced (Panceri, 1872). According to Crozier (quoted by Harvey, 1920), luminescence in *Chaetopterus* is not affected by an exposure to 3000 metre-candles for 6 hr. The luminescent substances, luciferin and luciferase, which have been distinguished in marine ostracods, fire-flies (beetles), *Pholas* and *Odontosyllis*, have not been demonstrated in *Chaetopterus* (Dubois, 1887; Harvey, 1920, 1926, 1940, 1948). Neither do dried preparations of the animal luminesce on moistening. A luciferin-luciferase reaction may still be present, but may escape detection by biochemical methods hitherto employed. Harvey (1940) has reviewed this aspect of the subject.

Young free-swimming larvae of *Chaetopterus* are also capable of producing light (Dahlgren, 1916). Enders (1909), describing larvae about 1·5 cm. long and ready to metamorphose, states that luminosity is noticeable in the region of the ciliated rings, and in the mucus which the animals discharge. It is still more apparent in older larvae, where it appears in the anterior region and about the ciliated rings as the result of stimulation.

In another luminous chaetopterid, *Mesochaetopterus japonicus*, Fujiwara (1934, 1935) found that light is produced by the tentacles, by large areas of glandular epithelium on the dorsal surface of the first segment of the middle region, by a paired scyphiform organ on the second segment, by the dorsal ciliated region of the third segment of the middle region and by notopodia of the posterior region. These regions, in a general way, are similar to those of *Chaetopterus variopedatus*. Fujiwara's description (1935) of luminosity in this animal is difficult to follow. He states that brightest light is produced by the glandular epithelium of the first segment of the middle region, as in *Chaetopterus*. A luminescent secretion is also produced by cells in the walls of the dorsal ciliated groove, and the basal regions of the posterior notopodia are also luminous. He appears to imply that an animal removed from its tube shines continuously, but I interpret his account to mean that the luminescent secretion from the middle region of the body shines for some considerable time, but that light from notopodia of the posterior region, in contrast, appears in quick flashes. Moreover, the posterior segments flash alternately. Fujiwara further states that the luminescent activity can be increased by electrical, mechanical, or chemical stimulation. Electrical stimulation of the tentacles causes the appearance of light both in these structures, and in the luminescent organs of the posterior region. In *Mesochaetopterus japonicus*, therefore, it seems that excitation of luminescent

organs, induced electrically, is transmitted by the nervous system throughout the length of the body; sensitivity to stimulation leading to a luminous response appears to be most pronounced in the tentacles.

Material and Methods

Specimens of *Chaetopterus variopedatus* used in this investigation were maintained under circulation in the laboratory. Before use they were removed carefully from their tubes so as not to stimulate them to produce their luminous secretion before being experimented upon. This no doubt occurred on occasion, and any specimens which responded poorly to subsequent stimulation were discarded.

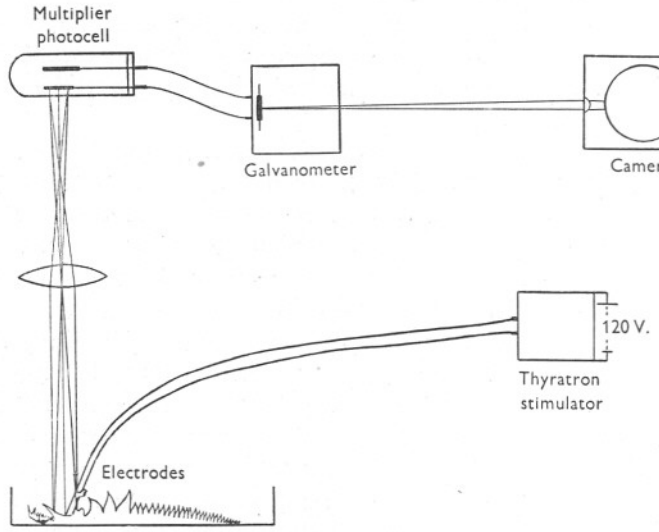

Fig. 1. Arrangement for investigating and recording luminescence, with the aid of a photocell and galvanometer.

Many of the experiments to be described merely depended on observing whether an animal did or did not luminesce, that is, whether the result was positive or negative. When it was necessary to obtain quantitative data, the light produced by the worm was focused on the photocathode of a photomultiplier cell (RCA 931 A). This was usually maintained at 1000 V., 100 V. per stage at which, according to specifications, it has a sensitivity of 3 A. per lumen and a magnification of 2×10^5 with a lamp of colour temperature 2870 K. The arrangement is shown in Fig. 1. As only comparative results within short time-periods were sought, no calibrations of the actual sensitivity of the cell were attempted. In most experiments the light from the basal glandular areas on segment XII only was measured. Photocurrent from the cell activated a moving-coil mirror galvanometer. This was a Tinsley

instrument having a resistance of 337 Ω; deflexion of 130 mm./μA. at 2·16 m.; and a periodic time of 2 sec. Light reflected from the galvanometer mirror fell upon a sheet of moving bromide paper in a camera travelling with a speed of 6 mm./min. Two other spot-lights were thrown on the same paper, one a time marker flashing once per minute, the other a stimulus marker, flashing when the stimulus key was depressed.

There was perceptible dark current in all records, and some drift of dark current base-line. At the beginning and end of each experiment, and at appropriate intervening intervals, the animal was covered so as to record the level of dark current. Some galvanometer records have been replotted to allow for basic level of dark current, drift, and any initial luminescence upon which the effect of a specific stimulus was superimposed.

Success was also attained in recording photocurrent with an oscilloscope, and this method was used when it was desirable to obtain maximal sensitivity, and fast records showing the initial phases of the luminescent reaction. The apparatus employed was a double beam oscilloscope with d.c. amplifier and attached camera.

Other particulars about methods used are described later under appropriate headings.

Observations

Effects of Mechanical Stimulation

Mechanical stimulation, by pulling, pinching, or tapping the animal, causes luminescence. As other observers have noted, light is produced, in consequence, from the peristomial tentacles, edges of the aliform notopodia, cup organ or dorsal tubercle, edges of the fans and notopodia of the posterior region. The response to stimulation tends to be very localized: thus pinching a fan or the cup organ of the middle region results in a faint flash of light in the organ directly stimulated. Similarly, mechanical stimulation of the posterior region causes the appearance of light in a few parapodia in the area directly affected.

It is more difficult to determine the effect of mechanical stimulation on the aliform notopodia of the XIIth segment. Light appears on the borders of the aliform notopodia as the direct result of pinching or touching these structures, and sometimes in the basal glandular areas on the dorsal surface as well. Luminous secretion appears from the latter glands as the direct result of touching them, or indirectly from pulling on the animal so as to produce tension in that region. No luminescent secretion is produced in the XIIth segment as the result of tactile stimulation of other parts of the middle region, and of the anterior and posterior regions, as long as the XIIth segment itself is not disturbed. Strong mechancial stimulation of the glands at the bases of the aliform notopodia causes a profuse discharge of luminous slime. It is probable that actual cellular destruction as well as indirect

nervous stimulation is involved in this display. As in other regions of the body, it appears from these results that the aliform notopodia and basal glands produce light only as the result of stimulation directly impinging on that segment. Light production in the aliform notopodia due to pulling or moving the animal seems to result from mechanical effects transmitted to the XIIth segment. There is, consequently, no definite evidence that mechanical stimulation in one region gives rise to a propagated excitation causing luminescence in more distant regions of the body. It is evident, however, that mechanical stimulation of *Chaetopterus* is very difficult to regulate quantitatively and spatially, and that more exact control can be exercised with electrical stimuli.

Effects of Electrical Stimulation

Direct current, faradic stimulation, and condenser discharges all produce luminescence. Quantitative studies were confined to the use of condenser discharges from a thyratron stimulator, since they allow careful control of strength, duration and frequency. Stimuli were delivered through a pair of platinum electrodes laid on the surface of the animal.

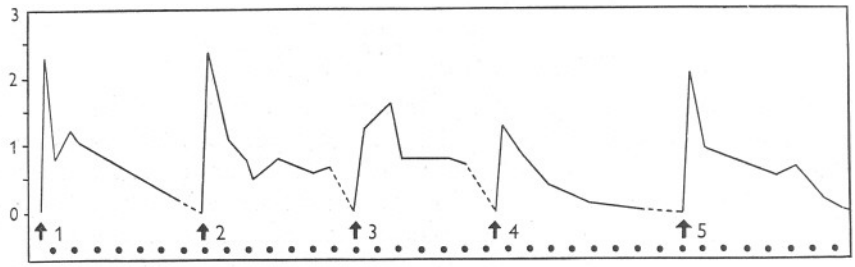

Fig. 2. Record of light produced by the photogenic glands on the aliform notopodia of *Chaetopterus* under electrical stimulation. Vertical arrows indicate application of stimuli. These were: 1 and 2, single stimuli; 3, two stimuli at 2 per sec.; 4, three stimuli at 3 per sec.; 5, one sec. burst at 5 per sec. Light intensity to the left in arbitrary units. Time scale below, 1 per min.

With the electrodes on the dorsal surface of the XIIth segment, a single electrical stimulus, above threshold, causes the production of luminescent secretion from the glands at the bases of the aliform notopodia (Fig. 2). The light appears quickly, within a few seconds of stimulation. Within a minute it begins to fade away, quickly at first, then more slowly, and becomes very dim and almost extinguished in 5 min.

The latent period and the time relations of the first phase of the luminescent response were determined from oscilloscope records (Fig. 3). In one series of experiments twenty animals were stimulated with a 2 sec. burst at 7 stimuli per sec. Latent periods measured from the beginning of stimulation varied from 3·0 to 4·4 sec., with a mean of 4·2 sec. The interval between first

deflexion and maximal height on the records ranged from 3·4 to 24 sec., with a mean value of 10·3 sec. Measurements made by eye (light-adapted) and a stop-watch gave a mean latent period of $2{\cdot}6 \pm 1{\cdot}8$ sec. (minimal value 1·5 sec.). The eye is more sensitive than the photocell, and this figure would be reduced further by dark adaptation of the observer. Animals in the dark, therefore, would become visible in about 2 sec., and would attain maximal luminescence in about 12 sec. after stimulation, the exact times depending on the animal.

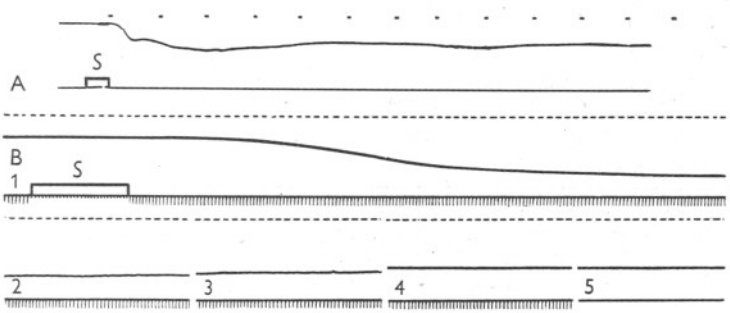

Fig. 3. Oscilloscope records of light produced by glands of aliform notopodia under electrical stimulation. A, 2 sec. burst of stimuli, at 9 per sec., at *S*. Time scale above, 1 per 5 sec. Latent period, 2·7 sec.; time to reach maximal intensity from first deflexion was 9·5 sec. B, 2 sec. burst at 14 per sec. at *S*. Time scale above, 1 per $\frac{1}{5}$ sec. There are 5 sec. intervals between 1–2, 2–3, 3–4, 4–5. Latent period, 3·6 sec.; time to reach maximal intensity from first deflexion was 11·4 sec.

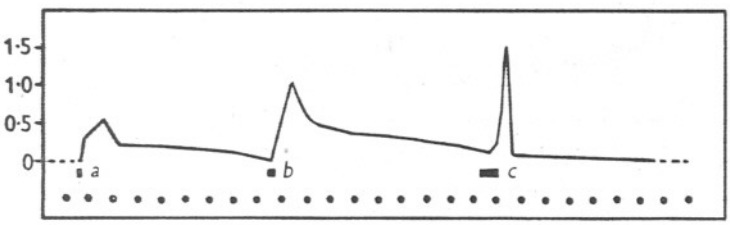

Fig. 4. Records of light produced by the photogenic glands on the aliform notopodia. Bursts of stimuli at 5 per sec. for 5 sec. at *a*, 30 sec. at *b*, and 1 min. at *c*. Stimulation indicated by dashes under record of light intensity. Time scale below, 1 per min.

The production of light by a single shock shows that there is a one-to-one relationship between single impulses and the light response: the arrival of an impulse at the neuro-effector junction excites the cell sufficiently to discharge. By increasing the number of stimuli, other factors, voltage and frequency, remaining constant, the light intensity and the amount of luminescent material secreted become greater. Fig. 4 is a record obtained in investigating this effect. Examination of the record shows that the initial luminescence increased greatly as the stimulation time was prolonged and the number of stimuli increased. With stimulation periods of 1:6:12, the

maximal intensity of luminescence resulting was 1:2:3. The total amount of light produced lay in the ratio of about 1:2:0·6. Since the responses to the second and third bursts of stimuli were certainly diminished by a fatigue effect, the absolute luminescence which would have followed stimulation for a given period, if diminution due to previous stimulation were excluded, probably would have been much greater.

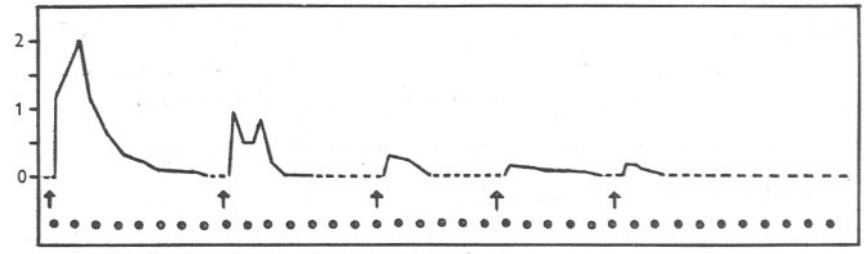

Fig. 5. Record of light produced by the photogenic glands on the aliform notopodia under repetitive electrical stimulation. Stimulation, indicated by vertical arrows under the light record, consisted of 5 sec. bursts at 8 per sec. except the last, which had a duration of 1 min. Time scale below, 1 per min. Intensity, to the left, in arbitrary units.

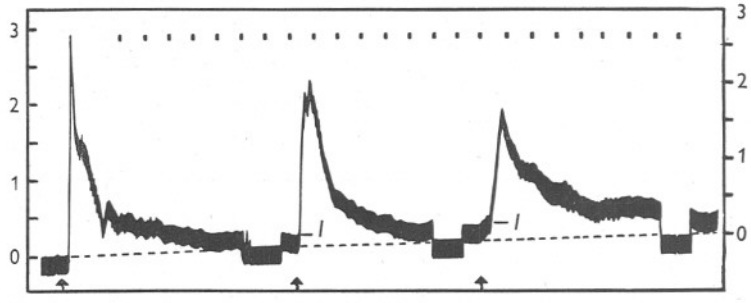

Fig. 6. Fatigue of luminescent power in the photogenic glands on the aliform notopodia. Stimulation, indicated by triangles below, 5 sec. periods at 4 per sec. The dotted line represents the level of dark current; *I*, indicates the initial level of residual luminescence on which a new response is superimposed. Time scale above, 1 per min. Light intensities to left and right in arbitrary units.

The light-producing glands soon fatigue on repeated stimulation, and this makes the interpretation of results more difficult. Information about the onset and course of fatigue was obtained by subjecting specimens to successive bursts of electrical stimuli. Figs. 5 and 6 show records obtained from two animals. In Fig. 5 the animal was stimulated by a succession of 5 sec. bursts at 8 per sec., except the last which lasted 1 min. An interval of about 6 min. between bursts permitted the luminescence to fade. It will be seen that each successive burst resulted in a fall in light production as the gland fatigued. Fig. 6 shows a similar result.

Recovery from fatigue was not observed in experimental animals. Fig. 7 shows the result of an experiment on an animal in which rest periods of

1 and 3 hr. intervened between successive periods of stimulation. In these times the response failed to recover to any extent, and much less luminescent material was secreted than at the beginning of the experiment. Other workers, however, have noted some recovery of luminescent ability after a rest period of several hours (see p. 434), but their observations were subjective. In any event, it is certainly a very slow process, and demonstrates that luminescence cannot function as a frequently repeatable event in the normal economy of this species.

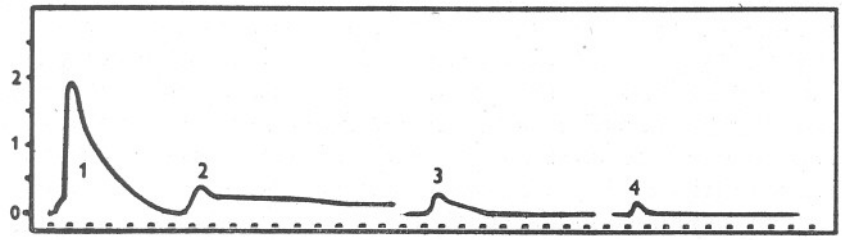

Fig. 7. Record of light produced by photogenic glands on the aliform notopodia. Fatigue in light-producing ability as the result of repeated electrical stimulation is demonstrated. 1, 2, 3, 4, light produced by 30 sec. periods of stimulation at a frequency of 2 per sec. Pause of 7 min. between 1 and 2; 1 hr. between 2 and 3; and 3 hr. between 3 and 4. Time scale below, 1 per min. Intensity, to the left, in arbitrary units.

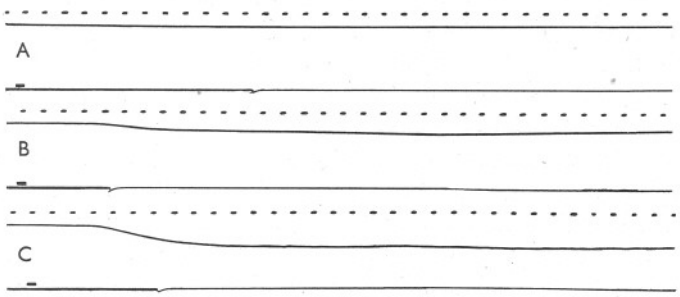

Fig. 8. Effect of voltage increases on the luminescent response. Oscilloscope records of light produced by the aliform notopodia. Stimulation consisted of 0·5 sec. bursts at 25 per sec., A, at 20 V., B, at 40 V., and C, at 60 V. Stimulation indicated below each record by a short horizontal line; time scale above each record, 1 per sec.

Gradually increasing the voltage, other factors remaining constant, increases the light response. Fig. 8 shows the result of an experiment in which the voltage was gradually increased, stepwise. For each rise in stimulus strength above threshold there is a corresponding increase in the resultant light intensity. The effect is probably due to the stimulation of more and more nerve fibres as the electric current becomes more widespread.

At a low frequency of stimulation (1·5 per sec.) light is confined to the region stimulated. Thus, when the stimulating electrodes are applied to the ventral surface of segment XII, against the nerve cord, and low frequency

stimulation is applied, light appears in the aliform notopodia of that segment only. Stimulation of segments XIII, XIV, XV, or XVI, results in luminescence of the dorsal tubercle or fan in the segment stimulated (Fig. 9). Stimulation of the posterior region results in the appearance of light in a few (2–3) pairs of notopodia in the neighbourhood of the electrodes. Stimulation of segments anterior to XII at a low frequency has no effect. At a higher frequency, beginning at about 6 per sec., the excitation spreads to other segments, and the area affected increases as the frequency is raised. Thus, when the ventral surface of the posterior region is stimulated at frequencies of 6–9 per sec., the notopodia of about 10 posterior segments in the region of the electrodes luminesce. Further increase in frequency causes all notopodia of the posterior region to luminesce. Similarly, stimulation of the ventral surface of segments III–V at frequencies of 6 or more per sec. causes the aliform notopodia to luminesce. In some animals stimulation of the anterior region at high frequencies (9 or more per sec.) causes the excitation to be transmitted to middle and posterior regions of the body, as well. This was observed in only certain animals, however, and often excitation was confined to the anterior, middle, or posterior region, whichever was stimulated.

Transmission of excitation in these experiments is through the nerve cord. When the nerve cord is cut, and the animal is stimulated at a high frequency on one side of the incision, the excitation fails to jump the gap.

These observations point to the existence of internuncial facilitation in the nerve cord of *Chaetopterus*. The transmission of excitation from segment to segment presumably depends upon linked neurones arranged in series along the cord, and in connexion with this thesis it may be noted that giant axon systems are wanting in the nerve cord of *Chaetopterus*. In the nervous pathways involved in luminescence, single impulses, or impulses at low frequencies, are not transmitted from one neurone to the next along the cord. When the frequency is raised above a critical level, however, augmentation occurs at intervening synapses, and impulses can sweep through to successive segments.

Effects of Autonomic Drugs

The cholinergic nature of the nerve fibres innervating certain glands in mammals is well established, and acetylcholine has been implicated as a chemical transmitter in the submaxillary and adrenal glands. Chemical transmitters have also been proposed in connexion with certain observations on neuro-muscular functioning of various annelids (Bacq, 1947; Botsford, 1941). It is of interest, therefore, to determine whether similar processes are involved in the nervous control of light production in *Chaetopterus*. Towards this end, the pharmacological effects of several autonomic drugs were tried on this animal.

The drugs employed were adrenaline, acetylcholine, nicotine, and eserine

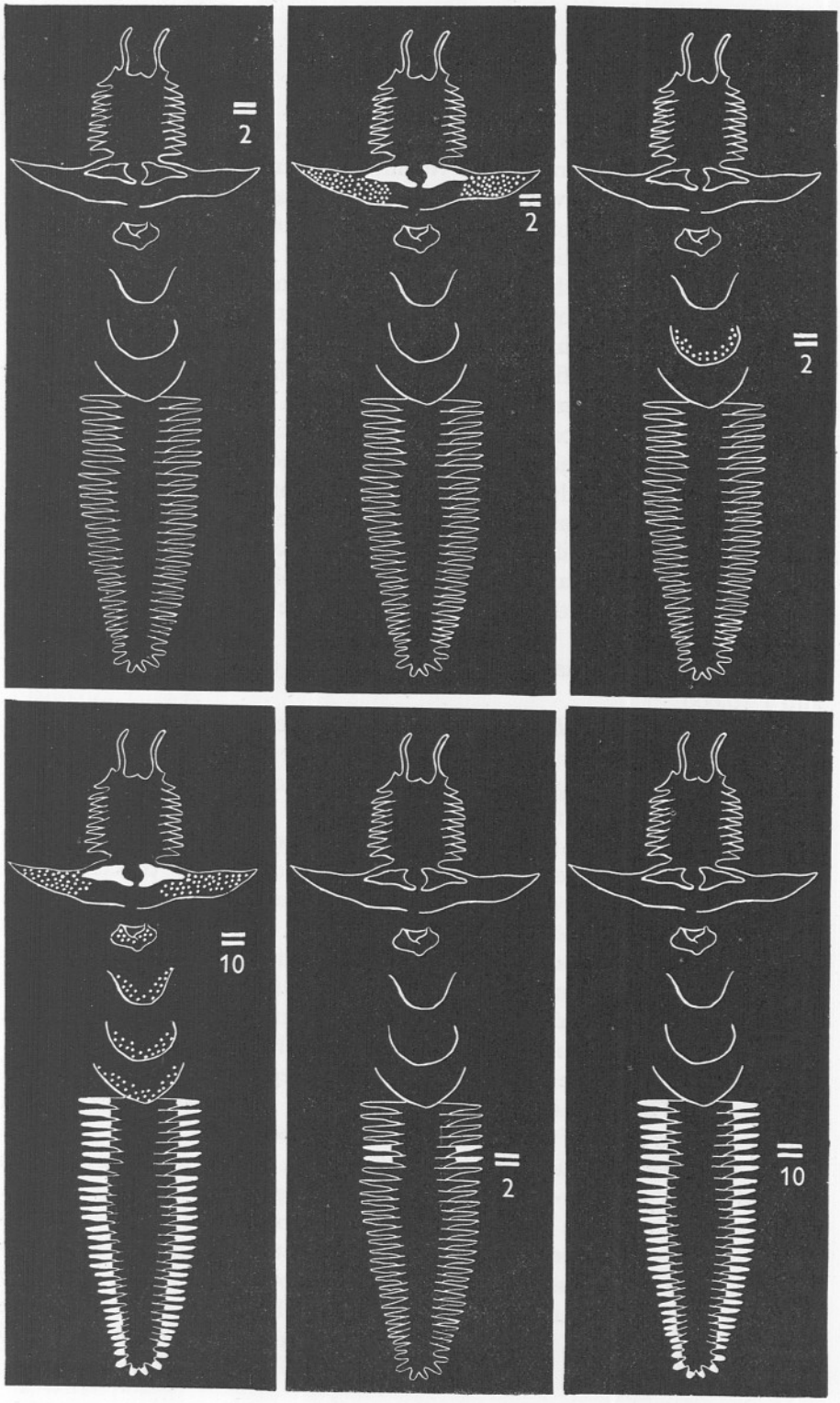

Fig. 9. The effects of stimulating the nerve cord at various frequencies. The double bar indicates the position of the stimulating electrodes. The numbers refer to the frequency of stimulation. Note the tendency for the excitation to spread as the frequency is raised.

(physostigmine salicylate). They were dissolved in sea water, in concentrations which are given as weight by volume, except for nicotine where the figures refer to concentrations in volume by volume. The solutions were applied in one of three ways: an intact animal was placed in a solution of the drug to be tested; or excised pieces of potentially luminescent tissues were placed in the solution; or solutions of drugs were injected into intact animals. The results of these experiments are summarized as follows.

Adrenaline. In concentrations of 1/1000 and 1/10,000 this drug failed to induce luminescence. This confirms an earlier observation of Harvey (1931) that adrenaline has no effect on luminescence in *Chaetopterus*.

Acetylcholine. Five intact animals were placed in a solution of acetylcholine (1/10,000), and one responded by luminescing brightly in all regions after intervals of 4–17 min., depending on the region lighting up. Injecting 0·1 or 0·2 c.c. of acetylcholine (1/100 to 1/5000) into the anterior or middle regions caused the appearance of flashes or persistent weak light in the fans, dorsal tubercle, and aliform notopodia. Pieces of the animal containing light-producing tissues and nerve cord shone feebly in solutions containing 1/1000 acetylcholine. Other pieces, from which the nerve cord was removed, behaved similarly.

Eserine. This drug had no apparent effect in concentrations of 1/1000 and 1/10,000.

Eserine and Acetylcholine. These two drugs, used together (both in concentrations of 1/1000 or 1/10,000) failed to evoke luminescence in isolated pieces of light-producing tissues. Injection of 0·2 c.c. of 1/1000 eserine and 1/1000 acetylcholine into the fans and anterior region resulted in some transitory flashes of light from the fans, dorsal tubercle, and aliform notopodia.

Nicotine. When tested on intact animals nicotine, in concentrations 1/1000 and 1/10,000, evoked a faint brief appearance of luminescence in about half the animals tested.

It is apparent from these results that sympathomimetic and parasympathomimetic drugs, which are frequently effective in inducing activity in other animals, have slight and rather inconsistent effects on light production in *Chaetopterus*. Acetylcholine and nicotine definitely induce luminescence in some animals, but the effect is somewhat irregular in occurrence and distribution. There is no evidence that eserine is effective by itself, or that it enhances the effect of acetylcholine in these experiments.

It is interesting that acetylcholine is effective in inducing luminescence in isolated pieces of light-producing tissues lacking central nervous system. This provides evidence that the drug is acting peripherally on the neuroglandular junction, although it does not exclude the possibility that it may be acting at other loci as well. The action of nicotine recalls its stimulatory effect on cholinergic neurones of other animals. The light produced by these drugs is usually rather weak and ephemeral, and probably reflects a slow

rate of diffusion of the acetylcholine or nicotine through the tissues of the body wall. In general, it appears that acetylcholine exerts a nicotine-like action on the nervous system of this worm, and stimulates the neuro-effector junctions in the photogenic tissues.

Autonomic drugs have, of course, been used in the study of the luminescence of other animals. Adrenaline evokes the appearance of light in the photophores of the deep-sea fish *Echiostoma ctenobarba*, and of the midshipman *Porichthys notatus* from shallow waters (both teleosts) (Greene & Greene, 1924; Harvey, 1931, 1940). Adrenaline also produces a constant glow lasting several hours in the lampyrid *Photuris pennsylvanica* (Creighton, 1926; Emerson & Emerson, 1941.)

It is doubtful whether any useful comparisons can be made of the action of drugs on bioluminescence *per se* in such widely unrelated animals as those just mentioned, without first assembling detailed information about the action of those drugs on the nervous system and various effectors in each particular form. Adrenaline, for example, is a normal constituent of fish and is produced by suprarenal tissue. Its effectiveness in producing luminescence in *Porichthys* and *Echiostoma* suggests that the nerve fibres supplying the photophores in teleosts are adrenergic, and that the secretion of adrenaline into the blood stream may also be a factor in evoking luminescence. Chromaffin tissue, on the other hand, is rare in polychaetes (Bacq, 1947; Gaskell, 1914). There is now some evidence that cholinergic fibres are widespread in annelids. Acetylcholine brings about muscular contractions in *Arenicola*, *Branchiomma*, *Hirudo* and *Lumbricus*, and eserine augments and prolongs the muscular response to electrical stimulation in some of these animals (Bacq, 1947; Bacq & Coppée, 1937; Katz, 1949; Wu, 1939). Tonic contracture is induced in the isolated extrovert of *Arenicola* by acetylcholine, presumably through excitation of the oesophageal pace-maker (Wells, 1937), and a cholinesterase has been identified in the body wall of *Myxicola* (Bacq, 1937). The positive response of acetylcholine on bioluminescence in *Chaetopterus* fits into this picture, and suggests that cholinergic neurones are involved in the light response.

Effects of Various Cations and Unbalanced Salt Solutions

The effects of various cations on light production were investigated by immersing whole animals in solutions of the several salts. These were all chlorides of Na, K, Ca and Mg. The salts were employed singly and in different combinations to reveal their balancing or antagonistic effects. The solutions, listed below, were used as made up, and also after readjustment of the pH to 8·2 by the addition of NaOH, KOH, HCl, or MgO, as necessary. Variations in pH from 7 to 9 were found not to be a limiting factor in these experiments. Each cation or combination of cations was tried on at least three animals.

1. 0·54M-NaCl 2. 0·54M-KCl
3. 0·36M-$CaCl_2$ 4. 0·36M-$MgCl_2$
5. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol.
6. 0·54M-NaCl, 25 vol. + 0·36M-$CaCl_2$, ½ vol.
7. 0·54M-NaCl, 25 vol. + 0·36M-$MgCl_2$, 2 vol.
8. 0·54M-KCl, 25 vol. + 0·54M-NaCl, ½ vol.
9. 0·54M-KCl, 25 vol. + 0·36M-$CaCl_2$, ½ vol.
10. 0·54M-KCl, 25 vol. + 0·36M-$MgCl_2$, 2 vol.
11. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$CaCl_2$, ½ vol.
12. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$MgCl_2$, 2 vol.
13. 0·54M-NaCl, 25 vol. + 0·54M-KCl, ½ vol. + 0·36M-$CaCl_2$, ½ vol. + 0·36M-$MgCl_2$, 2 vol.

Certain cations and combinations of cations had marked stimulatory effects, as the following summaries of the experimental protocols show.

1. *Isotonic* NaCl. Addition of this solution caused luminescence in most or all of the notopodia of the posterior region, followed by weak lighting of the fans in the middle region, and in the aliform notopodia and tentacles.

2. *Isotonic* KCl. This solution immediately caused brilliant and lasting luminescence of all areas: posterior notopodia, dorsal tubercle and fans of the middle region, aliform notopodia and peristomial tentacles. A copious secretion was also discharged from the glands at the bases of the aliform notopodia. This brilliant illumination lasted about 15 min., and then faded away.

3. *Isotonic* $CaCl_2$ had no apparent effect.

4. *Isotonic* $MgCl_2$ had no apparent effect.

5. *Isotonic* NaCl + KCl. This solution produced a bright display almost at once from the notopodia of the posterior region, the dorsal tubercle, and the aliform notopodia.

6. *Isotonic* NaCl + $CaCl_2$. In two specimens a few faint pin-points of light appeared momentarily on some notopodia of the posterior region. Two other specimens were negative.

7. *Isotonic* NaCl + $MgCl_2$. This solution caused luminescence of posterior notopodia, fans, dorsal tubercle, aliform notopodia, and the glands at the bases of the aliform notopodia. The light appeared after about 2 min., was usually brief and rather faint, and affected different specimens in varying degree.

8. 9, 10. *Isotonic* KCl + *either* NaCl, *or* $CaCl_2$, *or* $MgCl_2$. Each of these solutions caused a bright and lasting glow from all luminescent areas, and a copious amount of luminescent secretion from the glandular areas at the bases of the aliform notopodia.

11. *Isotonic* NaCl + KCl + $CaCl_2$. Addition of this solution produced a few faint points of light in the posterior notopodia of one specimen, but had no effect on three others.

12. *Isotonic* NaCl + KCl + $MgCl_2$. This solution caused some notopodia in the posterior region of five specimens to glow brightly, and in two animals evoked brief bright flashes in the alar notopodia, and a brief glow from the dorsal tubercle and glands at the bases of the aliform notopodia as well.

13. *Isotonic* NaCl + KCl + $CaCl_2$ + $MgCl_2$. This solution had no visible effect.

The stimulatory effect of both sodium and potassium on nerve and muscle is well known, and has been reviewed, among others, by Heilbrunn (1943). Sodium stimulates the cardiac ganglion of *Limulus*, and renews rhythmic pulsations in Scyphomedusae on removal of the marginal sense-organs. Potassium stimulates the marginal sense-organs of Scyphomedusae, excites

the isolated extrovert of *Arenicola*, and generally stimulates nerve cells and nerve fibres. Magnesium usually exerts a depressive effect and is a general anaesthetic for invertebrates, and calcium, in small amounts, offsets the toxic properties of sodium and potassium (Brown & MacIntosh, 1939; Hodgkin & Huxley, 1945; Rosenblueth, 1950; Wells & Ledingham, 1942).

Studies dealing with the effects of ions on the luminescent response of Metazoa have been confined, hitherto, to coelenterates and ctenophores. There is general agreement that in Scyphomedusae and in ctenophores potassium and calcium evoke and augment luminescence, which fails when these ions are omitted. Sodium, by itself, has little effect. Magnesium reduces luminescence, but when this ion is absent the ability to luminesce is increased (Hykes, 1928; Heymans & Moore, 1924, 1925; Moore, 1926). In general, potassium and calcium are stimulatory in these animals, and the effect is offset by magnesium. These results are somewhat divergent from those obtained with *Chaetopterus*. In this animal potassium has the greatest stimulatory effect, evoking bright luminescence of all regions, and it is seconded by sodium. By itself calcium evokes no luminescence and it fails to suppress the luminescence evoked by potassium. The addition of calcium to a solution of potassium and sodium, however, results in a more balanced physiological solution that fails to stimulate. Magnesium also reduces the stimulatory powers of sodium and potassium. These effects are referred to stimulation of the nerve cells and nerve fibres supplying the luminescent gland cells by sodium and potassium, rather than to any action of these ions directly on the glandular cells. Even after a period of maximal glow evoked by the application of KCl it is still possible to produce the release of further luminescent secretion by direct mechanical stimulation of the photogenic cells in the aliform notopodia. This shows that the glandular cells are still intact and contain a considerable residual amount of photogenic material. Calcium and magnesium, in turn, oppose the stimulatory action of potassium and sodium on the nervous elements.

Effects of Hypotonic and Hypertonic Solutions

Many of the older accounts dealing with bioluminescence refer to the stimulatory effect of fresh water in evoking a luminous response. Panceri (1872, 1878), for example, in studies dealing with the luminescence of marine animals, consistently made use of fresh water to bring about the production of light. This earlier work has been followed up by investigating the effects of various hypotonic and hypertonic solutions of sea water on light production in *Chaetopterus*. To test the effect of a solution, an animal was placed in a dish, dorsal side uppermost, and all sea water was drained off; the solution in question was then added to the dish in sufficient quantity to submerge the animal. The effect of each solution was tested on four or more animals.

Hypotonic Solutions

(1) Distilled water evoked luminescence in about 1 min. Light appeared at first towards the posterior end of the worm, and spread anteriorly to involve the fans, dorsal tubercle, and aliform notopodia.

(2) 20, 30, 40 % sea water. All these solutions caused luminescence in about 1 min. The posterior notopodia lighted first, and the effect gradually spread orally to involve more anterior luminescent regions (fans, dorsal tubercle, aliform notopodia), in varying degree, depending on the animal.

(3) 50 % sea water. This solution evoked luminescence in the posterior notopodia of two out of four animals examined.

(4) 60 % sea water. Three animals gave no response. In a fourth animal there were a few weak flashes from notopodia of the posterior region and from the aliform notopodia after about 1 min.

(5) 70 and 90 % solutions of sea water were without effect.

Hypertonic Solutions

Hypertonic sea water, at strength 150 %, was tried on six specimens. The concentrated sea water was prepared by boiling, and the pH was returned to 8·2 with sodium bicarbonate. It failed to induce luminescence.

These experiments reveal that diluted sea water first evokes luminescence at a strength of about 60 %. The effect increases with greater dilutions, and reaches a maximum in distilled water. Hypertonic sea water (150 %) has no effect.

The mode of action of hypotonic solutions is not clear. They may excite luminescence by a direct osmotic effect, causing cytolysis of the glandular cells; or they may act by differential leaching of ions from nervous elements, giving rise to nervous excitation. *Chaetopterus* is not an estuarine form, and would not be expected to possess any power of osmotic regulation. A tendency is noted for the posterior notopodia to lighten first in hypotonic solution, showing that the profuse mucous secretion of the anterior and middle regions exerts some protective effect.

Discussion and Conclusions

The present investigation demonstrates that luminescence in *Chaetopterus* is under nervous control. Under localized tactile stimulation light appears only in a restricted area, and even severe injury, amounting to mutilation, fails to evoke widespread luminescence.

Information about the transmission processes involved in the luminous responses is revealed by electrical stimulation of the animal. It is found that low frequencies give a very localized response, confined to a segment or a few segments stimulated, but as the frequency is raised, excitation is transmitted to other regions, until finally the whole animal may lighten. It is

concluded that the spread of excitation is a process depending upon the existence of internuncial facilitation in the nerve cord. Through pathways for the luminescent response appear to be lacking, and transmission through the central nervous system involves the build up of an excitatory state at synapses with the arrival of successive stimuli.

The results obtained by electrical stimulation suggest certain ways in which the luminescent response can be regulated. The latter is in some way dependent on the degree of peripheral stimulation. Increased tactile stimulation, presumably, will evoke a higher frequency of discharge, and maintained stimulation a prolonged volley in sensory pathways. At least two factors are operating on the efferent side which determine the magnitude of the response, namely number of neuro-effector units brought into activity and number of nervous impulses discharged. Increase in either the number of efferent stimuli or the number of gland cells excited will result in more light. The significance of the high frequency effect on central nervous transmission in the normal functioning of the animal is more doubtful, but it may represent a mechanism whereby prolonged and vigorous tactile stimulation will bring glandular cells of more distant regions into activity.

There are few comparable studies on other species for comparison. The interesting physiological investigations on nervous control of luminescence in coelenterates and ctenophores show features peculiar to those groups, and necessitate interpretation in terms of the nerve-net existing in those forms. Fujiwara (1935) has shown in *Mesochaetopterus* that electrical stimulation causes the transmission of an excitatory process along the body, resulting in luminescence. Thus, there are certain physiological features common to two genera of chaetopterids, *Chaetopterus* and *Mesochaetopterus*. Other patterns of nervous control in polychaetes are suggested from studies of luminescence in polynoids. Thus in *Acholoë* it has been found that light tactile stimulation gives rise to a local luminescent response, but strong stimulation evokes more widespread luminescence. Transection of the animal causes the posterior fragment to luminesce, but not the anterior piece (Kutschera, 1909). One explanation advanced is that the excitation can only be transmitted caudally, but the reason for this restriction is not clear, and further physiological studies on polynoids and other luminescent forms would be of great interest.

I should like to express my thanks to Dr W. R. G. Atkins, F.R.S., for some helpful criticisms about several aspects of the work, and for the loan of a camera and galvanometer. It is a pleasure to acknowledge technical assistance from Mr F. J. Warren. Part of the expenses incurred in this research was defrayed by a grant from the Government Grant Committee of the Royal Society.

Summary

The nervous control of luminescence in *Chaetopterus variopedatus* was investigated by various direct and indirect means. Quantitative measurements of the light produced by the animal were obtained by the use of a multiplier photocell and sensitive galvanometer or oscilloscope.

Tactile or mechanical stimulation gives a rather localized luminescent response. The most effective stimuli for evoking luminescence of the conspicuous light glands of the aliform notopodia are tension and pressure acting on segment XII.

Electrical stimulation of segment XII (condenser discharges) causes the appearance of light in the glands on the aliform notopodia. The mean latent period, as determined from oscilloscope records, was 4·2 sec., and the time taken to reach maximal intensity from first deflexion was 10·3 sec.

A single shock causes the appearance of light, and the intensity of the response is increased by increasing the voltage or the number of stimuli. Raising the voltage throws more efferent neurones into activity. Augmenting the number of stimuli results in an enhanced effect, and more luminescent material is secreted.

The preparation fatigues readily, and successive periods of stimulation give greatly decreased responses. No recovery was observed under experimental conditions after a rest period of 3 hr.

At low frequencies of stimulation the response is restricted to the segment or few segments directly stimulated. Raising the frequency brings more segments into luminescence. This effect is ascribed to some process of internuncial facilitation in the nerve cord.

The effects of four autonomic drugs were tried. Adrenaline had no effect. Acetylcholine and nicotine were weakly excitatory. Acetylcholine produced luminescence in fragments lacking central nervous tissue as well as in pieces containing nerve cord; it has an excitatory effect, therefore, on peripheral elements. There was no noticeable augmentatory effect with eserine. The evidence suggests a nicotine-like action of acetylcholine acting peripherally.

Isotonic solutions of NaCl, KCl, $CaCl_2$ and $MgCl_2$ were tried on the preparation. K and Na were excitatory, particularly the former. Addition of Mg reduced the excitatory effect of K and Na, and Ca inhibited the luminescence usually evoked by K and Na salts. A balanced salt solution, containing K, Na, Ca, and Mg, in the proportions in which they occur in sea water, failed to produce luminescence. The excitatory effects of K and Na, and the opposing effects of Ca and Mg, are ascribed to stimulation of nervous elements concerned with luminescence.

Hypotonic solutions and fresh water are stimulatory, luminescence appearing in about 60% sea water. The effect is not clear; it may act through cytolysis of glandular cells, or by differential leaching of ions.

Hypertonic solutions (150% sea water) have no excitatory effect.

A review of the literature dealing with luminescence in *Chaetopterus* is given, and the physiological results obtained in the present investigation are compared with observations on several other forms.

REFERENCES

BACQ, Z. M., 1937. Nouvelles observations sur l'acétylcholine et la choline-estérase chez les Invertébrés. *Arch. Internat. Physiol.*, T. 44, pp. 174–89.

—— 1947. L'acétylcholine et l'adrénaline chez les Invertébrés. *Biol. Rev.*, Vol. 22, pp. 73–91.

BACQ, Z. M. & COPPÉE, G., 1937. Réaction des Vers et des Mollusques à l'éserine. Existence de nerfs cholinergiques chez les Vers. *Arch. Internat. Physiol.*, T. 45, pp. 310–24.

BONHOMME, C., 1943. L'appareil lumineux de *Chaetopterus variopedatus* Clap. Recherches histologiques. *Bull. Inst. Océanogr. Monaco*, No. 843, 7 pp.

BOTSFORD, E. F., 1941. The effect of physostigmine on the responses of earthworm body wall preparations to successive stimuli. *Biol. Bull. Woods Hole*, Vol. 80, pp. 299–313.

BROWN, G. L. & MACINTOSH, F. C., 1939. Discharges in nerve fibres produced by potassium ions. *Journ. Physiol. (Proc.)*, Vol. 96, 10*P*–11*P*.

CREIGHTON, W. S., 1926. The effect of adrenalin on the luminescence of fireflies. *Science*, Vol. 63, pp. 600–1.

DAHLGREN, U., 1916. The production of light by animals. *Journ. Frank. Inst.*, Vol. 181, pp. 659–96, 804–43.

DUBOIS, R., 1887. De la fonction photogénique chez le *Pholas dactylus*. *C.R. Acad. Sci. Paris.*, T. 105, pp. 690–2.

EMERSON, G. A. & EMERSON, M. J., 1941. Mechanism of the effect of epinephrine on bioluminescence of the firefly. *Proc. Soc. Exp. Biol., N.Y.*, Vol. 48, pp. 700–3.

ENDERS, H. E., 1909. A study of the life history and habits of *Chaetopterus variopedatus* Renier et Claperède. *Journ. Morph.*, Vol. 20, pp. 479–531.

FAUVEL, P., 1927. *Polychètes sédentaires*. Faune de France, Vol. 16. Paris.

FUJIWARA, T., 1934. On a new chaetopterid, *Mesochaetopterus japonicus* sp.nov. *Journ. Sci. Hiroshima Univ.*, Ser. B, Div. 1, Zool., Vol. 3, pp. 1–14.

—— 1935. On the light production and the luminous organs in a Japanese chaetopterid, *Mesochaetopterus japonicus* Fujiwara. *Journ. Sci. Hiroshima Univ.*, Ser. B, Div. 1, Zool., Vol. 3, pp. 185–92.

GASKELL, J. F., 1914. The chromaffine system of annelids and the relation of this system to the contractile vascular system of the leech, *Hirudo medicinalis*. *Phil. Trans. Roy. Soc.*, B, Vol. 205, pp. 153–211.

GREENE, C. W. & GREENE, H. H., 1924. Phosphorescence of *Porichthys notatus*, the California singing fish. *Amer. Journ. Physiol.*, Vol. 70, pp. 500–6.

HARVEY, E. N., 1920. *The Nature of Animal Light*. Philadelphia and London.

—— 1926. Bioluminescence and fluorescence in the living world. *Amer. Journ. Physiol.*, Vol. 77, pp. 555-61.

—— 1931. Stimulation by adrenalin of the luminescence of deep-sea fish. *Zoologica, N.Y.*, Vol. 12, pp. 67–9.

—— 1940. *Living Light*. Princeton, N.J.

—— 1948. Introductory remarks: a general survey of bioluminescence. *Ann. N.Y. Acad. Sci.*, Vol. 49, pp. 329–36.

HEILBRUNN, L. V., 1943. *An Outline of General Physiology*. Philadelphia and London.

HEMPELMANN, F., 1934. Polychaeta. In Kükenthal's *Handbuch der Zoologie*, 2 Bd., 2 Hälfte. Leuchten, S. 131–3. Berlin u. Leipzig.

HEYMANS, C. & MOORE, A. R., 1924. Luminescence in *Pelagia noctiluca*. *Journ. Gen. Physiol.*, Vol. 6, pp. 273–80.

—— —— 1925. Note on the excitation and inhibition of luminescence in *Beroe*. *Journ. Gen. Physiol.*, Vol. 7, pp. 345–8.

HODGKIN, A. L. & HUXLEY, A. F., 1945. Resting and action potentials in single nerve fibres. *Journ. Physiol.*, Vol. 104, pp. 176–95.

HYKES, O. V., 1928. Contribution à la physiologie de la luminescence et de la motilité des Coelentérés. *C.R. Soc. Biol.*, T. 98, pp. 259–61.

JOYEUX-LAFFUIE, J., 1890. Étude monographique du Chétoptère (*Chaetopterus variopedatus*, Renier) suivie d'une revision des espèces du genre *Chaetopterus*. *Arch. Zool. Exp. Gén.*, T. 8, pp. 245–360.

KATZ, B., 1949. Neuro-muscular transmission in invertebrates. *Biol. Rev.*, Vol. 24, pp. 1–20.

KREKEL, A., 1920. Das Leuchtorgane von *Chaetopterus variopedatus* Clap. *Zeit. wiss. Zool.*, Bd. 118, pp. 480–509.

KUTSCHERA, F., 1909. Die Leuchtorgane von *Acholoe astericola* Clprd. *Zeit. wiss. Zool.*, Bd. 92, pp. 75–102.

LANKESTER, E. R., 1868. Preliminary notice of some observations with the spectroscope on animal substances. *Journ. Anat. Physiol.*, Vol. 2, pp. 114–16.

LESPÈS, C., 1872. Étude anatomique sur un Chétoptère. *Ann. Sci. Nat. Zool.*, T.15, No. 14, 17 pp.

MCINTOSH, W. C., 1915. *A Monograph of the British Marine Annelids*, Vol. 3. London: Ray Society.

MANGOLD, E., 1910–14. Die Produktion von Licht. In Winterstein's *Handbuch der vergleichenden Physiologie*, 3 Bd., 2 Hälfte, S. 225–392.

MOORE, A. R., 1926. Galvanic stimulation of luminescence in *Pelagia noctiluca*. *Journ. Gen. Physiol.*, Vol. 9, pp. 375–9.

NICOL, J. A. C., 1952. Studies on *Chaetopterus variopedatus* (Renier). I. The light-producing glands. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 417–31.

PANCERI, P., 1872. Études sur la phosphorescence des animaux marins. *Ann. Sci. Nat. Zool.*, T. 16, Art. 8, 66 pp.

—— 1878. La luce e gli organi luminosi di alcuni annelidi. *Atti. R. Accad.*, Napoli, Vol. 7, No. 1, 20 pp.

ROSENBLUETH, A., 1950. *The Transmission of Nerve Impulses at Neuroeffector Junctions and Peripheral Synapses*. London.

STEPHENSON, E. M., 1946. *Animal Camouflage*. Harmondsworth, England.

TROJAN, E., 1913. Ueber Hautdrüsen des *Chaetopterus variopedatus* Clap. *S.B. Akad. Wiss. Wien*, Bd. 122, pp. 565–96.

TROJAN, E., 1914. Ueber die Bedeutung der 'follicules bacillipares' Claparède's bei *Chaetopterus variopedatus*. *Proc. IX Int. Zool. Congr. Monaco*, 1913, pp. 390–5.

WELLS, G. P., 1937. Studies on the physiology of *Arenicola marina* L. I. The pace-maker role of the oesophagus, and the action of adrenaline and acetylcholine. *Journ. Exp. Biol.*, Vol. 14, pp. 117–57.

WELLS, G. P. & LEDINGHAM, I. C., 1942. Studies on the physiology of *Arenicola marina* L. III. The potassium relations of the isolated extrovert. *Journ. Exp. Biol.*, Vol. 19, pp. 176–85.

WILL, F., 1844. In Krekel, 1920. (See above.)

WU, K. S., 1939. The action of drugs, especially acetylcholine, on the annelid body wall (*Lumbricus*, *Arenicola*). *Journ. Exp. Biol.*, Vol. 16, pp. 251–7.

PROCESSES OF ENRICHMENT OF SURFACE WATER WITH NUTRIENTS DUE TO STRONG WINDS BLOWING ON TO A CONTINENTAL SLOPE

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(Text-figs. 1–4)

Biological and physical evidence suggests that the area south-west of Ireland is one of loss from the Celtic Sea. In winter the shelf water there may cascade to 400 m. or even deeper (Cooper & Vaux, 1949). All the evidence suggests that new water enters the Celtic Sea and English Channel over the continental slope between Ushant and the Sole submarine promontory 250 miles to the west. No evidence exists that the Atlantic surface waters are ever rich enough to account for the enrichment of the English Channel observed in the nineteen-twenties. Although the existence then of sufficiently rich oceanic surface water cannot be excluded, it is much more probable that the enrichment was brought about by some form of upwelling. The cause of this is thought to be composite. Only a few times in a century may the component phenomena work together to produce the maximum effect. Each component needs separate study.

There may be two distinct effects of a strong wind blowing on to the continental slope from the south. Such a wind will force light nutrient-poor water against the slope (assumed to extend to the surface of the sea) to form a cushion of considerable depth above sloping isosteres—surfaces of equal density—stable only while the wind lasts (Sandström, 1918; reproduced by Harvey, 1928, fig. 25A). Potential energy has become stored in the water. As soon as the wind dies down and the stress is removed from the sea surface, the potential energy is converted to kinetic energy. Each isosteric surface would then oscillate about its mean level. If there were no frictional losses, this oscillation would go on for ever.

The conditions against an actual continental slope are rather different, since it is usually bordered by a continental shelf. There, when the heavy deeper water rises against the slope, it would spill over the edge on to the continental shelf. Some mixing and enrichment with nutrients of continental shelf water would occur, but the effect is unlikely to be great and it would be important only locally.

But in a submarine valley, such as that at 48° 13′ N., 9° 21′ W., which becomes narrower and shallower as it cuts back into the shelf, such spillage

water would become canalized. Conditions would come to resemble those which create a tidal bore or eagre in the Rivers Severn and Trent. It would seem probable that such a constricted core or eagre of deep water could be projected for many miles on to the continental shelf whence it would return only slowly on the next downward swing of the boundary layer over deep water. This mechanism would be especially favoured if a submarine valley in the slope heads into one of the shallow troughs which dissect the south-western Celtic Sea. Indeed it would provide a means for preventing such troughs from silting up.

The inference is that areas of the sea lying immediately shorewards of a submarine valley should be especially favourable for outbursts of phyto-plankton not only in spring but in summer as well. Submarine eagres of this kind may well often occur but seem insufficient to account for much enrich-ment of large areas such as the Celtic Sea.

Except when cascading is occurring (Cooper & Vaux, 1949), waters near the headings of submarine valleys should become richer in total phosphorus and other 'total' nutrients than those lying near to an undissected continental slope.

Sandström (1918, p. 234) further developed this idea into his concept of 'jibing' of water masses in a high wind. When the external forces, such as wind stress, acting on the sea water reach a magnitude exceeding the highest possible value which can be sustained by the Archimedean forces, a catastrophe takes place and an entirely new state of affairs is brought about, exactly as when the limit of elasticity of a solid is exceeded.

The maximal value of the Archimedean forces is reached when the isosteres become vertical. Should the external forces exceed that required to produce vertical isosteres, then the surface waters will *capsize*, as exemplified in detail in Fig. 1. Then, light water is brought down beneath heavier, the stability is upset and a strong vertical convection ensues whereby the *whole of the water affected is mixed up into one single homogeneous layer*. The specific volume of this layer will be equal to the mean specific volume of the strata of which it is composed, and between this and the water beneath there will be a sharply defined difference of density. In the homogeneous layer there will be no isosteres and, consequently, no Archimedean forces will arise, so that the water therein contained will follow without resistance the direction of any external force acting upon it. The circulation will be highly intensive so that the water will continue homogeneous, and exert a continual friction upon the layer beneath, thus maintaining the sharply defined limit of density between the two. This friction occasions a gradual absorption of the water from the lower layer, so that the upper one will tend to increase in volume, density and nutrient content.

Sandström gave to this process the name 'to jibe'. 'Jibe' is a variant of 'gibe' and means 'to taunt'; either 'gybe' or 'jib' may have been intended.

Their meaning is to swing from one side of a mast to the other. 'Jib' has other meanings; applied to a horse it signifies to stop suddenly, to move restively sideways and backwards. The term 'to jib' could be used but is not particularly appropriate for the present purpose. 'Capsize' is more fitting.[1]

In Fig. 1, panels C and D, as applied to the Celtic Sea, part of the energy of the wind will be expended on raising the level of the water over the continental shelf (i.e. in the Celtic Sea), part in forcing water through escape channels, such as the Straits of Dover and the North Channel, and part in initiating a cyclonic circulation of water to escape south-west of Ireland.

South-west of Ireland the gales most likely to provoke capsizing of water masses will be from the south-west and west, and these are the prevailing winds and those which most often reach gale force. They are commonest in winter and will then combine with cascading and resonance phenomena in the 'South Porcupine submarine indentation' to produce vertical mixing to a very considerable depth (cf. Fig. 2). The waters most concerned will be either oceanic surface waters or water recently cascaded from the continental shelf. There is in this area only rarely a mechanism for enriching the continental shelf with deep nutrients on any considerable scale. Even when enrichment occurs here, the dominant cyclonic circulation will tend to carry the surface water away from the Celtic Sea. The waters over the Porcupine Bank might, however, benefit. Whenever cascading plays a part it will tend to reduce enrichment from deep water by any other mechanism.

Along the southern edge of the Celtic Sea, the strong winds most favourable for capsizing would blow from the south-east or south. These winds are less common than the south-westerlies and westerlies. Moreover, in this area, there is much less cascade water so that, if capsizing occurs, it may bring about mixing with the deeper North Atlantic Central water and even with the Mediterranean or Gulf of Gibraltar water at 800–1200 m. depth, both relatively rich in nutrients (Cooper, 1952). All in all, the most favourable conditions for enrichment of the southernmost Celtic Sea by capsizing are likely to occur after the breakdown of the summer thermocline in autumn. Southerly gales in November and December are likely to be more effective in bringing up nutrients than those in February or March. The usual cyclonic circulation of the Celtic Sea will tend to transport such enriched water on to the continental shelf and into the English Channel.

Conditions to initiate capsizing of water masses are likely to occur over continental slopes backed by extensive shallow seas, for there the surface ocean waters are relatively free to press inwards, whereas the root of the water mass will be stopped completely by the continental slope.

[1] The writer would prefer to introduce the term 'culbute' derived from the French *culbuter* which suggests all that 'capsize' and 'somersault' do, but much destructive power as well. Majority opinion in this laboratory is that addition of yet another word to the technical jargon of science cannot be justified and that 'capsize' will serve (see Addendum, p. 463).

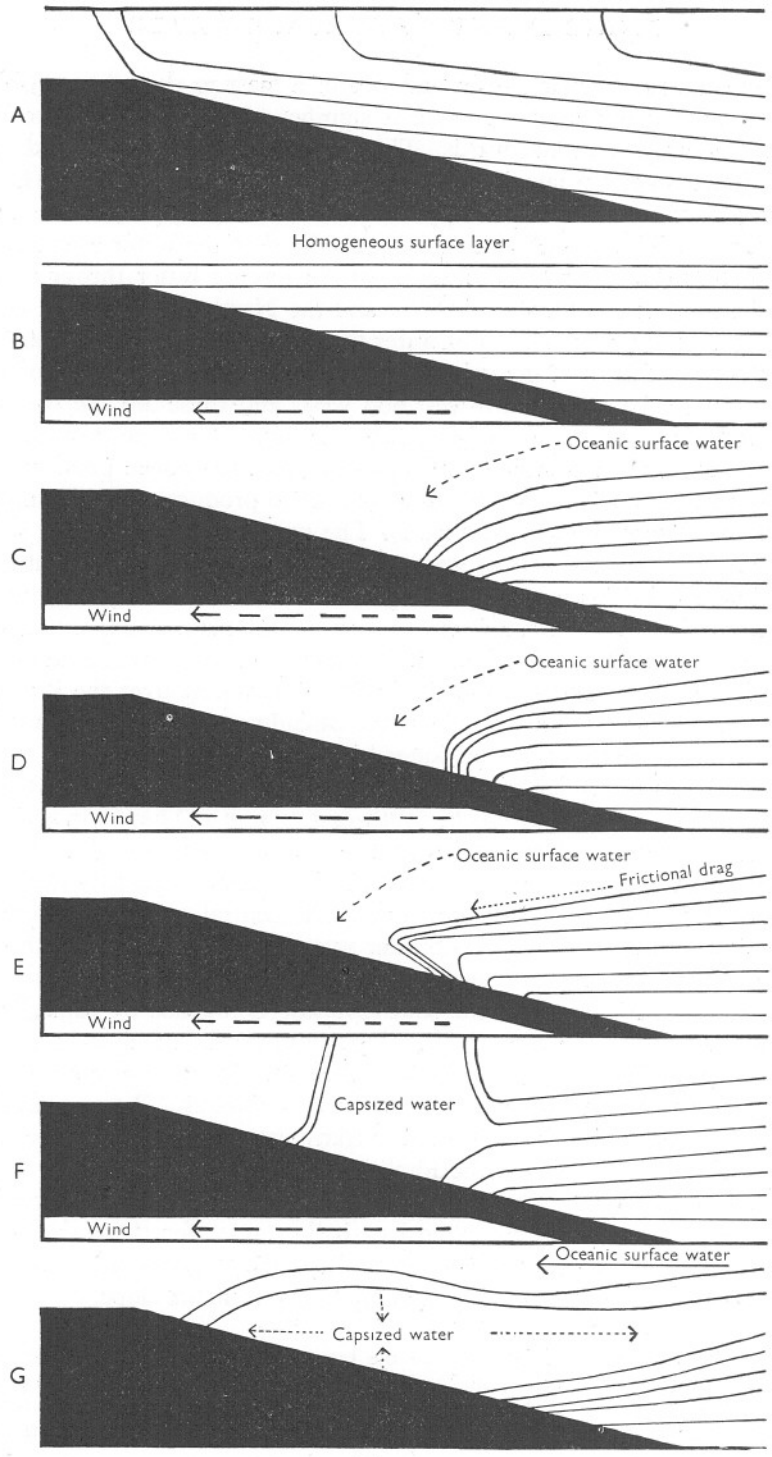
A
Homogeneous surface layer
B
Wind
Oceanic surface water
C
Wind
Oceanic surface water
D
Wind
Oceanic surface water
Frictional drag
E
Wind
Capsized water
F
Wind
Oceanic surface water
Capsized water
G

Fig. 1.

Capsizing is essentially a wave phenomenon and may be compared with the breaking of a roller approaching a beach. By analogy with what happens to a swell approaching an ordinary coastal bay, over a submarine terrain such as that illustrated by Cooper (1952, fig. 10), there should be a tendency for the destructive energy created by capsizing to be concentrated over the submarine spurs and for the headings of the valleys to be relatively quiet. Capsizing as a mechanism for surface enrichment with nutrients is likely to be more effective over strongly dissected sections of the continental slope than over smooth areas.

In September 1950, Dr C. F. Mortimer kindly allowed me to experiment with his model built to illustrate the observed effect on water movements of a strong wind blowing along a stratified lake, Windermere. Mortimer's model, developed quite independently, resembles that illustrated by Sandström (1918, fig. 45), except that it has sloping ends. At the time interest was concentrated on establishing that internal waves from a distant source could produce upwelling phenomena. Although something of the sort could be made to happen, the scale did not seem adequate to account for observations in the ocean.

In these experiments the process of capsizing and the destructive turbulence resulting was demonstrated, yet, I regret to say, it was not until 6 months later, when the theory of capsizing over a continental slope had been further developed from Sandström's work, that the behaviour of the model was understood (see Addendum, p. 462).

A number of phenomena, such as the distribution of mass and of nutrients which would result from currents running parallel to the continental slope

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Legend to Fig. 1.

Fig. 1. A, a frequent pattern of isosteres south of the Celtic Sea in winter when the uppermost 75–100 m. of water in the ocean is homogeneous and is overlying water with density and content of nutrient salts increasing downwards. B, a pattern of isosteres in winter over the continental slope, drawn to a scale of 1:4, with no forces operative. The amount of light water which will later lie to windward is considered unlimited. C and D, cushioning of light oceanic surface water against the continental slope brought about by on-slope gales. The resistance of the solid slope to further progress of the foot of the light water is, however, absolute causing the isosteres to curl and ultimately to become vertical. Restoring Archimedean forces in D have then become zero. E, the drag of the surface wind current will draw the upper strata of stratified water with it leading to an unstable density inversion as illustrated. F, the unstable tongue of heavier water will capsize violently, leading to a homogeneous mass of mixed water extending from the surface to the depth of the bottom of the capsizing water mass. New isosteres, bracketing the capsized water mass, are so created. G, the newly formed surface water will be heavier than the surface water inshore and to seaward and will subside to form a lens of homogeneous water at its appropriate density level and will be replaced by fresh oceanic surface water blown in from seaward. Processes D–G must be considered as simultaneous parts of a continuous process, with the line of capsizing receding from the continental slope and the maximum depth of the phenomenon increasing as the gale proceeds. Consequently the water blown on to the continental shelf of the Celtic Sea by a strong southerly gale should be entirely capsized water and richer in nutrients than it would be if it were solely oceanic surface water. Moreover, the nutrient content of the water passing on to the shelf should increase as the gale proceeds, and the depth of capsizing becomes greater.

have been considered as means of enrichment of surface water with nutrients from deeper layers. None, considered singly, seems able to account for the observed occurrence of nutrients. The concept of capsizing of a water mass over the southern continental slope of the Celtic Sea during strong southerly gales is the first to promise a mechanism on a scale great enough to explain the observed results.

No research ship is ever likely to make direct observations of capsizing water masses during strong on-slope gales. Indeed a shipmaster is likely to take steps to get away from an area of capsizing as quickly as possible. By the time the wind had dropped sufficiently to allow of observations, much of the direct evidence would have vanished. Confirmation will need to be sought by indirect means.

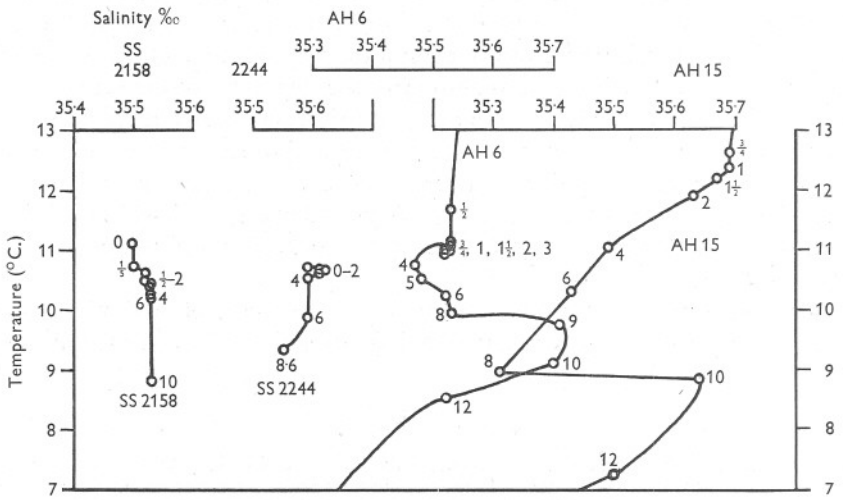

Fig. 2. Temperature-salinity relationships: on two occasions at station SS, 50° 34′ N., 11° 17′ W., on the edge of the 'South Porcupine' submarine bight, south-west of Ireland (SS2158, 14. v. 25, and SS 2244, 19. ii. 27); at *Armauer Hansen* station 1914/6 (5. vi. 14) on the southern edge of the Celtic Sea (cf. Cooper, 1952, figs. 8 and 9); and at *Armauer Hansen* station 15 (9. vi. 14) in the North Atlantic 400 miles from the continental slope. The small figures represent depths in hundreds of metres. The diagram illustrates the vertical compression of properties which may occur in the submarine bight and to a lesser extent anywhere on the continental slope.

A greater understanding of the process of capsizing may contribute to the safety of vessels passing over the continental slope, in particular those engaged in the hake fishery.

Capsizing has to be considered as one only of a number of mechanisms peculiar to the region of the continental slope which contribute in different degrees to the enrichment of the English Channel with nutrients. Atkins's (1923) first measurements on 7 March 1923 showed that the phosphate content of the English Channel at E1 (50° 04′ N., 4° 22′ W.) was then very high

(0·71 μg.-atom/l.). It is of interest that the table of mean wind conditions over the western English Channel (Dietrich & Wyrtki, 1951, used by permission of the Hydrographer of the Navy) shows that in February 1923 the monthly mean wind blew at 8·1 m./sec. from direction true 214°, a monthly mean velocity which has never been exceeded since from any direction. None the less, detailed examination of records shows that it would be too facile to attribute the observed distribution of nutrients in March 1923 solely to capsizing water masses over the continental slope during the preceding south-westerly gales. The event needs to be remembered as one only in the complex of events we are seeking to understand.

Temperature-salinity diagrams for stations 49, 51 and 68 (Cooper, 1952, fig. 4) worked by the *Thor* in 1906 (Schmidt, 1912) are shown in Fig. 3. The middle station 51 is strikingly different from stations 49 and 68, from all others worked by the *Thor* and from International Station E4 (48° 27′ N., 6° 35′ W.) worked 6 days earlier. The isohaline water extended from 50 to 800 m., suggesting that the waters at station 51 had been subjected to more intense vertical mixing. At all the nine deep-water stations worked, except one, marked thermal stratification of the uppermost water layers had become established. The exception was again station 51, where the surface water was only 0·15° C. warmer than at 100 m., the uppermost 50 m. being completely isothermal. The maintenance of such homogeneity in late spring must have demanded powerful forces bringing about vertical mixing.

The position of station no. 51, 48° 07′ N., 9° 03′ W. shown by Cooper (1952, fig. 10), was near a dissected section of the continental slope. Any water movements in such an area should facilitate vertical mixing and capsizing there is likely to be especially strongly developed.

The Daily Weather Reports of the Meteorological Office for November 1905–May 1906 have been examined. The winter was not notably stormy. There were south-westerly gales (Beaufort force 7 or 8) in the area on 22 and 26 November, and a south-south-easterly gale on 18 December. The stormiest period was the first fortnight of January. These were the only gales which could have caused severe capsizing, but they were at the season suspected of being most favourable for nutrient enrichment. The north-westerly gales of 8, 11 and 12 February and 12 March could not have caused capsizing in the southern area. There have been many winters more favourable for capsizing than that of 1905–6.

It has been earlier suggested (Cooper, 1947) that internal waves may play a part in raising nutrient-rich deep water on to the continental shelf. So they may, but now it seems that in this area their influence will be very small compared with that of capsizing. It seems more likely that some internal waves in the ocean may arise from intermittent capsizing over distant continental slopes. This is a process which could be readily established by repeated observations of temperature and salinity at standard depths at a position some

hundreds of miles off a continental slope against which a heavy gale was known to be blowing.

The exceptionally powerful vertical thrusts visualized as occurring beneath a capsizing water mass, followed by subsiding of the relatively heavy new

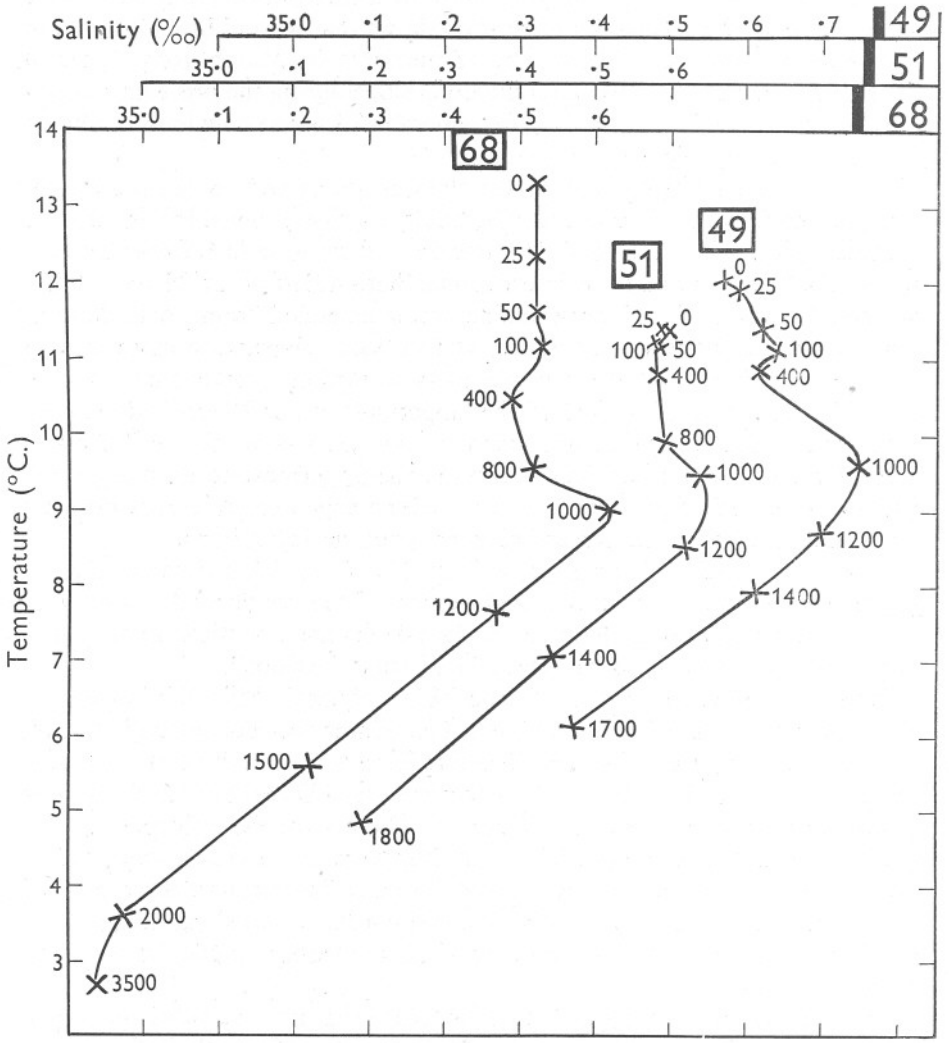

Fig. 3. Temperature-salinity diagrams for three stations (49, 51, 68) worked by *Thor* in May 1906 (see Cooper, 1952, fig. 4). The numbers refer to depths in metres.

surface water and recovery of the deeper water of the same density into a thinner but more extensive lenticular water mass at mid-depths, is a process which must necessarily initiate wave motion in the lower boundary of the

homogeneous water. Internal waves may be a result, not a cause, of a process that leads to enrichment with nutrients of surface waters.

A stratified or laminated water mass underlying a quiescent one, already homogenized by capsizing, may be compared with the leaf-spring of a railway wagon or motor car at rest. In the open ocean, the vertical thrust due to subsequent capsizing of a water mass—if indeed such ever occurs there—would be taken up by the laminated water mass as by a leaf-spring and the energy smoothly dissipated as internal waves. There is no reason to suspect that much dissipation of energy would occur due to friction or turbulence. But against a continental slope, and especially against a strongly dissected one, this 'leaf-spring' of laminated water masses would grind forcibly, so that much of the energy of the vertical thrust due to overhead capsizing would be dissipated by turbulent mixing.

The detailed examination of the Irish records at station SS (Cooper, 1952) has shown that much vertical mixing occurs between 600 and 1000 m. Two of the most extreme occurrences are presented in Fig. 2. On occasion cascading from the north would provide a partial explanation of the observed distribution of properties, but it is clear that it cannot always do so. On some occasions the distribution of temperature has been such as to make it highly improbable that any considerable proportion of the surface water immediately overhead had been carried down. The phenomenon is one of mixing, confined to the deeper strata, without complete homogenization.

It is inconceivable that this phenomenon arises from the mixing action of surface waves. Much thought has been given to internal waves as a cause of such deep turbulence, but no records exist of internal waves in the ocean of sufficient magnitude to produce the observed distribution of properties against the slope.

'Leaf-spring' dissipation of energy beneath a capsizing water mass against a dissected continental slope promises a mechanism able to transmit to very considerable depths energy imparted to the sea surface, and of sufficient magnitude to produce the observed distribution of properties between 600 and 1000 m.

This process of capsizing, if it can be firmly established, would influence the biological cycle in the sea in many very varied ways. The hypothesis fits qualitatively with such local observations as have been examined. It is not proven, and is presented solely as a basis for further quantitative work.

Summary

Some physical processes are examined which may cause enrichment of the surface layers of the sea from deep reserves of nutrients.

Winds blowing intermittently towards a continental slope may produce vertical oscillations which bring about spillage of deeper nutrient-richer water

from the ocean on to the continental shelf. Submarine valleys cut in the continental slope should canalize such spillage water into narrow streams.

Sandström's concept of capsizing of water masses in a high wind has been further developed for the conditions existing over a continental slope. Capsizing of water masses is more likely to enrich the surface layers over the southern rather than over the western continental slope of the Celtic Sea. Capsizing is likely to be especially intense over submarine spurs projecting from dissected regions of the continental slope.

Data collected by the Danish research ship *Thor* in 1906 is adduced as evidence for capsizing over a dissected slope.

Internal waves in the open ocean may possibly be created by the vertical thrusting of capsizing water masses over a continental slope.

The deeper stratified water underlying a region of capsizing has been compared with a leaf-spring of a vehicle. Dissipation of the energy of capsizing in such a leaf-spring of stratified water would produce a distribution of properties such as that often reported from the Irish investigations.

ADDENDUM (Added in Proof)

Photographs to illustrate the process of capsizing have been obtained at the Windermere Laboratory of the Freshwater Biological Association in Dr C. H. Mortimer's (1951) experimental tank. In this the surface layer of water may be warmed and made lighter by two hot wires stretched the length of the tank, and then labelled by means of a dye. Electric blowers simulate wind blowing over a stratified lake or sea.

In the ocean the theory of capsizing of water masses over a continental slope requires a very large reservoir of light surface water lying in the ocean to windward and opportunity for some surface water to be driven on to the continental shelf to leeward. In our area the Celtic Sea and its neighbouring channels provide such opportunity. These conditions the tank cannot provide. Although capsizing has been observed on the 'lee slope' of the tank, it has not been possible to photograph it.

When the blowers are stopped the light surface water in the tank swings from the leeward to the windward end of the tank where a process closely akin to but not identical with capsizing occurs. This is illustrated in Fig. 4. The uncoloured water is heavier than the coloured water and, in the ocean, the condition illustrated should be quickly followed by cataclysmic mixing. Though there is an element of fake in these pictures, none the less they should assist the reader to visualize the process of capsizing which has been described.

The writer is indebted to Mr H. C. Gilson, Director, for placing the facilities of the Windermere Laboratory at his disposal, to Dr Mortimer for the use of the tank and to him and Mr E. Ramsbottom for experimental and photographic assistance.

The term 'capsizing' (see p. 455, footnote) has been discussed with hydrographers during the meeting of the International Council for the Exploration of the Sea at Amsterdam in October 1951. It was clear that to some people the word conjured up a picture of a complete turning-turtle without very much mixing. The most essential part of the process is cataclysmic mixing; overturning is also essential, but in any one incident it need not be complete.

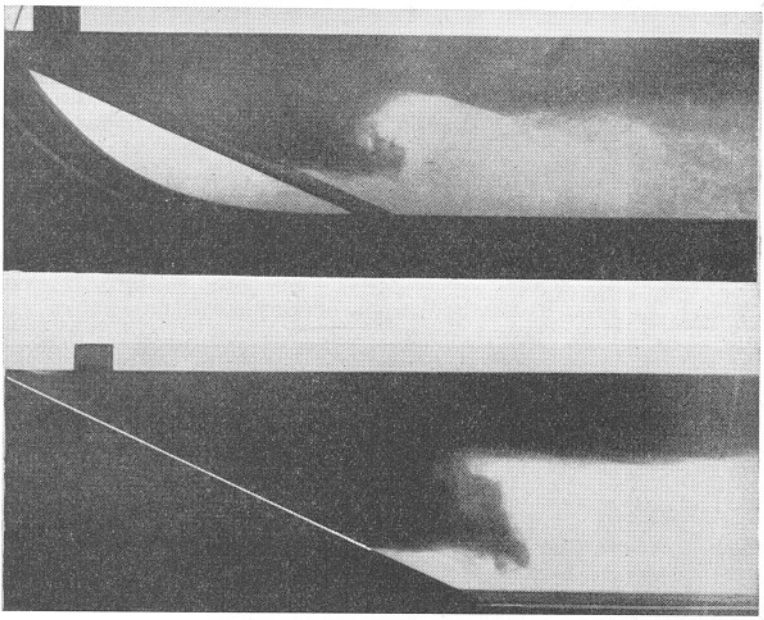

Fig. 4. Two photographs in a model tank to illustrate the process of capsizing of water masses over a continental slope. In both pictures the continental slope is represented by a sheet of metal; in the lower one the dead water beneath the plate has been masked and the boundary between the capsized water and the 'continental slope' has been lightly touched up.

The French word *culbuter*, meaning 'to upset violently resulting in a confused heap or jumble', expresses much better than any English word what is in mind. Mr G. A. Steven, who suggested the apt word 'cascade' for another kind of event over the continental slope, feels strongly that 'culbute' is much the more descriptive word and that its introduction into oceanography is justified. Oceanographers, if they find the need to use the hypothesis, are left to choose the term they think most fitting. If accepted for use in English speech the pronunciation of 'culbute' would be better anglicized.

REFERENCES

ATKINS, W. R. G., 1923. The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. *Journ. Mar. Biol. Assoc.*, Vol. 13, pp. 119–50.

COOPER, L. H. N., 1947. Internal waves and upwelling of oceanic water from mid-depths on to a continental shelf. *Nature, Lond.*, Vol. 159, p. 579.

—— 1952. The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 465–510.

COOPER, L. H. N. & VAUX, D., 1949. Cascading over the continental slope of water from the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 719–50.

DIETRICH, D. & WYRTKI, K., 1951. Tables of monthly mean wind vectors and components for the English Channel as deduced from barometric gradients over the years 1881 to 1949 (less 1943). Admiralty: Hydrographic Department (Oceanographic Branch).

HARVEY, H. W., 1928. *Biological Chemistry and Physics of Sea Water*, 189 pp. Cambridge.

MORTIMER, C. H., 1951. The use of models in the study of water movements in stratified lakes. *Proc. Int. Assoc. Theoretical and Applied Limnology*, Vol. 11, pp. 254–60.

SANDSTRÖM, J. W., 1918. The hydrodynamics of Canadian Atlantic waters. *Canadian Fisheries Expedition*, 1914–15, pp. 221–343. Ottawa.

SCHMIDT, J., 1912. Hydrographical observations. *Rep. Danish Ocean. Exp. 1908–1910*, Vol. 1, pp. 53–75. Copenhagen.

THE PHYSICAL AND CHEMICAL OCEANOGRAPHY OF THE WATERS BATHING THE CONTINENTAL SLOPE OF THE CELTIC SEA

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(Text-figs. 1–15)

CONTENTS

Knowledge of the hydrography of the English Channel and Celtic Sea is needed as a background for the life histories of the mackerel, pilchard and herring and, indeed, of every organism living within range of the Plymouth Laboratory. Such knowledge can never be fully attained until we know more of the exchanges with the deep Atlantic Ocean which take place 200–300 miles to the south-west and west over the continental slope. Moreover, at the slope we shall need to know not only what waters move in and out but what move up and down. Long ago Storrow (1925), and no doubt others, saw clearly some of the problems here to be discussed, but they were unable to bring factual evidence to bear. A critical reconstruction of the considerable but fragmentary observations in the neighbourhood of the continental slope of the Celtic Sea will be presented here and supplemented by observations made in 1950 with the generous co-operation of the vessels of the National Institute

of Oceanography (Discovery Committee) and in 1948 by H.M. Surveying Ship *Dalrymple*. Though many of the conclusions remain tentative, it should now be easier to design observational work at sea to test specific hypotheses at the right time and place by the methods of experimental oceanography. The numerical results in 1950 will be published by the Conseil International pour l'Exploration de la Mer.

In addition to acknowledgements in the text and to many colleagues at the Plymouth Laboratory, thanks are due to the Hydrographer of the Navy for his cordial assistance in many ways and to Dr J. N. Carruthers of the Hydrographic Office, who has frequently constructively assisted from his unrivalled knowledge of the literature. He and Mr G. A. Steven of this laboratory have provided anvils upon which some of the ideas and nomenclature have been hammered out. Mr F. A. J. Armstrong, not only by carrying out all the laboratory analyses and by his critical faculty but by relieving me of many day to day duties, has much furthered this work. Insufficient acknowledgement has been made in the text of the great debt due to the writings of the Scandinavian school of oceanographers, in particular those of B. Helland-Hansen, F. Nansen, J. W. Sandström and H. U. Sverdrup and to those of the Canadian investigator, A. G. Huntsman, and the American, C. G. Rossby.

The Mediterranean or Gulf of Gibraltar Water

The highly saline deeper water (salinity > 38‰) from the Mediterranean Sea spills over the sill of the Straits of Gibraltar and flows downhill, mixing vigorously the while with Atlantic water mostly North Atlantic Central water (p. 479) with a salinity around 36‰. The mixed water attains a density around σ_t 27·6–27·8 and spreads out as an intrusive plate or tongue into the Atlantic at around 1000 m. depth, slowly mixing further with the waters above and below (Helland-Hansen & Nansen, 1927). This 'Mediterranean' water has never been shown to be of importance for studies of surface hydrography in our area, but there is little doubt that it is.

When only salinity, temperature and oxygen have been considered the name 'Mediterranean' has been clear and unambiguous but, when applied in nutrient and productivity studies, it is misleading. 'Mediterranean' suggests a water very poor in nutrients. In fact the 1000 m. stratum here is relatively rich, since it includes a large component of enriched Intermediate or Central water from the equatorial Atlantic at 700–1200 m. depth. When this water upwells here, the upper layers will not be seriously impoverished, as the name 'Mediterranean' would suggest, but enriched. A truly descriptive name should suggest that we have to do with a new water mass created in the Atlantic Ocean west of the Straits of Gibraltar which Vallaux (1936) has neatly described as the 'Gulf of Gibraltar'. In this paper, henceforth, the

term 'Mediterranean water' will be replaced by 'Gulf of Gibraltar water'. I am indebted to Dr J. N. Carruthers for suggesting this.

From the way in which this water has been formed one would expect it to be markedly heterogeneous (Nielsen, 1912, pp. 179–82), and in our area it is. It cannot be identified by any point on a temperature-salinity diagram but only by an area. The point G (9·00° C., 35·70‰ S) which we shall use to represent it on T–S diagrams is a useful statistical fiction which expresses the fact that, during the slow mixing of Gulf of Gibraltar water with North Atlantic deep water (and no doubt with North Atlantic Central and cascade waters), short-period and considerable fluctuations in the properties of the former become ironed out so that the mixed water approximates closely to the linear temperature-salinity relation:

$$S = 35{\cdot}25_8 + 0{\cdot}14_7(T-6). \qquad (1)$$

Before the results of the 1938 International Gulf Stream Expeditions had reached this country (see p. 486) this expression had been derived by the method of least squares from *Armauer Hansen* stations 7–15 of 1914 (Helland-Hansen & Nansen, 1927), and other scattered observations where oxygen observations were available.

Although the temperature and salinity of the Gulf of Gibraltar water vary much, the percentage saturation with oxygen does not. Between *Armauer Hansen* stations 7 and 15 (Gaarder, 1927) the temperature of this water ranged from 8·37 to 10·44° C. and the salinity from 35·52 to 35·75‰, whereas the oxygen content lay always between 65 and 68·$_5$% saturated. This property will sharply distinguish Gulf of Gibraltar water from cascaded or 'capsized' water (Cooper, 1952*a*) of similar temperature and salinity, but not from North Atlantic Central water which at similar depths has similar oxygen percentage saturation.

The impoverished deeper water of the Mediterranean is even more deficient in phosphate than it is in nitrate; it has a large positive anomaly of the nitrate-phosphate ratio. In the Gulf of Gibraltar this Mediterranean water mixes with North Atlantic Central having (for the North Atlantic) a high content of nutrients and a normal nitrate-N–phosphate-P ratio of about 15:1. Off the Iberian Peninsula, Thomsen's (1931) results showed that the nitrate-phosphate ratio in the newly formed Gulf of Gibraltar water, after correction for phosphate salt error, may be as high as 40:1. By the time it has flowed to the border of the Celtic Sea, this water may be still poorer than North Atlantic Central water at the same depth but, from the point of view of upwelling, it must be regarded as a relatively rich water, in which the anomalous nitrate-phosphate ratio has almost disappeared (Cooper, 1937, 1938*a*).

The very variable extension from time to time of Gulf of Gibraltar water was shown by five stations worked by the present H.M.S. *Challenger* at a single truly oceanic position 44° 36′ N., 20° 00′ W. (Cons. Int., *Bull. Hydrogr.*

for the respective years), supplemented by the nearby *Deutschland* station (Reihe) 4 (Brennecke, 1921) (Table I).

For standard depths on the six occasions mean values of temperature and salinity have been calculated; the deviations from these means are presented in Fig. 1, from which it will be seen that between 0 and 700 m. depth the range of temperature and salinity was 1·2° C. and 0·20‰ respectively. The relatively much larger fluctuations at 750 and 1000 m. depth are more clearly shown by the standard deviations at standard depths graphed in Fig 2. Most striking of all was the very rapid increase in both temperature and salinity in the $4\frac{1}{2}$ months between 29 November 1932 and 14 April 1933

TABLE I

Ship	Station no.	Date	Lat.	Long.	Depth (m.)
Deutschland	4	20. v. 11	45° 13′ N.	20° 07′ W.	—
Challenger	1292	29. ix. 32	44° 37′ N.	20° 00′ W.	4372
Challenger	1318	14. iv. 33	44° 35′ N.	19° 56′ W.	4170
Challenger	1556	18. iv. 34	44° 35′ N.	20° 00′ W.	4315
Challenger	1666	14. iv. 35	44° 40′ N.	20° 00′ W.	4546
Challenger	1772	13. iv. 36	44° 36′ N.	20° 00′ W.	4546

TABLE II

Depth (m.)	Temperature (° C.)			Salinity (‰)		
	29. ix. 32	14. iv. 33	ΔT	29. ix. 32	14. iv. 33	ΔS
750	8·84	9·76	0·92	35·37	35·56	0·19
1000	7·26	7·86	0·60	35·35	35·76	0·41

(Fig. 3 and Table II). Thus at the level of the Gulf of Gibraltar water there were large variations from year to year in the middle of April and very rapid changes in the course of a few months. This conclusion is confirmed by the findings at the Irish station SS on the continental slope (Table XV and Fig. 2), and would probably have been found anywhere in the eastern North Atlantic.

The capacity of these deep-water movements to transport heat about the world is great. Thus this short-period increase in heat content at 44° 36′ N., 20° 00′ W. of a column of water 1 cm.^{2} cross-section would have been sufficient to raise the temperature of all the air above a surface of 308 cm.^{2} by 1° C. Otherwise stated, the increase in temperature of the water below 100 square sea miles would have been sufficient to raise the temperature of all the air over Great Britain by 0·5° C. The Gulf of Gibraltar water should not be regarded as permanently sealed down and of no account in surface oceanography and meteorology.

Vallaux (1936) has already directed attention to the highly heterogeneous nature of the Gulf of Gibraltar water. He pictures it as fragmented into a series of globular masses dispersing both in depth and expanse through the North Atlantic and gradually merging with it.

In 1906 the *Thor* (Schmidt, 1912), in the course of her investigations on the breeding place of the eel, worked a number of hydrographical stations along

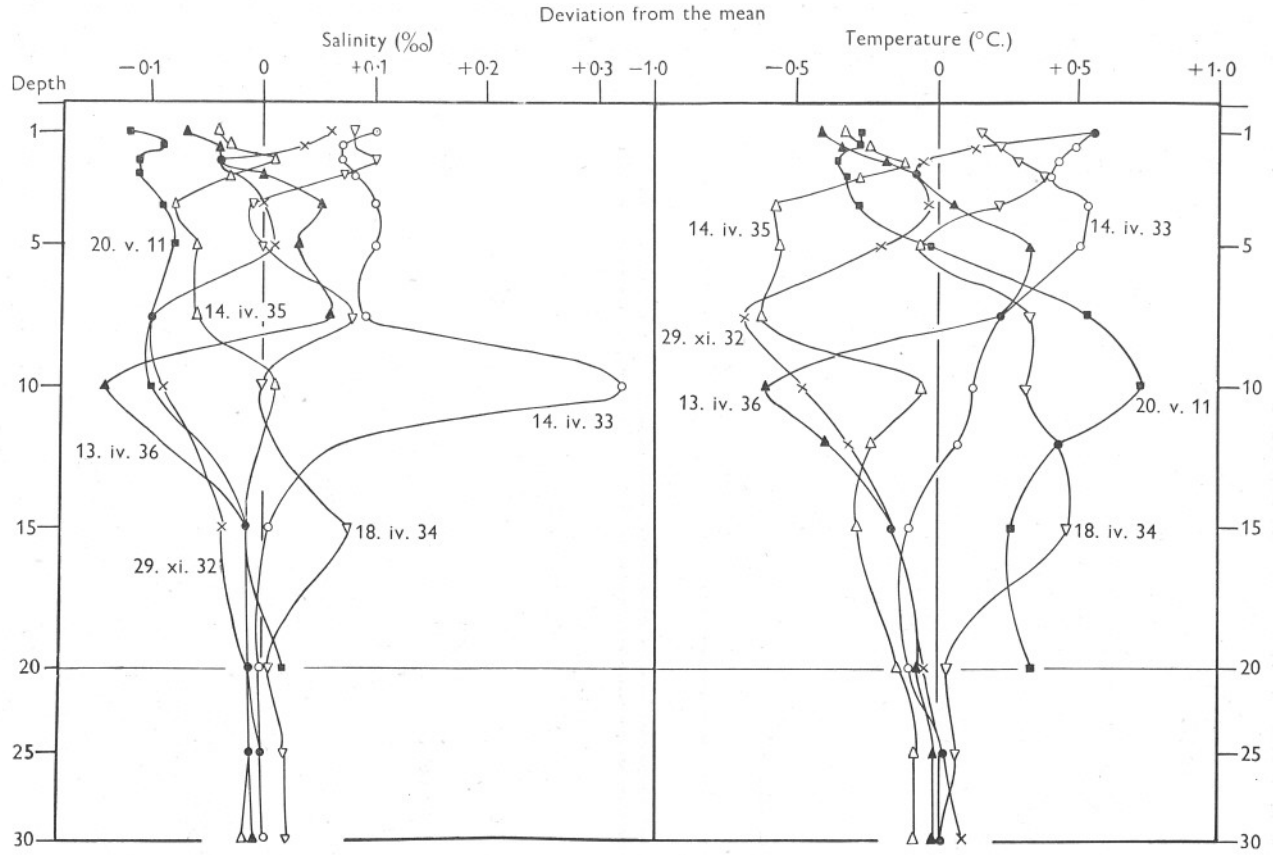

Fig. 1. Salinities (left) and temperatures (right) from standard depths at six stations in the North Atlantic near 44° 36′ N., 20° 00′ W. (Table I), expressed as deviations from the respective mean values at each depth. Black circles indicate coincident points on two or more curves. Depths in hundreds of metres.

Fig. 2. Standard deviations of temperature and salinity based on six sets of observations at or near 44° 36′ N., 20° 00′ W.; also (open circles) standard deviations of temperature from twenty-nine sets of observations at the Irish station SS (50° 34′ N., 11° 17′ W.) from Table XV. Depths in hundreds of metres.

Fig. 3. Increase in temperature and salinity between 29 November 1932 and 14 April 1933 at 44° 36′ N., 19° 58′ W. Depths in hundreds of metres.

the slope of the Celtic Sea and Bay of Biscay. On Fig. 4 some stations worked between 10 May and 17 June are denoted by circles and some between 26 August and 3 September by crosses. Section I (Fig. 5) ran in deep water along the edge of the slope. It is clear that the wedge of highly saline Gulf of Gibraltar water was held into the right on the Franco-Iberian coast, and

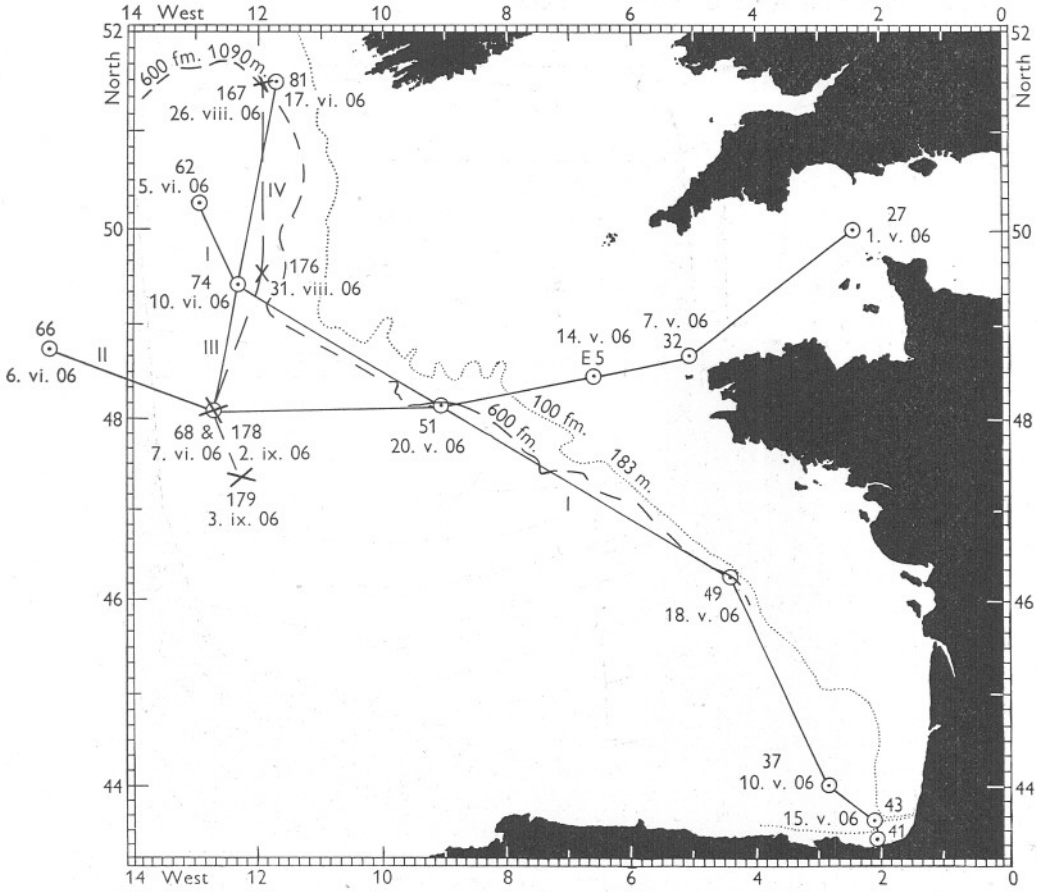

Fig. 4. Positions of some stations worked by the Danish research vessel *Thor* in 1906 and the International Hydrographic Station E5.

on 20 May was strongly represented as far north as station 51 (48° 07′ N., 9° 03′ W.), south of the Celtic Sea. Between stations 51 and 74, worked 3 weeks later, a slight bulge in the continental shelf has to be shown in section I. The submarine promontory west of the Little Sole and Great Sole Banks, shown by the 100 and 600 fm. contours on Fig. 4, seems to play a large part in the hydrography of the area and needs constantly to be in mind. In its neighbourhood there seems to have been a marked attenuation in the

strength of the Gibraltar water then at station 74 and on other occasions. The continental slope changes in direction from west-north-west to north-north-east and becomes the eastern boundary of a submarine gulf, bight or indentation.[1] If Gibraltar water is to enter this indentation, the water already there must escape either as an eddy in a horizontal plane or by upwelling to levels where movement is less restricted.

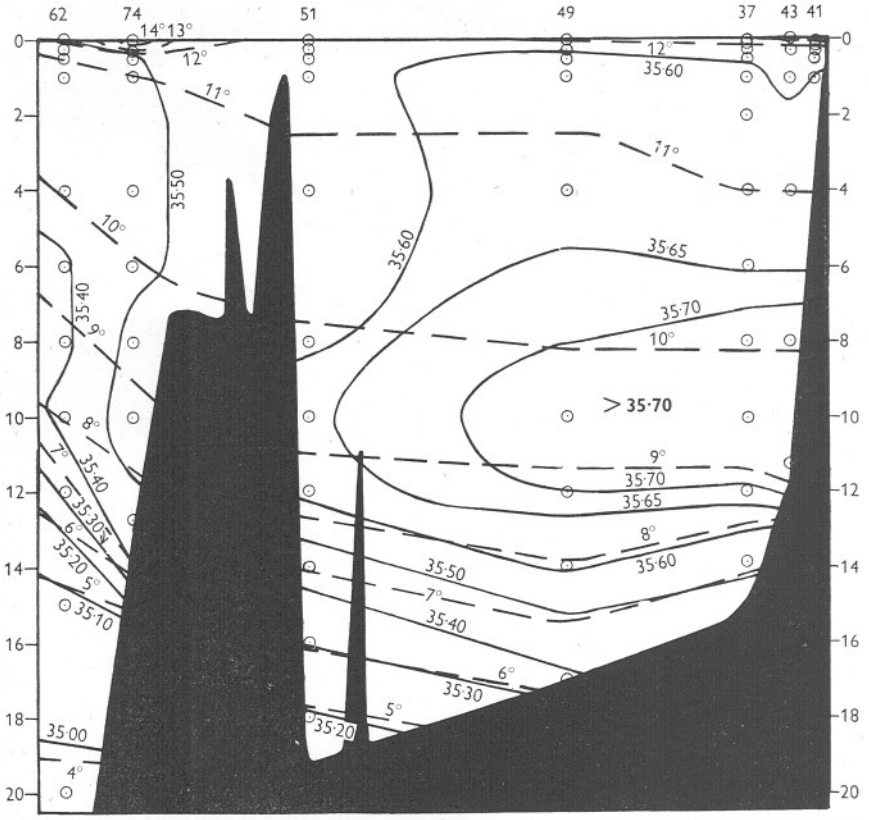

Fig. 5. Section I of Fig. 4 (stations 62–41), based on temperatures and salinities observed by *Thor* between 10 May and 10 June 1906. Bottom topography assessed from Admiralty charts. Depths in hundreds of metres.

Through or around this submarine promontory it is not easy to draw continuous curves for temperature and salinity between stations 51, 74 and 62, spread over 200 miles. The waters north-west and south-east of the 'Sole' submarine promontory evidently have markedly different properties (Fig. 5).

[1] The nomenclature of features such as this is at present under discussion. Possible confusion may be avoided by using the term 'indentation', unlikely to be acceptable to anyone as a permanent name for anything. Since it bites into the continental shelf of which the Porcupine Bank is a part it will here, for convenience of repeated reference, be called the 'South Porcupine submarine indentation'.

Section II (Fig. 6) ran down the English Channel and over the continental slope south of the Little Sole Bank, crossing section I at station 51. In the

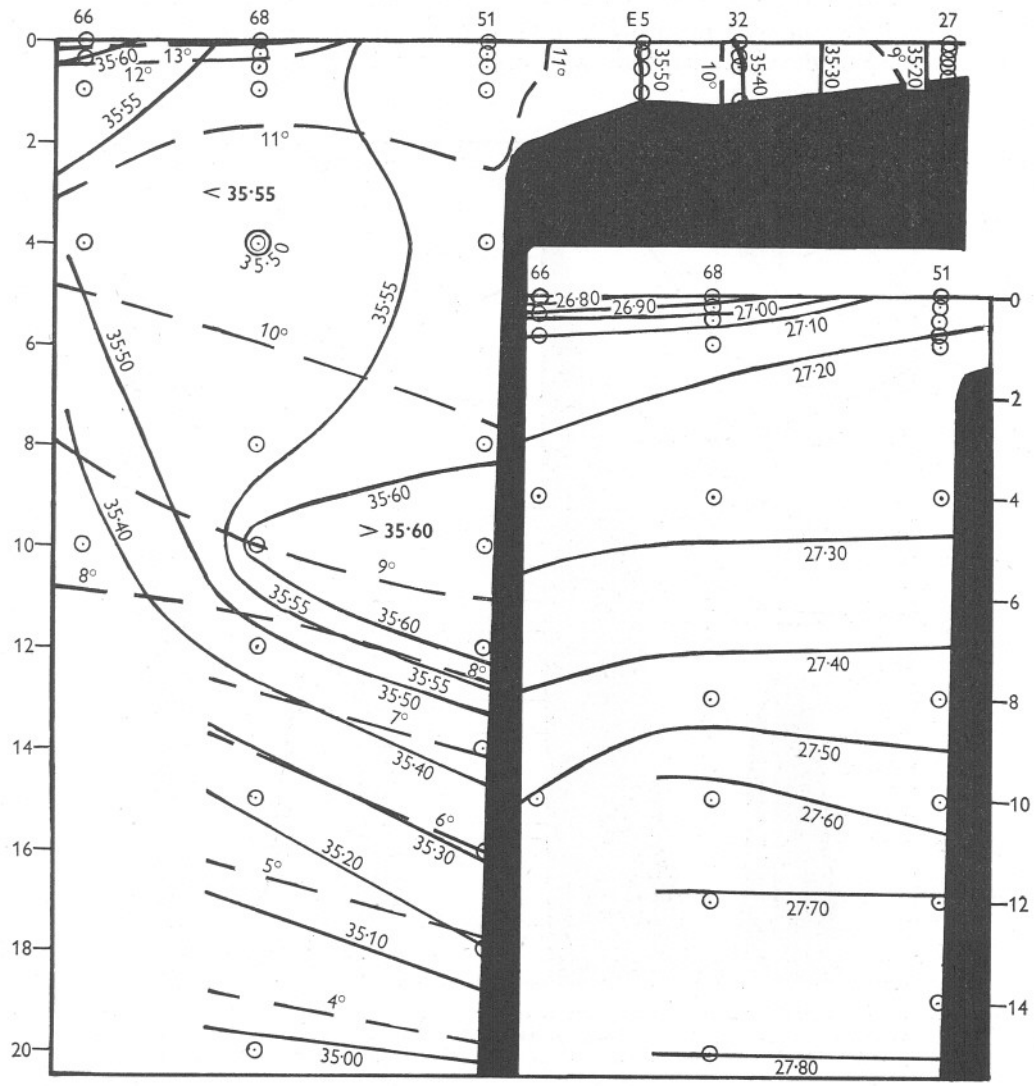

Fig. 6. Section II of Fig. 4 (stations 66–27), based on temperatures and salinities observed by *Thor* between 1 May and 7 June 1906. Inset bottom right, distribution of density (σ_t). Depths in hundreds of metres.

uppermost 400 m. the isopycnals incline downwards away from the continental slope (Fig. 6, inset) suggesting a weak surface current towards the south-east, confirmed from a study of the geopotential topography of the surface against

the 100-decibar surface. Abreast of Ushant the Gulf of Gibraltar water at 1000 m. was held in against the slope and did not extend very far westwards. The slope of the isopycnals for σ_t 27·50 and 27·60 suggests that this water mass was still moving west-north-west. Eighty miles off the slope at station 66 the influence of the Gibraltar water was very slight (salinity maximum 35·34‰).

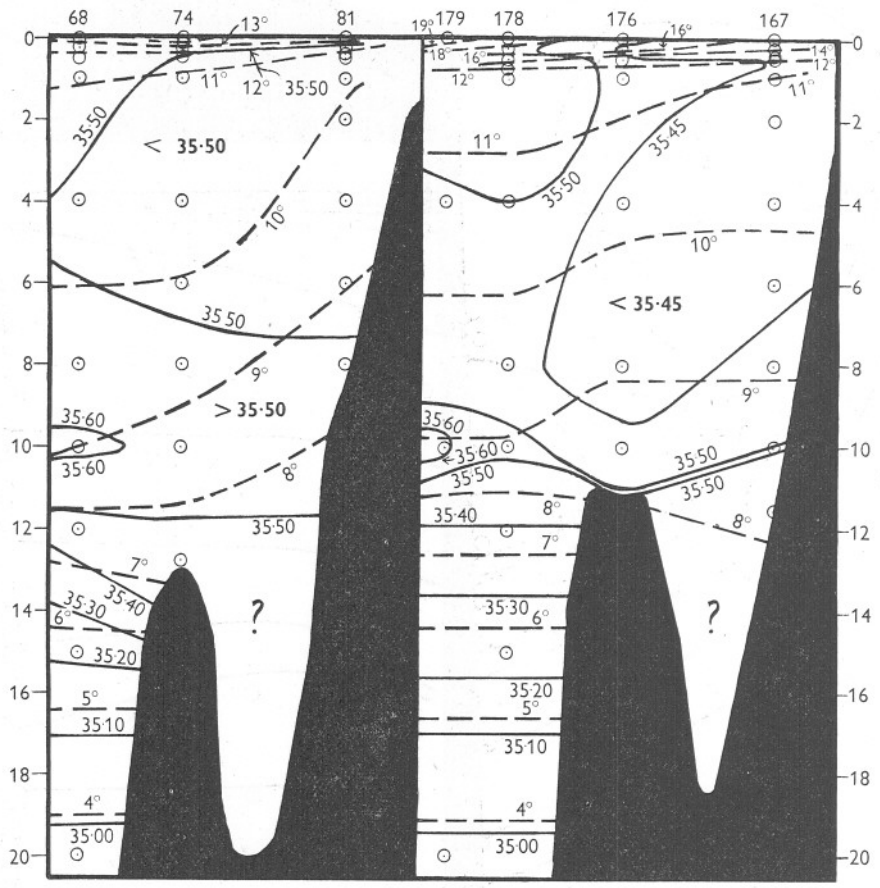

Fig. 7. North-south sections based on temperatures and salinities observed by *Thor*. Section III of Fig. 4 (stations 68, 74, 81), 7–17 June 1906; Section IV (stations 179, 178, 176, 167), 26 August–3 September, 1906. Depths in hundreds of metres.

On the north-south section III (Fig. 7, left), although the water at station 68 undoubtedly included a strong Gibraltar component, one cannot feel the same confidence about the water to the north within the submarine indentation with a salinity of 35·52–35·55‰, a temperature of 8·5–9·3° C. and a density σ_t of 27·51–27·63. These are compatible with a very considerable proportion of water cascaded from the Rockall Table Mount.

Section IV (Fig. 7, right) shows the change, essentially along section III, in the next 3 months. There had been a marked withdrawal of the saline water at 800–1200 m., causing a decrease in salinity of 0·06–0·10‰. The shape of the surfaces of equal density between stations 178 and 179 (not reproduced) also suggests a south-east-going current at these depths, where the water movements evidently are considerable.

The North Atlantic Deep Water

The deep water of the eastern North Atlantic can only remotely affect the surface water and is of importance to us only for the effect it may have on the stratum of Gulf of Gibraltar water around 1000 m. depth, and as a component of a current system which impoverishes the nutrient regime of the whole of the North Atlantic compared with the other oceans (Sverdrup, Johnson & Fleming, 1942, p. 754).

It is of interest, none the less, that the variations in temperature and salinity of the deep water near the continental slope at the positions italicized in Fig. 8 are quite considerable (Table III). This deep water has been formed, according to Nansen (1912), chiefly at the surface in a limited area south-west of Greenland and to some extent by the outflow from the Norwegian Sea through the bottom of the Faeroe-Shetland Channel (but see Cooper, 1952*b*). According to Helland-Hansen (1930, p. 75) a certain amount of Gulf of Gibraltar water appears to mix downwards to 5000 m.

For the construction of temperature-salinity diagrams in this area the deep water may be characterized by the point *D* having temperature 3·9° and salinity 34·95‰. This point is not quite the same as Jacobsen's (1929) point *B*, derived from and employed for a much wider area.

The distribution of silicate in the deep water is discussed in a separate paper (Cooper, 1952*b*).

Phosphorus below 1000 m. Depth

There have been very few determinations of phosphate in the deep water near the continental slope of the Celtic Sea. On 17–19 June 1930 the *Dana* (*Dana Report*, No. 12, 1937) worked for inorganic phosphate two stations 56 miles south and east respectively of *Discovery II* station 2659 of 12 May 1950. The *Dana* results (Table IV) have been multiplied by 1·35 to correct for salt error (Cooper, 1938*b*). They may be compared with the *Discovery II* results for total phosphorus which would be expected to be about 0·1 μg.-atom/l. greater. Actually below 1200 m. depth they were about 0·2 μg.-atom/l. less, a notable result if it is correct. The following comments may be made:

(i) Although, for reasons to be given (Appendix, p. 509), the accuracy of the analyses made on the *Discovery II* samples is not very high, there is little reason to doubt their accuracy to one decimal place as reported.

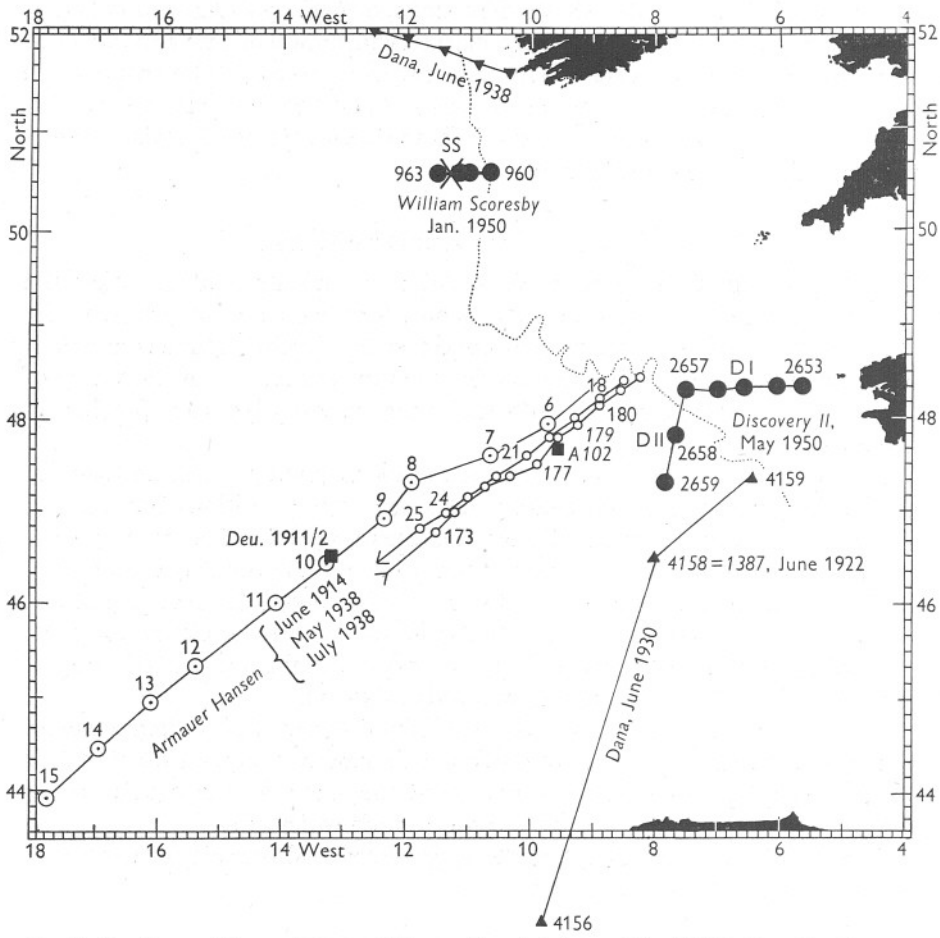

Fig. 8. Positions of deep stations off the continental slope of the Celtic Sea: ⊙, *Armauer Hansen* stations in June 1914; ○, *Armauer Hansen* stations in May and July 1938; ▲, *Dana* stations in June 1930 and one in June 1922; ▼, *Dana* stations in June 1938; ■, *Deutschland* Reihe 2 in May 1911 and *Altair* station 102 in July 1938; ●, stations by R.R.S. *William Scoresby* in January 1950 and by R.R.S. *Discovery II* in May 1950; ×, position of the Irish station SS.

Table III. Range of Temperatures and Salinities Recorded at the Deep Stations Italicized on Fig. 8

Depth (m.)	ΔT (° C.)	ΔS (‰)
2000	0·6	0·09
2500	0·3	0·07
3000	0·1	0·04
3500	0·05	0·04

(ii) Although Dr H. Thomsen and Dr A. Fr. Bruun, the skilful observers who made the analyses at sea on board *Dana*, make no high claim for the accuracy of their inorganic phosphate analyses, an error of greater than $\pm 0{\cdot}1$ μg.-atom/l. seems unlikely.

(iii) The salt error correction factor is not a true constant, but only a factor less than 1·1 could make the deep water results consistent. Such a factor was highly unlikely.

TABLE IV. VERTICAL DISTRIBUTION OF PHOSPHORUS (μG.-ATOM/L.) IN THE BAY OF BISCAY IN 1930 AND 1950. INORGANIC PHOSPHATE OR TOTAL PHOSPHORUS

Ship ...	*Dana*	*Dana*	*William Scoresby*		*Discovery II*
Station no. ...	4158	4159	963		2659
Lat. N. ...	46° 28′	47° 20′	50° 34′		47° 24′
Long. W. ...	8° 01′	6° 28′	11° 30′		7° 52′
Date ...	17. vi. 30	19. vi. 30	19. i. 50		12. v. 50
Depth (m.)	Inorganic phosphate	Inorganic phosphate	Inorganic phosphate	Total phosphorus	Total phosphorus
100	$0{\cdot}5_7$	$0{\cdot}5_7$	0·55	0·70	0·5
150	$0{\cdot}6_7$	$0{\cdot}5_7$	0·53	—	0·6
200	$0{\cdot}7_6$	$0{\cdot}5_7$	0·54	0·70	0·6
300	$0{\cdot}6_7$	$0{\cdot}6_7$	0·65	—	0·8
400	$0{\cdot}7_6$	$0{\cdot}7_6$	0·75	0·93	0·8
500	$0{\cdot}9_5$	$0{\cdot}9_5$	0·96	—	—
600	$1{\cdot}1_4$	$1{\cdot}0_5$	0·97	1·08	1·0
800	$1{\cdot}1_4$	$1{\cdot}1_4$	1·13	1·26	1·3
900	—	—	1·13	1·33	1·2
1000	$1{\cdot}1_4$	$1{\cdot}1_4$	1·17	1·30	1·2
1100	—	—	1·20	1·33	1·3
1200	$1{\cdot}2_3$	—	1·19	1·33	1·2
1500	$1{\cdot}5_2$	—	—	—	1·3
2000	$1{\cdot}5_2$	—	—	—	1·3
2500	$1{\cdot}7_1$	—	—	—	1·4
3000	$1{\cdot}8_0$	—	—	—	1·6
3500	$1{\cdot}8_0$	—	—	—	1·5
3800	—	—	—	—	1·6
4000	$1{\cdot}8_0$	—	—	—	—
4500	$1{\cdot}9_0$	—	—	—	—

(iv) The *Dana* results at stations 4158 and 4159 between 400 and 1200 m. agree closely with the relatively accurate analyses for inorganic phosphate made 20 years later on *William Scoresby* samples from a position about 280 miles to the north-north-west (Table IV).

(v) The *Dana* results of a week earlier at station 4149, 11 miles off Cape Espichel, Portugal, below the productive zone, lie within the range of variation of inorganic phosphate established in the neighbourhood by Bôto (1945; also in Cons. Int., *Bull. Hydrogr.* for 1934) on the Portuguese research vessel *Albacora* 4 years later (Table V).

(vi) The *Dana* results in 1930 show a steady increase in inorganic phosphate at 1000–2000 m. from the neighbourhood of Lisbon northwards to the border of the Celtic Sea (Table VI).

(vii) The *Discovery II* results between 200 and 1300 m. check well with the more accurate analyses of total phosphorus made on *William Scoresby* samples from a position about 280 miles to the north-north-west in the same year 1950 (Table IV).

TABLE V. COMPARISON OF INORGANIC PHOSPHATE CONTENT (AS μG.-ATOM/L. P) AT *DANA* STATION 4149, 11 MILES OFF CAPE ESPICHEL (NEAR LISBON) WITH *ALBACORA* STATIONS WITHIN 22 MILES OF IT, AND WITH *ALBACORA* STATION 558

Ship ...	*Albacora*			*Dana*	*Albacora*		*Albacora*
Station no. ...	442	486	488	4149	448	556	558
Lat. N. ...	38° 26′	38° 27′	38° 27′	38° 19′	38° 17′	38° 15′	39° 29·5′
Long. W. ...	9° 30′	9° 28′	9° 20′	9° 26′	9° 13′	9° 10′	9° 37·5′
Date ...	8. ii. 34	9. v. 34	9. v. 34	11. vi. 30	9. ii. 34	14. viii. 34	17. viii. 34
Depth (m.)							
300	—	0·58	0·70	$0·7_7$	—	0·79	—
400	0·79	0·77	0·80	$0·8_5$	0·62	0·80	0·68
500	—	—	—	$0·9_5$	—	0·87	—
600	—	0·70	0·80	$0·5_7$	—	0·78	0·79
800	0·86	0·69	0·83	$0·5_7$	0·55	0·79	0·66
1000	0·70	0·75*	—	$0·5_7$	0·62	—	0·59
1200	0·70	0·83*	—	$0·8_5$	0·62	—	0·68
1300	—	0·89	—	—	—	—	—
1400	—	—	—	—	—	—	0·96
1500	—	—	—	$0·9_5$	—	—	—
1600	—	—	—	—	—	—	0·96

* Interpolated with 900 m. result.

TABLE VI. INORGANIC PHOSPHATE (AS μG.-ATOM/L. P) at *DANA* STATIONS BETWEEN 1000 AND 2000 M. DEPTH

Dana station ...	4148	4149	4156	4158	4159
Lat. N. ...	37° 02′	38° 19′	42° 41′	46° 28′	47° 20′
Long. W. ...	9° 17′	9° 26′	9° 49′	8° 01′	6° 28′
Date ...	11. vi. 30	11. vi. 30	16. vi. 30	17. vi. 30	19. vi. 30
Depth (m.)					
1000	$0·6_7$	$0·5_7$	$1·0_5$	$1·1_4$	$1·1_4$
1200	$0·7_6$	$0·8_5$	$1·0_5$	$1·2_3$	—
1400	$0·9_5$	—	—	—	—
1500	—	$0·9_5$	$1·3_3$	$1·5_2$	—
1600	$1·2_4$	—	—	—	—
2000	—	—	$1·3_3$	$1·5_2$	—

(viii) It would seem therefore that in the northern Bay of Biscay in June 1930 the phosphate content at 1200–2000 m. was higher than it is now in the same area or than it was then to the southward. Variations in phosphate content of at least 0·2 μg.-atom/l. have taken place. It may not be by chance that the decrease in the deep water has occurred at the same time as that in the English Channel near Plymouth.

North Atlantic Central Water

According to Sverdrup *et al.* (1942, p. 668) North Atlantic Central water characterized by a nearly straight T–S curve between $T=8°$, $S=35{\cdot}10‰$ and $T=19°$, $S=36{\cdot}70‰$ has been found over a very large area of the North Atlantic. In this area its presence has been masked below 10° and above 11·5° C. Below 10° its place is taken by Gulf of Gibraltar or cascade waters. Above 11·5° we find the zone of strong seasonal variations, due to solar heating of the surface waters in summer and of vertical mixing in winter. Between these limits occurs water resembling the Central water but, rather surprisingly, somewhat warmer, and needing its own T–S curve. This can be derived only from stations where oxygen determinations are available, such as stations 7–15 of *Armauer Hansen* in 1914. Those selected were:

Station *AH* 1914 ...	15	13	12	10	9	8	7
Depth range used (m.)	100–700	75–400	100–600	75–200	100–400	200–500	400 only

The linear T–S curve so calculated is

$$S=35{\cdot}50_8+0{\cdot}124(T-11). \qquad (2)$$

The temperature and salinity of North Atlantic Central water below 100 m. depth brought into this area should comply with this relation (see Fig. 9).

The Upper Limit of Central Water

The upper limit of North Atlantic Central Water is the point where the T–S curve ceases to follow equation (2). In winter and spring the upper waters are homogeneous, represented by a point, and in summer they are isohaline and represented by a vertical T–S curve. In June 1914 at the *Armauer Hansen* stations the upper limit was clearly definable within 25 m. (Table VII).

Table VII. The Upper Limit of North Atlantic Central Water at *Armauer Hansen* Stations 15 to 6 in June 1914

Station ...	15	14	13	12	11	10	9	8	7	6
Depth of upper limit (m.)	100	75	75	100	*c.*75	100*	100	200	200	Not present
Temperature (° C.)	12·37	12·50	12·59	11·53	11·27	11·64	11·02	11·10	10·93	
Salinity (‰)	35·69	35·69	35·72	35·59	35·54	35·57	35·51	35·55	35·53	
Oxygen (%)	92	93	92·5	96	98	94	96	95	—	

* High oxygen content (104%) shows that the 75 m. water belonged within the zone of winter mixing, not of Central Water.

From station 15 inwards to station 9, as at many other deep Atlantic stations, the limit of vertical mixing had been between 75 and 100 m. depth (Fig. 9). Moreover, at the more seaward stations 15, 14 and 13, the winter surface water had had a salinity of about 35·70‰ and a temperature of 12·4–12·6° C. Chemically it was essentially the same water as that underlying it.

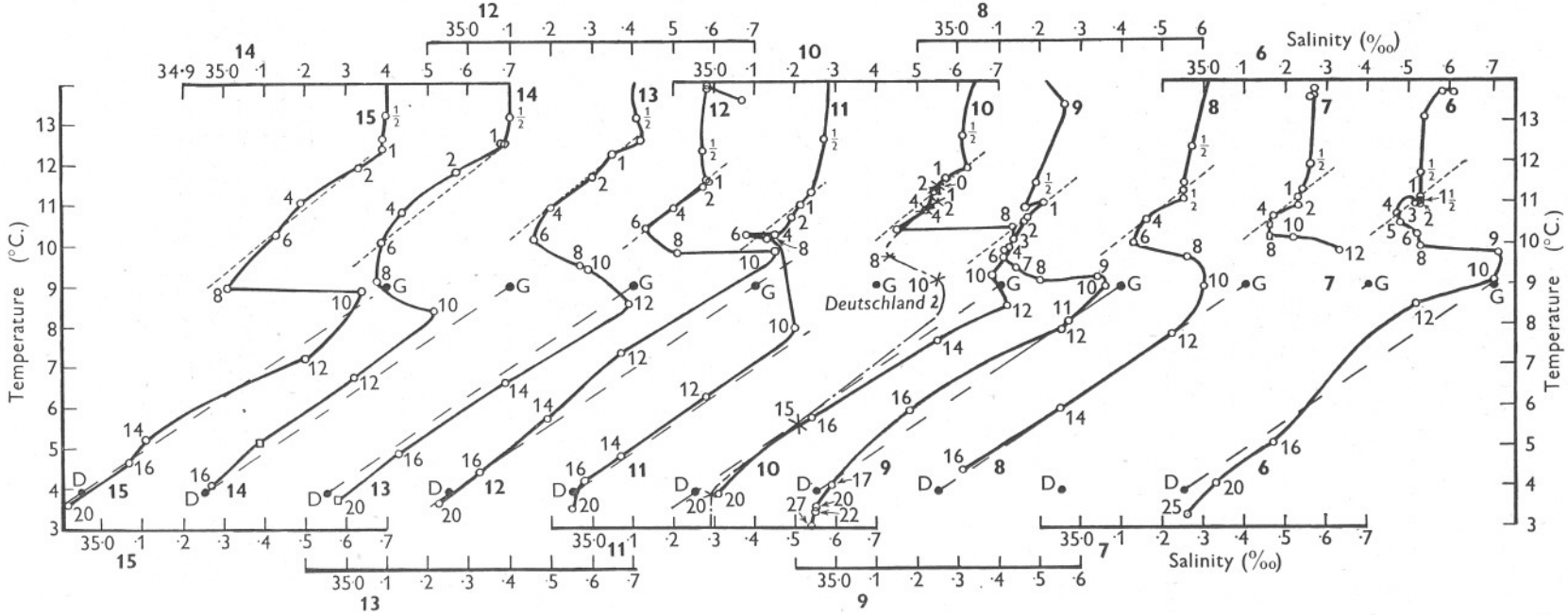

Fig. 9. Temperature-salinity relationships for *Armauer Hansen* stations 15–6 (see Fig. 8 for positions) worked in June 1914. The linear curves representing the properties of mixed Gulf of Gibraltar and Deep water (equation 1, p. 467) and North Atlantic Central water (equation 2, p. 479) are indicated by dashed and dotted lines respectively. *Deutschland* Reihe 2 is superimposed on *Armauer Hansen* station 10, from which it was distant about four miles. The points G and D represent the mean properties of Gulf of Gibraltar and North Atlantic Deep Water. The figures in bold-faced type denote station numbers. The remaining numbers against the curves denote depths of observations in hundreds of metres.

Approaching the continental slope at stations 8, 7 and 6 the apparent depth of vertical mixing was more than twice as great (Fig. 9). Meteorological conditions at these stations cannot have differed greatly from those farther out, and one is forced to seek another origin for the upper 200–300 m. of water with salinity between 35·51 and 35·55 ‰ and temperature between 10·9 and 11·1° C. We have to deal with a phenomenon peculiar to the neighbourhood of the continental slope (cf. Cooper, 1952*a*).

The Lower Limit of Central Water

The lower limit of the North Atlantic Central water rises as the continental slope is approached (Table VIII).

TABLE VIII. THE LOWER LIMIT OF NORTH ATLANTIC CENTRAL WATER AT *ARMAUER HANSEN* STATIONS 15 TO 6 IN JUNE 1914

Station ...	15	14	13	12	11	10	9	8	7	6
Depth of lower limit (m.)	750	500	500	600	400?	400?	500	500	400	Not present
Temperature (° C.)	9·35	10·40	10·55	10·34	10·25	10·82	9·90	10·32	10·69	
Salinity (‰)	35·33	35·41	35·47	35·43	35·45	35·52	35·41	35·43	35·47	
Oxygen (%)	*c.*73	84	82	85	85·5	86·5	84·5	81	83	

It extends down to 750 m. at station 15 and only to 400 m. at station 7. At station 6 it is not recognizable in the midst of more highly oxygenated water. It was underlain either by a mixed water formed between itself and Gulf of Gibraltar water as at stations 15, 14, 13, 12, 9 and 8 or by cascaded water as at stations 11, 10 and 7.

The stratum of Central water gets thinner as the slope is approached (Figs. 9 and 11). At station 15 it was 700 m. thick, whereas it was recognizable with certainty at station 7 only at 400 m. Evidently, in June 1914, the North Atlantic Central water had little direct effect on the Celtic Sea.

At the upper limit the Central water has an oxygen content 92–98 % saturated, at the lower 81–85 %. The high oxygen content (99 %) at stations 6 at 400 m. shows that this was not Central but 'capsized' or cascaded water. The temperature, salinity and density were appropriate to Celtic Sea water the previous winter. The arrival of cascade water in the ocean abreast of the slope may bring about a state of labile or metastable equilibrium to a considerable depth. Winds, which can mix the waters of the open ocean only to 75–100 m., can therefore with the same ease homogenize the waters near the slope by a 'capsizing' process (Cooper, 1952*a*) to a much greater depth.

SUBMARINE VALLEYS IN THE CONTINENTAL SLOPE

In February 1949 a survey of an area around 48° N. lat., 9° 30′ W. long. was carried out in good weather by the present Hydrographer of the Navy, Rear-Admiral A. Day, C.B.E., D.S.O., when in command of H.M. Surveying

Ship *Dalrymple*. The whole survey, based on a floating beacon anchored near the 100 fm. line and fixed by a series of star sights, was achieved by echo-sounding checked by the lead at intervals. A portion of the resulting document has been reproduced here (Fig. 10) by permission of the Hydrographer of the Navy.

If the sea-level were to fall by several hundred fathoms, a ria coast of strong relief would stand revealed. Thus the submarine valley at 48° 13′ N., 9° 21′ W. cuts back for about 9 sea miles (17 km.) and sections across it show that the maximum depth of the valley bottom below the containing spurs is about 1800 ft. (550 m.).

The French research vessel *Président Théodore Tissier* (Beaugé, 1934) has charted the continental slope between 48° 10′ N. lat., 9° 20′ W. long. and 49° 00′ N. lat., 11° 10′ W. long. I am much indebted to Monsieur P. Desbrosses for presenting me with a copy of this chart. The area surveyed was much greater and the density of soundings would seem to have been less, possibly considerably less, than in *Dalrymple's* survey so that the contoured chart is likely to be less accurate in detail than that reproduced in Fig. 10. However, great detail is not necessary to show that to the west-north-west there are a number of submarine canyons of even greater size. Thus the steep cliff shown in Fig. 10 (top left) would appear to be one jaw of a canyon about 15 miles long and with a maximum depth between and below the containing spurs of about 4000 ft. This canyon and others appear to be ideally shaped to create submarine eagres whilst the broad spurs shown in Fig. 10 and two similar ones at 48° 40′ N., 10° 22′ W. and 48° 35′ N., 10° 10′ W. appear likely to exacerbate the capsizing process suggested as occurring in southerly gales all along the continental slope. Continuous and extensive observations over these submarine canyons would be needed before well-placed standard hydrographical stations off the continental slope between 6 and 11° W. can be proposed.

The Vertical Distribution of Water Masses

Making use of the extensive information to be gleaned from Fig. 9 and from the sections and plots for temperature, salinity and density by Helland-Hansen & Nansen (1927, table II and plates 14 and 32) and from those for oxygen by Gaarder (1927, pp. 9–14, and Schnitt 1 *a* and *b*), it is possible to identify the several water masses in the *Armauer Hansen* section in June 1914 (Fig. 11). It is not possible to assess the importance of internal waves in causing the undulating boundaries, particularly of the Gulf of Gibraltar water. At station 11 this was completely squeezed out so that the Celtic Cascade Core (see below) and the Mixed Gibraltar-Deep water were in contact.

Station 15 was a typical and simple oceanic station with North Atlantic Central and Gulf of Gibraltar water clearly developed.

Stations 11 and 10 exhibited marked idiosyncrasies. At 800 m. at station 11

and at 600 m. at station 10 was a core of highly oxygenated water (Table IX, italicized), having properties appropriate to the north-western Celtic Sea the previous winter. There is little doubt that it had recently cascaded and had been forced out into the ocean as a core (cf. Cooper & Vaux, 1949), having been canalized in a submarine valley such as those shown in Fig. 10. The

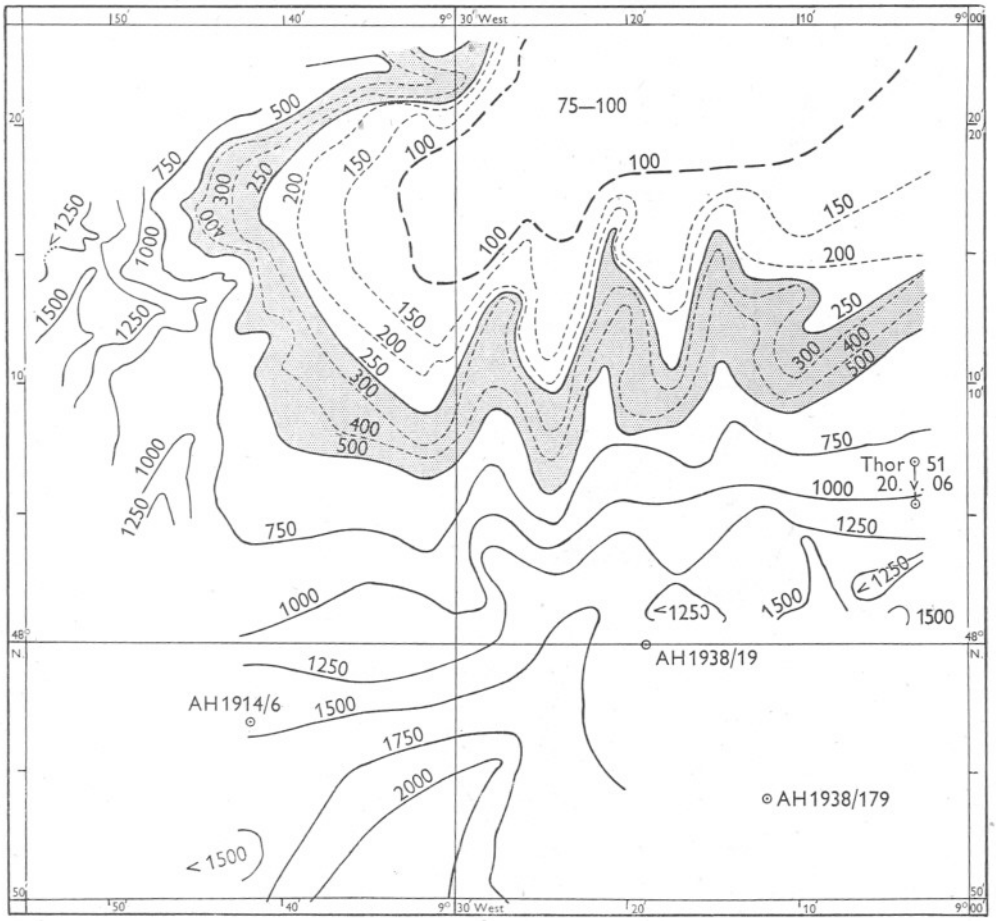

Fig. 10. Contoured bottom topography of the continental slope of the Celtic Sea in the neighbourhood of 48° N. lat., 9° 30′ W. long., making use, by permission of the Hydrographer of the Navy, of an original hydrographic survey carried out by H.M. Surveying Ship *Dalrymple* (Captain, now Rear-Admiral A. Day, C.B.E., D.S.O.) in February 1949. South of 48° N. lines of soundings are comparatively few. The contours at 250 and 1750 fm. have been added by the author. The 100 fm. contour is shown by a thick broken line. Contours at 250 fm. intervals are shown by thick continuous lines. Intermediate contours at 50 fm. intervals from 100 to 300 fm. and at 400 fm. are shown by thin dotted lines. The slope between the 250 and 500 fm. contours is stippled. The positions of the important station 6 worked by *Armauer Hansen* in June 1914 and of two stations worked by the same ship in 1938 are shown. The position of station 51, worked by *Thor* on 20 May 1906, is marked by an open circle, together with the adjustment necessary to bring the sounding reported by *Thor* into line with the chart.

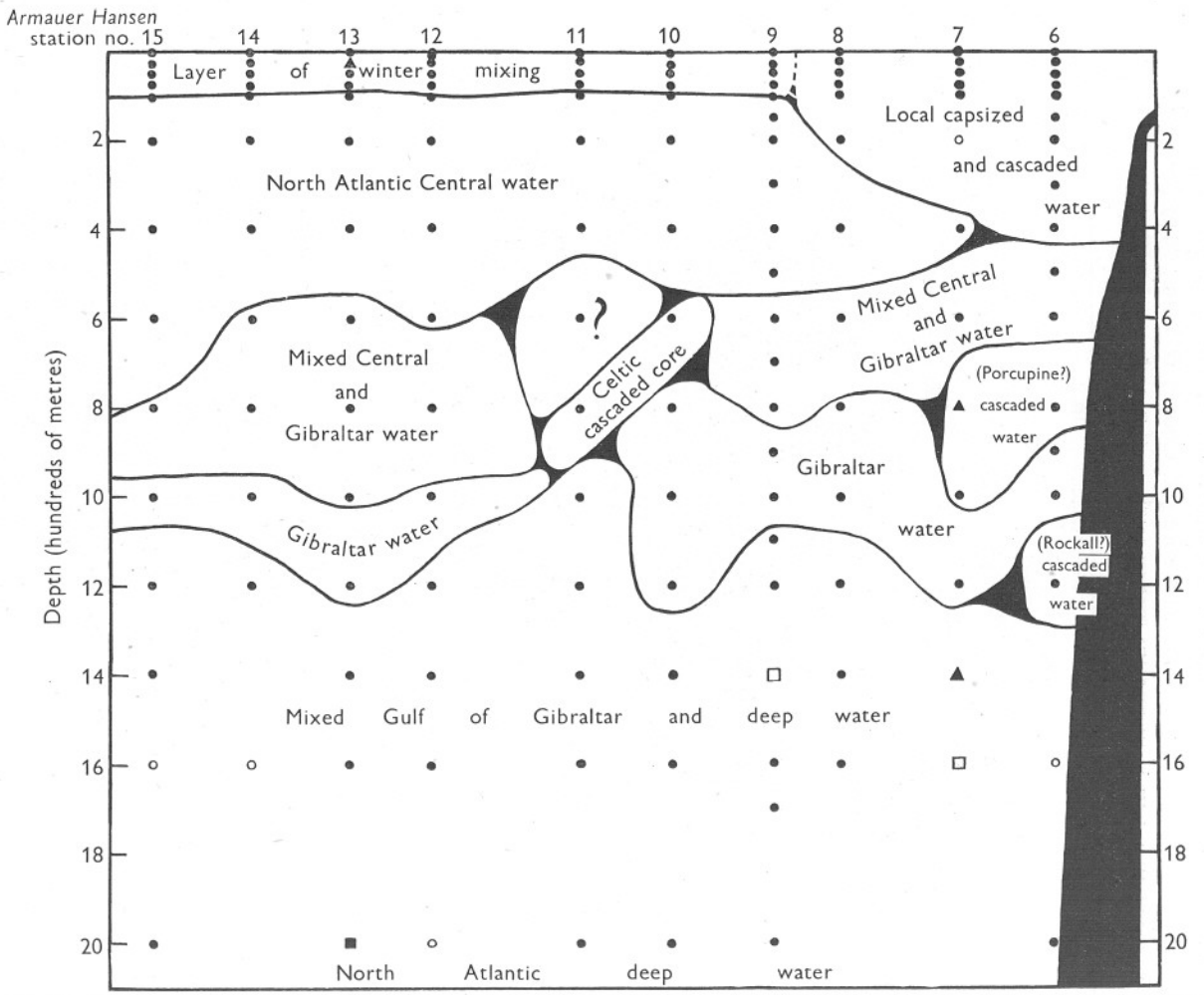

Fig. 11. Section illustrating distribution of water masses at *Armauer Hansen* stations 15–6, June 1914. Circles represent determinations of temperature and salinity, squares represent determinations of temperature only, and triangles of salinity only. Where oxygen determinations were also made these symbols are blacked in. Helland-Hansen and Nansen's interpolated results at intermediate depths have been used in constructing the section.

stability at the base of the core ($\Delta\sigma_t$ 0·41 in 200 m.) was remarkable. The core almost certainly originated north of the *Armauer Hansen* section, so that the fact that the oxygen-rich water lay deeper at the outer station no. 11 than at no. 10 agrees with a thesis, propounded by Sandström (1918, p. 241) and confirmed by other work at Plymouth, that such currents move forward in the northern hemisphere with a right-handed-screw motion.

The position of station 10 was within 5 miles of that of *Deutschland* Reihe 2 (46° 29′ N., 13° 11′ W.) on 16 May 1911, the temperature-salinity relation for which has been superimposed on Fig. 9 (Station 10) as a fine dashed and dotted line. The nature of the water masses on the two occasions differed greatly but, unfortunately, no depth was worked between 400 and 800 m. or between 1000 and 1500 m.

TABLE IX. CORE OF CELTIC SEA CASCADE WATER OBSERVED BY *ARMAUER HANSEN* ON 7 JUNE 1914

Depth (m.)	Oxygen (cc./l.)	Oxygen %	Salinity (‰)	Temp. (° C.)	Density σ_t	Nature of water
			Station 11, 46° 00′ N., 14° 03′ W.			
400	5·45	85·5	35·45	10·25	27·28	North Atlantic Central
600	4·83	76	35·38	10·24	27·22	?
800	*5·48*	*86*	*35·43*	*10·17*	*27·28*	*Celtic Cascade Core*
1000	4·55	68	35·50	7·95	27·69	Mixed Gulf of Gibraltar and Deep
			Station 10, 46° 25′ N., 13° 14′ W.			
400	5·44	86·5	35·52	10·82	27·23	North Atlantic Central
600	*6·01*	*94·5*	*35·45*	*10·36*	*27·26*	*Celtic Cascade Core*
800	4·07	64·5	35·73	10·44	27·48	Gulf of Gibraltar
1000	4·38	67·5	35·68	9·25	27·63	Gulf of Gibraltar

At station 6 against the slope, North Atlantic Central water was not recognizable and only vestigially at 400 m. at station 7. Gulf of Gibraltar water was present strongly at 900–1000 m. at station 6 and at 1200 m. at station 7.

Also at station 6 oxygenated water was banked against the slope in three separate strata. That above 400 m. depth was largely a mixed water formed by cascading from the continental shelf and by capsizing over the continental slope. For the highly oxygenated water at 800 m., there may be no need to seek an origin farther north than cascade water from the Porcupine Bank. That at 1200 m., beneath the Gulf of Gibraltar water, may have cascaded from the neighbourhood of the Rockall Table Mount, an event which will be further discussed below (p. 497, and Table XVIII). To these several water masses of very different histories but similar salinities, it is considered very probable that some organisms may react very differently, particularly at sensitive stages in their life histories, such as development of diatom resting spores, fertilization and hatching of eggs and moulting of crustaceans (cf. Wilson, 1951). Therefore, when discussing the hydrographical background of biological events it is never sufficient to speak of 'an influx of Atlantic Water'. The particular kind of Atlantic water needs to be identified.

Results of the International Gulf Stream Expeditions 1938

In June 1938 a section with stations 20 miles apart was worked by the Danish research vessel *Dana* from 51° 33′ N., 10° 22′ W. off Dursey Head, County Kerry, to 53° 48′ N., 20° 21′ W. (Fig. 8) (Cons. Int., *Bull. Hydrogr.* for 1938). The section crossed the submarine indentation and the southern spur of the Porcupine Bank into the deeper Eastern North Atlantic. The distribution of properties was complex and their interpretation will be difficult. Two similar but less complex sections were worked at the same time by the Norwegian vessel *Armauer Hansen*, south-west from the English Channel towards the Azores. No advantage is to be gained by a superficial examination of these valuable observations. Their application to our problems, especially to the Celtic Sea mackerel investigations in the same year, is deferred until the Scandinavian oceanographers have published their conclusions.

The Slope Waters off the Celtic Sea in 1950

On 18–19 January 1950, R.R.S. *William Scoresby* worked four stations along the parallel 50° 34′ N. between 10° 40′ and 11° 30′ W. (Fig. 8), where the results of the Irish investigations at station SS (50° 34′ N., 11° 17′ W.) had shown that vertical exchanges occur. Later, on 11–12 May, R.R.S. *Discovery II* worked a line of three stations (section D 11) over the slope between 48° 18′ N., 7° 30′ W. and 47° 24′ N., 7° 52′ W., the deepest being sampled to 3800 m. depth. She worked other stations on the shelf, which will be discussed in a later paper. Cordial thanks are due to Dr G. E. R. Deacon, F.R.S., and to Dr N. A. Mackintosh for arranging this co-operation, to Dr T. J. Hart and Dr H. P. F. Herdman, scientists in charge of the two ships, and to Mr R. I. Currie and Mr H. Cox, who were responsible for collecting many of the samples, and to Mr Currie for the analyses of oxygen. The results are presented graphically in Figs. 12–15.

The vertical variations in salinity and temperature between the surface and 1200 m. depth (Fig. 12) are smaller than in most parts of the world, but are characteristic of the waters bathing the Western European continental slope between Gibraltar and Western Ireland. Within this framework there is a very marked difference in the nature of the water masses encountered on the two cross-slope sections.

The Surface Waters

On the northern section worked by R.R.S. *William Scoresby* on 18–19 January 1950 vertical mixing was apparent down to 250 m., as on the *Armauer Hansen* section in June 1914 (Figs. 9, 12 and 13, panel 3). Along the 33-mile long section the distribution of density above 250 m. depth was almost uniform (27·05–27·11 σ_t), indicating very sluggish water movements parallel to the

continental slope and the results of capsizing. None the less the total phosphorus content showed a horizontal increase westward of about 0·1 μg.-atom/l. as the brim of the slope was crossed (Fig. 13, panel 4). Again, in spite of the generally vertically uniform temperature distribution, there were small density inversions which appear to be real at 20, 150 and 300 m. (Fig. 12). This phenomenon, frequently observed in this neighbourhood, will be discussed in another paper.

The content of nutrients at the easternmost station WS960 (50° 34′ N., 10° 40′ W.; total phosphorus 0·61–0·63, inorganic phosphate 0·48–0·53 μg.-atom/l. P) suggested that some areas of the northern Celtic Sea were little richer than the English Channel.

The phosphate content on 19 February 1927 at position SS, determined by Atkins (1928), may be compared with that at the same position and depths interpolated from stations WS962 and 963 (Table X).

TABLE X

Depth (m.)	19 February 1927	18–19 January 1950
0	0·46	0·55
402	0·72	0·73
860	0·91	1·13

The difference between the two water masses on the sections worked by R.R.S. *William Scoresby* in the north and R.R.S. *Discovery II* in the south shows up most clearly on a temperature-salinity diagram (Fig. 15). At no depth are the two waters closely related.

Along the southern (D II) section in May there was no relict isothermal, isopycnal layer remaining to indicate the lower limit of vertical mixing during the winter. It is unlikely that it extended down to 300 m. The contents of total phosphorus and of silicate-Si of the uppermost 100 m. (0·3–0·6 and 0·5–2·2 μg.-atom/l. respectively (Fig. 14, panels 4 and 5) were or had become low. It is probable that the relatively nutrient-rich winter surface water here (which should have been created by the gales of the first week of February) had been replaced by impoverished surface water from the ocean to the south or from the Biscayan shelf. If later such water moved into the English Channel it could bring only poor conditions with it.

In the southern section in May there was a density gradient (Fig. 14, panel 3). Assuming only horizontal water movements, this would indicate a weak eastbound current flowing along the edge of the slope, in agreement with the current system already deduced for the region by Helland-Hansen and Nansen (1927); but since vertical currents and internal waves may also have played a part no firm conclusion is possible. At least it seems that the impoverished warm saline surface water is more likely to have come from the ocean to the south-west or west than from the Biscayan shelf to the south-east.

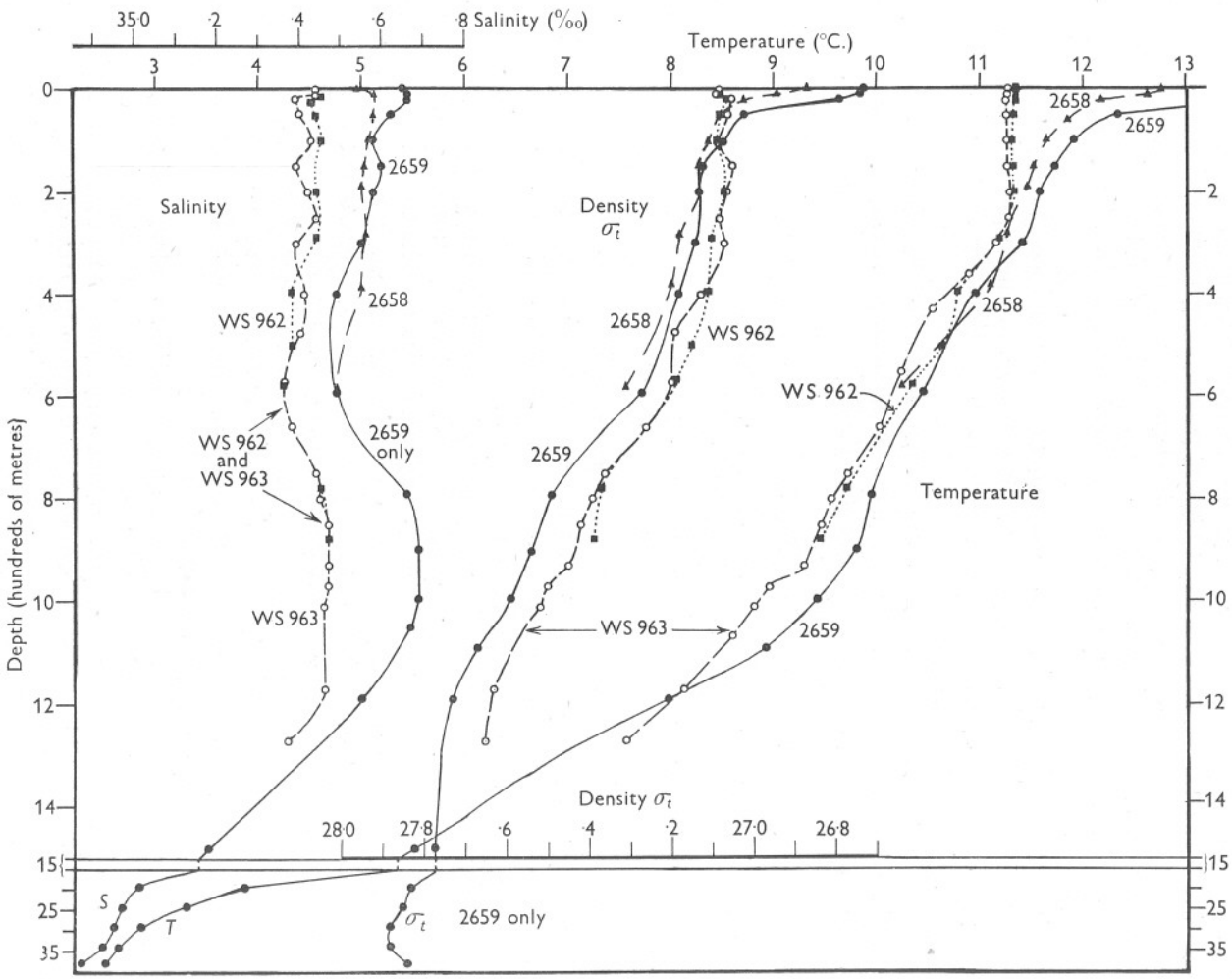

Fig. 12. Vertical distribution of salinity, density and temperature at *William Scoresby* stations 962 (···■···), 963 (---○---) on 18–19 January 1950, and *Discovery II* stations 2658 (— —▲— —) and 2659 (——●——) on 11–12 May 1950.

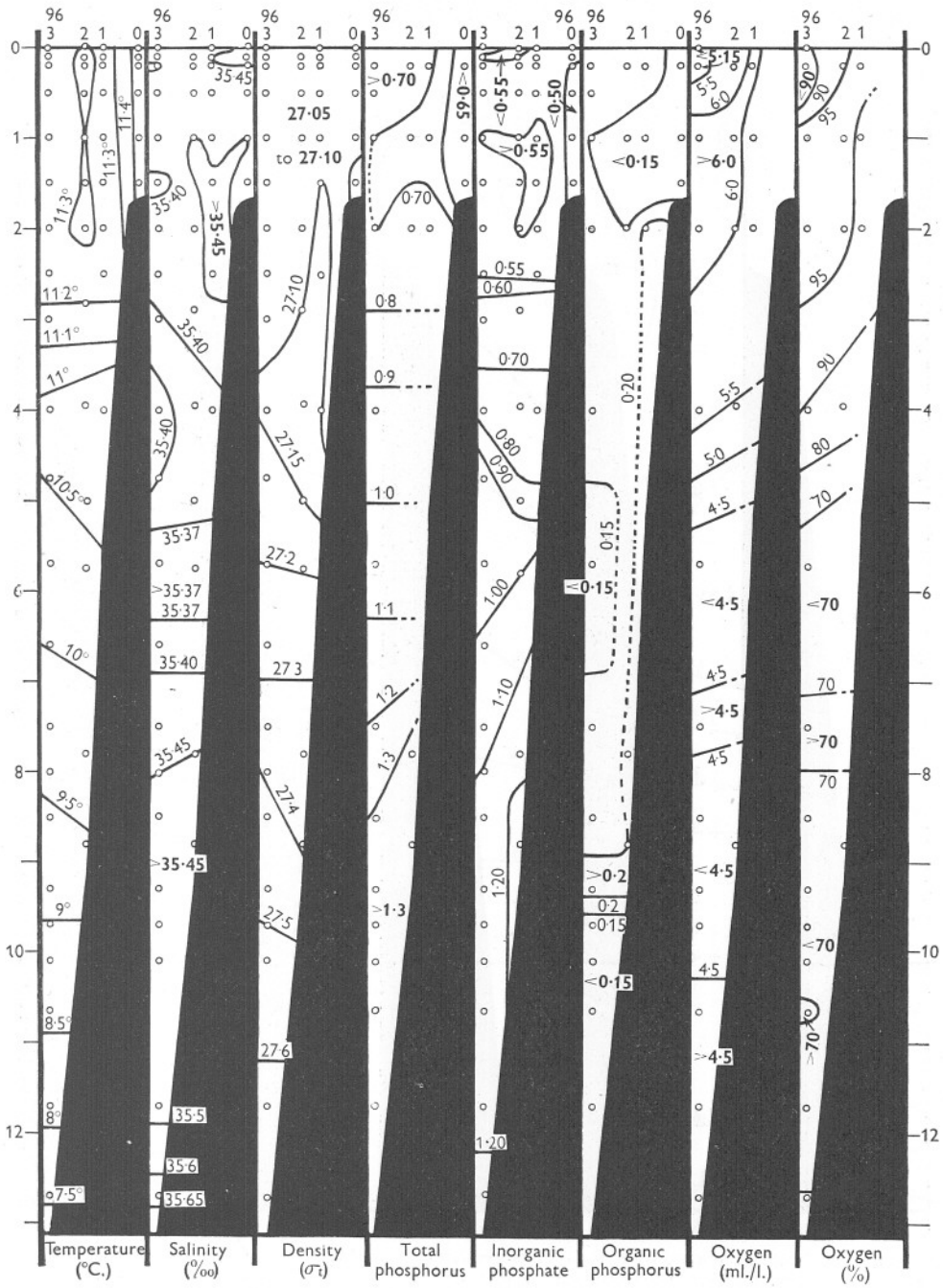

Fig. 13. Sections worked by R.R.S. *William Scoresby* on 18–19 January 1950, illustrating the distribution of properties over the continental slope west of the Celtic Sea along the parallel of latitude 50° 34′ N. Phosphorus and phosphate in μg.-atom/l. P. Depths in hundreds of metres.

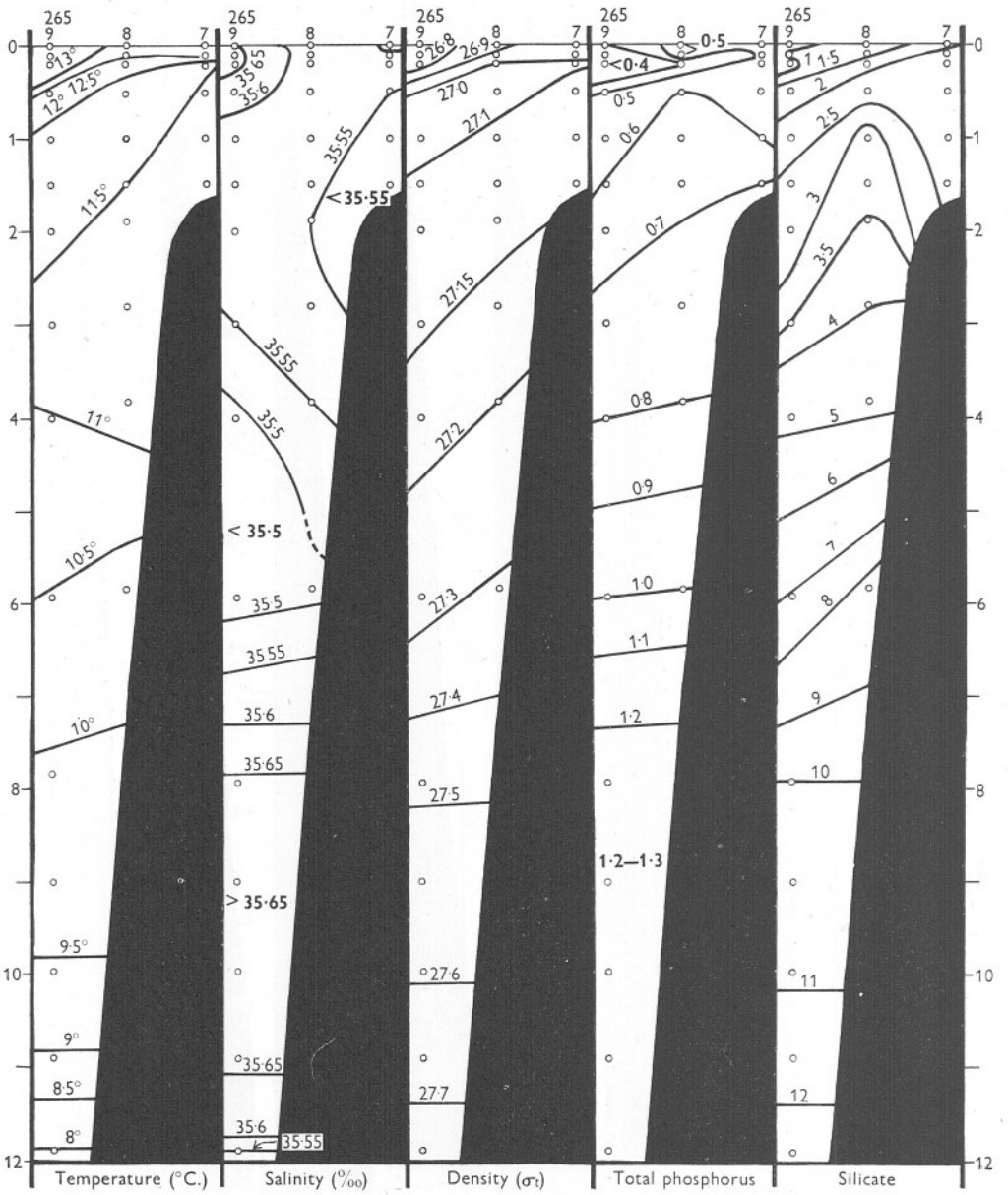

Fig. 14. Sections worked by R.R.S. *Discovery II* on 11–12 May 1950, illustrating distribution of properties over the continental slope south of the Celtic Sea approximately along the meridian 7° 40′ W. Phosphorus and silicate in μg.-atom/l. Depths in hundreds of metres.

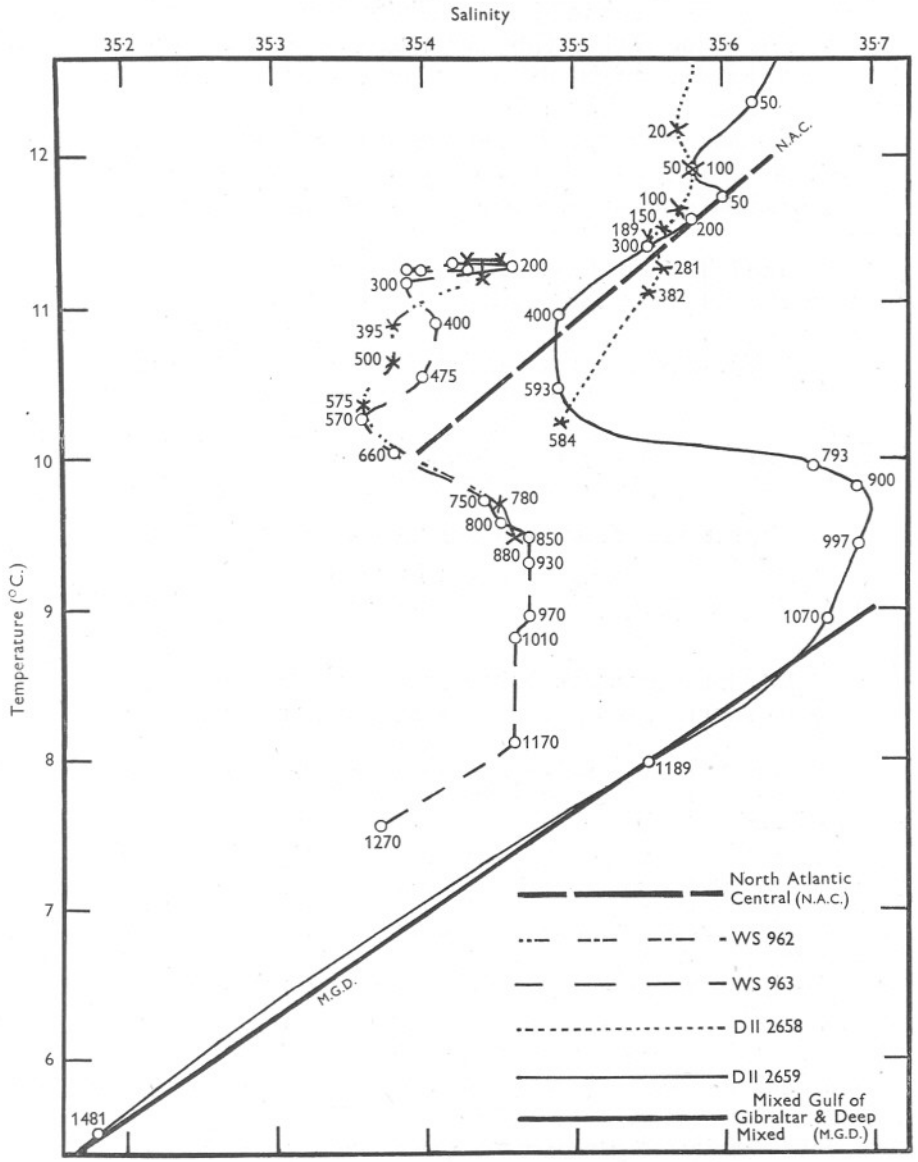

Fig. 15. Temperature-salinity relationships for the two *William Scoresby* stations (962, 963) and the two *Discovery II* stations (2658, 2659) over the continental slopes of the Celtic Sea in 1950.

The Deeper Waters

On the southern section in May, the salinity maximum at around 1000 m., characteristic of the Gulf of Gibraltar water, was well developed (Fig. 14, panel 2). It was also recognizable on the northern section in January. It had the properties set out in Table XI.

Determinations of silicate, in addition to those of oxygen, are likely to assist in distinguishing deep cascaded water from Gulf of Gibraltar water. Silicate determinations are also likely to distinguish cascaded from capsized water.

Above the Gulf of Gibraltar water lay water of minimum salinity and having the properties set out in Table XII.

TABLE XI. PROPERTIES OF THE GULF OF GIBRALTAR WATER IN THE EARLY MONTHS OF 1950

Salinity	35·6 ‰	Total phosphorus	1·2– 1·3 μg.-atom/l.
Temperature	8·9 –10·0° C.	Phosphate phosphorus	1·1– 1·2 μg.-atom/l.
σ_t	27·45–27·68	Silicate-Si	10 –11·5 μg.-atom/l.

TABLE XII. PROPERTIES OF MINIMUM SALINITY WATER

Salinity	35·49 ‰	Total phosphorus	0·6–1·0 μg.-atom/l.
Temperature	10·25–10·95° C.	Silicate-Si	4·8–8·3 μg.-atom/l.
σ_t	27·18–27·32		

TABLE XIII. SOME PREDICTED PROPERTIES OF THE SEVERAL TYPES OF WATER MASS FOUND NEAR THE CONTINENTAL SLOPE OF THE CELTIC SEA

	Oxygen (%)	Silicate-Si (μg.-atom/l.)	Total phosphorus (μg.-atom/l.)	Temperature (°C.)	Salinity (‰)
Cascaded water	>85	<4	<0·7	Uniform and dependent on origin	Uniform and dependent on origin
Capsized water	High and uniform	*c.* 6	*c.* 0·9	Uniform and >10	Uniform and >35·5
Gulf of Gibraltar water	65–69	10–11·5	1·2–1·3	9·0±0·5	Maximal and >35·5
Deeper North Atlantic Central water	65–70	>10	>1·3	Conforming to standard *T–S* diagram	Conforming to standard *T–S* diagram

The rapid increase in nutrient content through the layer of minimum salinity is very striking.

The low-salinity component of this water can come neither from above nor below. It can arise only by lateral mixing. Two origins are possible, either North Atlantic Central water from much the same depth to the south-west, or cascaded water directly from the Porcupine Bank or round by the South Porcupine submarine promontory from the Hebridean continental shelf. At *William Scoresby* station 963 on 19 January 1950 the low oxygen content

(63·5 % saturated) at the salinity minimum at 575 m. indicates surely that then North Atlantic Central water was dominant there.

The predicted properties set out in Table XIII will certainly be modified in detail by further knowledge. They are meant to show how, by combining several determinations, it should become possible in this area to recognize with certainty the several water masses and admixtures of them.

The Hydrography of the Submarine Indentation South of the Porcupine Bank and South-west of County Kerry

On twenty-seven occasions the Irish Fisheries Service, under the direction of the late Mr G. P. Farran, has made observations at the station SS (50° 34′ N., 11° 17′ W. approximately) on the eastern side of the submarine indentation

Table XIV. Observations at the Irish Station SS, 50° 34′ N., 11° 17′ W. approximately

Station no.	Lat. 50° N.+	Long. 11° W.+	Date	Depth to bottom (m.)	Depth of samples taken below 601 m.
SR 992	34′	29′	9. viii. 10	1452	713, 1225
SR 1098	37½′	16′	11/12. ii. 11	1006	700, 956
SR 1158	33′	21′	15. v. 11	1234–1478	731, 1234
SR 1228	36′	19′	10. viii. 11	1167	823, 1097
SR 1379	31′	16′	11. v. 12	977	731, 914
SR 1439	27′	20′	14. viii. 12	951	640, 914
SR 1613	29′	22′	15. v. 13	960	640, 914
SR 1677	35′	18′	14. viii. 13	1072	731, 987
SR 1824	33′	23′	14. v. 14	1379	914, 1280
SR 2158	34′	17′	14. v. 25	1037	1000
SR 2173	34′	17′	24. xi. 25	1152	1097
SR 2221	34′	17′	17. viii. 26	797	768
SR 2244	34′	17′	19. ii. 27	906	860
SR 2270	34′	17′	10. v. 27	1004	966
SR 2290	34′	17′	27. xi. 27	1049	1024
SR 2311	34′	16′	14. iv. 28	906	878
SR 2353	34′	16′	21. ii. 29	1016	986
SR 2382	35′	12′	3. vi. 29	843	800
SR 2404	36′	15′	12. viii. 29	873	840
SR 2420	34′	16′	1. xii. 29	1027	750, 978
SR 2487	37′	19′	26. v. 31	856	695
SR 2509	34′	14′	17. viii. 31	767	750
SR 2533	38′	14′	3. ii. 32	769	720
Challenger 1	25′	15′	26. vi. 32	815	750, 795
SR 2585	41′	17′	8. viii. 32	989	700, 800, 950
SR 2648	35′	16′	17. v. 33	1016	700, 800, 969
SR 2664	35′	16′	8. viii. 33	1073	700, 800, 1042
SR 2725	34′	15′	12. vi. 34	847	700, 800
WS 962	34′	10′	18. i. 50	922	780, 880
WS 963	34′	30′	19. i. 50	1311	660, 750, 800, 850, 930, 970, 1010, 1065, 1170, 1270

(Table XIV). The results for the years 1910–14 have been read from Mr D. J. Matthews's record cards, now in the writer's possession, and those for later years have been extracted from the *Bulletins Atlantiques* and *Bulletins Hydrographiques* published by the International Council for the Exploration of the

Sea. The series has been supplemented by one by H.M.S. *Challenger* in 1932 (Cons. Int., *Bull. Hydrogr.* for 1932) and by interpolated results from the two outermost *William Scoresby* stations in 1950 (Cons. Int., *Bull. Hydrogr.* for 1950). Depths observed ranged from 767 to 1478 m.

Mean temperatures, salinities and densities have been evaluated (Table XV), by interpolation where necessary, for standard depths at intervals of 100 m. from 100 to 1000 m. Down to 600 m., the sampling intervals were small enough to make interpolation safe except on 17 August 1931. Below 601 m. in many years only one depth was sampled so that interpolation may have caused error. The curves have been slightly adjusted so that salinity, temperature and density are consistent. Moreover, on some occasions, bottom was found above 800 m. Although the assessment of mean values at 800–1000 m. must be subject to greater error than in the upper waters, the error of the temperature mean appears not to exceed $\pm 0{\cdot}02^\circ$ C. Standard deviations of the means are also included in Table XV.

TABLE XV. MEAN TEMPERATURES, SALINITIES AND DENSITIES AT STANDARD DEPTHS AT OR NEAR THE IRISH STATION SS (50° 34′ N., 11° 17′ W.) FOR TWENTY-NINE OCCASIONS, WITH STANDARD DEVIATIONS

Depth (m.)	Temperature (° C.)	Salinity (‰)	Density (σ_t)
100	$11{\cdot}02 \pm 0{\cdot}43$	$35{\cdot}52 \pm 0{\cdot}04_9$	$27{\cdot}19 \pm 0{\cdot}08_2$
200	$10{\cdot}74 \pm 0{\cdot}26$	$35{\cdot}52 \pm 0{\cdot}06_2$	$27{\cdot}24 \pm 0{\cdot}05_0$
300	$10{\cdot}62 \pm 0{\cdot}22$	$35{\cdot}52 \pm 0{\cdot}05_1$	$27{\cdot}26 \pm 0{\cdot}03_6$
400	$10{\cdot}50 \pm 0{\cdot}19$	$35{\cdot}51 \pm 0{\cdot}06_0$	$27{\cdot}28 \pm 0{\cdot}03_5$
500	$10{\cdot}31 \pm 0{\cdot}14$	$35{\cdot}50 \pm 0{\cdot}04_4$	$27{\cdot}30 \pm 0{\cdot}03_8$
600	$10{\cdot}09 \pm 0{\cdot}14$	$35{\cdot}50 \pm 0{\cdot}05_5$	$27{\cdot}34 \pm 0{\cdot}04_7$
700	$9{\cdot}83 \pm 0{\cdot}20$	$35{\cdot}51 \pm 0{\cdot}04_5$	$27{\cdot}40 \pm 0{\cdot}04_5$
800	$9{\cdot}54 \pm 0{\cdot}27$	$35{\cdot}54 \pm 0{\cdot}04_0$	$27{\cdot}47 \pm 0{\cdot}04_8$
900	$9{\cdot}28 \pm 0{\cdot}31$	$35{\cdot}55 \pm 0{\cdot}04_5$	$27{\cdot}52 \pm 0{\cdot}05_0$
1000	$8{\cdot}92 \pm 0{\cdot}43$	$35{\cdot}54 \pm 0{\cdot}04$	$27{\cdot}57 \pm 0{\cdot}06_2$

Vertical mixing would seem to proceed at all depths on a considerable scale (Cooper, 1952*a*, fig. 2). Although the water at 1000 m. is commonly of very different origin from that at 100 m., the uniformity in salinity from top to bottom is notable. The result illustrates the futility of treating all high-salinity waters in the Celtic Sea as carrying uniform chemical and biological properties.

The stratum of most constant temperature lies between 500 and 600 m., that of most constant density between 300 and 500 m. The deepest water at 1000 m. shows a greater range of temperature and of density than any other stratum below 150 m. A similar result has been found in the open Atlantic at 44° 36′ N., 20° 00′ W. (Fig. 2). The relatively large standard deviation of the density at 1000 m. must mean that the currents there are of the same order of magnitude as those at 100 m. These deep currents will affect all attempts at dynamic computation of surface currents. The reference level of assumed no motion in the Eastern North Atlantic needs to be taken very deep. Moreover, the strong slope of deep geopotential topographies should

have a very pronounced effect, possibly a controlling effect, on surface currents. It may explain, in part, the great difficulty in assessing surface currents in the Atlantic near the continental slope of the Celtic Sea.

Variations in the Gulf of Gibraltar and 'Rockall Cascade' Waters at Station SS

The strength of the tongue of Gulf of Gibraltar water varies much from time to time. The largest changes between successive observations are given in Table XVI. Between May and August 1911 water entered between 700 and at least 820 m. depth which was both much warmer and more saline; it was undoubtedly Gulf of Gibraltar water. Between the same months in 1933, the converse happened, the Gulf of Gibraltar water was pushed out by colder and less saline water. This is the more usual occurrence.

TABLE XVI

Dates	Increase in salinity (‰)			Increase in temperature (° C.)		
	800 m.	900 m.	1000 m.	800 m.	900 m.	1000 m.
(*a*) Salinity and temperature increased or decreased together						
15. v.–10. viii. 11	+0·09	—	—	+0·63	+0·69	+0·70
17. v.–8. viii. 33	−0·07	−0·09	−0·09	−0·30	−0·40	−0·52
(*b*) Salinity and temperature moved in opposite phase						
27. xi. 27–14. iv. 28	+0·06	+0·08	—	−0·62	−0·78	—
14. viii. 12–13. v. 13	−0·06	−0·06	—	+0·23	+0·21	—

During the winter of 1927–8 between November and April at about 880 m. water about 0·08 ‰ more saline but half a degree colder came in; yet in the winter of 1912–13 at about 900 m. water 0·06 ‰ less saline and 0·20° C. warmer entered. These last events cannot be correlated with changes in the Gulf of Gibraltar component. A detailed study of variations in salinity on the lines of the analysis of temperature to follow has not revealed any rhythmic change in the distribution of salinity.

There are striking variations in temperature at 800–1000 m. depth, but owing to the heterogeneous nature of the data they are not presentable in a simple form. They may be most surely shown by the following procedure.

(i) The temperatures at 100 m. intervals from 100 to 1000 m. were tabulated, when necessary interpolating graphically and checking that temperatures, salinity and density are mutually consistent. (ii) The mean temperature at each standard depth for all observations at station SS was then evaluated. (iii) At 800, at 900 and at 1000 m., the deviations of each observed or interpolated temperature from the mean for the depth was worked out. (iv) The deviations at 800 m. and, when available, at 900 and 1000 m., were then averaged to give the best assessment possible of the mean deviation of the temperature of the 800–1000 m. stratum from its overall average. (v) The changes in these mean deviations as measured on cruises a quarter or half year apart were then computed (Table XVII).

The result is no more than a measure of the changes in the temperature of the 800–1000 m. stratum considered as a whole. The summer of 1911 was exceptional (p. 495), and all results involving it are enclosed in square brackets and omitted from the means.

There is a seasonal change in temperature with a range of about 0·5° C. The water at 800–1000 m. has been warmest in November and coldest in August. Nearly all the warming up occurs between August and November.

TABLE XVII. CHANGES IN THE MEAN TEMPERATURE OF THE 800–1000 M. STRATUM AT STATION SS BETWEEN CRUISES A QUARTER AND A HALF-YEAR APART

Quarterly intervals

	1911	1927	1929*				*Mean*
Feb.–May	[−0·48]	−0·60	−0·17				*−0·39*
	1911	1912	1913	1929	1932†	1933	
May–Aug.	[+0·68]	−0·14	−0·04	−0·04	−0·22	−0·40	*−0·17*
	1929						
Aug.–Nov.	+0·28						*+0·28*
Nov.–Feb.	No pairs of observations available						—

Half-yearly intervals

	1927/8			*Mean*
Nov.–Apr.	−0·78			*−0·78*
	1911	1929		
Feb.–Aug.	[+0·20]	−0·25		*−0·25*
	1925	1927	1929	
May–Nov.	+0·01	+1·16	+0·24	*+0·47*
	1910/11	1926/27		
Aug.–Feb.	+0·12	+0·44		*+0·28*

Also

	1910/11	1911/12	1912/13	1913/14	1926/27	1931/32‡	1932/33	1933/34	*Mean*
Aug.–May	[−0·36]	[+0·23]	+0·22	+0·08	−0·16	+0·42	+0·51	+0·31	*+0·23*

* 21 Feb.–3 June. † 26 June (*Challenger* Station 1)–8 Aug.
‡ 17 Aug. 1931–26 June 1932.

Analysis of the observations by other methods has shown that the extent of the cooling between May and August has been somewhat exaggerated; most of the cooling occurs between February and May, the season of cascading of shelf water (Cooper & Vaux, 1949), which undoubtedly may affect the water down to 1000 m. depth.

Water in the Celtic Sea never becomes heavy enough to sink so far and it is doubtful if Porcupine Bank water could either. Water of sufficient density could only be found at the surface still farther north. None the less, north of 60° N. and also over the Rosemary Knoll[1] the salinity is almost always too low. Over the extensive Rockall Table Mount[1] water of appropriate density,

[1] Name in accordance with the recommendations of the British National Subcommittee on Nomenclature of Ocean Bottom Features.

salinity and temperature often occurs. I am much indebted to Lt.-Cmdr. J. R. Lumby, R.N., for providing me from his card index with a complete set of surface hydrographical observations for the months of January to April over the Rockall Table Mount between 56° 30′ and 58° 15′ N. lat. and 13° and 15° W. long. From them the mean surface density there has been computed for each month (Table XVIII); 21% of these observations show a surface salinity of 35·45 ‰ or more. During passage south the salinity of Rockall cascade water would be expected to increase somewhat, due to lateral mixing.

Considering only the statics of the system, heavy saline water formed in winter over the Rockall Table Mount could account for the fairly regular seasonal fluctuation of the water at 800–1000 m. depth at station SS (cf. also Nansen, 1912). However, the dynamics of a north-south section across the North Atlantic Drift requires a density distribution in this sense with heavy surface water on the left or north and light water on the right or south. Even

TABLE XVIII

Month	Mean density of surface water over Rockall Table Mount: No. of observations	Mean density of surface water over Rockall Table Mount: σ_t	Depth at station SS at which such a mean density is recorded; from Table XV (m.)
January	12	27·46	790
February	12	27·57	1000
March	26	27·50	860
April	33	27·44	750

so, if a cold winter produces a sudden increase in the density of the water overlying the shallow Rockall Table Mount, then the steady state of the drift would be upset. Either its speed towards the east or north-east must increase to carry a greater volume of saline water into the northern North Sea, or the heavy water must cascade towards the south, undercutting the North Atlantic Drift. Both may probably happen to different degrees in different years. Tait (1951) has remarked that in the northern North Sea the predominance of oceanic influence is in most years at a maximum in spring and early summer and at a minimum in autumn and winter, and that these seasonal variations are subject to annual fluctuations in their magnitude and incidence. This, qualitatively, is the effect which increase in density during cold weather in February and March over the shallow Rockall Table Mount and the neighbouring banks or knolls would produce. The evidence from station SS and from *Armauer Hansen* station 1914/6 is that this heavy water may also cascade and then flow southwards along the continental slope in some winters for over 500 miles.

Although incursions of Gulf of Gibraltar water will lead to warming up at any season, it seems clear that only in the summer of 1911 was it dominant over the seasonal oscillation due to the 'Rockall cascade' current. The greatest

changes in density occurred: (i) August 1910–February–May 1911 when the overall increase much exceeded 0·10 σ_t-unit; (ii) February–May 1927 when the density increased by 0·09 σ_t-unit due entirely to a fall in temperature of 0·5° C. On the latter occasion the salinity scarcely changed. The phenomenon was probably associated with cascading from the continental shelf of water having salinity 35·55 ‰, temperature 8·2–9·2° C. and density 27·54–27·68 σ_t-unit. Such water cannot have originated in the Celtic Sea and can only have come from farther north. On 1 February 1927 water having salinity 35·48 ‰, temperature 8·2° C. and σ_t 27·65 was reported (Cons. Int., *Bull. Hydrogr.* for 1927) on the Danish line of surface stations between Copenhagen and New York at 59° 02′ N., 11° 00′ W. It is likely, therefore, that the chilled water at station SS (50° 34′ N., 11° 17′ W.) had been formed by cooling and

TABLE XIX

Date	Lat. N.	Long. W.	Depth (m.)	Temp. (° C.)	Salinity (‰)	Density (σ_t)	Oxygen (%)
			Over Rockall Table Mount				
15. i. 34	58° 09′	14° 21′	0	8·7	35·40	27·50	—
4. ii. 34	57° 48′	13° 04′	0	9·1	35·46	27·48	—
12. iii. 34	58° 03′	13° 09′	0	8·7	35·52	27·59	—
25. iii. 34	58° 05′	13° 03′	0	9·2	35·48	27·48	—
16. iv. 34	57° 39′	13° 37′	0	9·6	35·59	27·49	—
			Station SS				
12. vi. 34	50° 34′	11° 15′	600	9·81	35·57	27·45	—
			700	9·81	35·55	27·43	—
			800	9·41	35·57	27·52	—
			Also *Armauer Hansen* station 1914/6				
5. vi. 14	47° 57′	9° 42′	800	9·94	35·53	27·39	90
			1200	8·51	35·52	27·62	89

cascading of the water in the North Atlantic Drift passing over the Rockall Table Mount. North Atlantic Central water carried towards Rockall is likely, whilst on passage around and over the Table Mount, to be modified by capsizing against the island slope during high winds. If the Rockall Table Mount was indeed its origin it had subsequently moved south at the rate of about 5 miles a day. The year 1934 showed the effect particularly clearly (Table XIX).

There is little doubt that at station SS in June 1934 there was a large northern component at 600–800 m. Similarly, the highly oxygenated waters reported from the *Armauer Hansen* expedition in 1914 by Gaarder (1927) at station 6 at 800 and 1200 m., sandwiching oxygen-depleted water (72 and 77·5% saturated) at 900 and 1000 m., would seem certainly to have been of northern surface origin.

Ability to cascade from north to south depends not on any absolute but on relative values of density. Thus ten observations of computed surface density by Ocean Weather ships over the Rockall Table Mount in February–April 1950 revealed a somewhat low mean density of 27·41 σ_t. Nevertheless, the

waters at station SS in the 'South Porcupine submarine indentation' in January 1950, also light relative to earlier years, could have subsequently accommodated such water down to 900 m. Considerable north-south cascading was possible.

The dynamics of such a descending mid-water current of cascade origin, hugging the continental slope on its left, needs attention. It is clear that immediately west of the British Isles in spring and summer geopotential topographies (for definition see Sverdrup *et al.* (1942, p. 404)), suggesting surface currents to the north and north-east, need to be interpreted with especial care. A mid-water descending current in the opposite direction and of considerable magnitude is always likely. It is now realized that such a current system would contribute to the difficulty experienced in interpreting the *Dana* section across it in June 1938. This has not been re-examined.

In March and April and even perhaps in May, severe gales from between south-west and north-west would, by causing capsizing, destroy this descending mid-water cascade current during its passage along the western fringe of the British Isles. Northern cascade water would not then reach south-west Ireland in an identifiable form.

The winter and spring of 1927 was a period of strong cascading (Cooper & Vaux, 1949). The low inorganic phosphate found that year by Atkins at 860 m. at station SS (Table X, and compare Cooper 1952*a*, fig. 2) suggests that by mid-February little water from the south was present. During the spring cascading from the Celtic Sea continued strongly, followed during the summer and autumn by a very strong recession of cascade water. By November the water at 1000 m. had warmed up by $1\frac{1}{4}^{\circ}$ C. and had become lighter than any water recorded there between 1910 and 1934. By April 1928 this warm light water had again been displaced by a dense, saline water of intermediate temperature (35·61‰, 9·0–9·4° C. and σ_t 27·58–27·61), this water having a strong Gulf of Gibraltar component. It is clear that during 1927, as a whole, water movements around 800–1000 m. were on a scale greater than in any other year for which we have sufficient records (Table XIV). Quite apart from vertical exchanges, the resulting alterations of deep geopotential topographies must have had a very considerable effect on those at the surface. Unusual surface currents above the continental slope of the western Celtic Sea were likely in that year.

Seasonal Variations at Station SS in the 200–400 m. Water Stratum

The seasonal variations for the 200–400 m. stratum have been worked out in the same way as those at 800–1000 m. (Table XX). The scarcity of observations in November has made difficult the distribution of changes as between autumn and early winter. Most surprising was that the changes in temperature from season to season at 200–400 m. were on an average less than one-fifth of those at 800–1000 m. The remaining conclusions are tabulated in Table XXI.

TABLE XX. CHANGES IN THE MEAN SALINITY AND TEMPERATURE OF THE 200–400 M. STRATUM AT STATION SS BETWEEN CRUISES A QUARTER OR A HALF-YEAR APART

Salinity

Quarterly intervals

	1911	1927	1929*	1932				*Mean*
Feb.–May	+0·05	−0·10	+0·11	+0·01				*+0·02*
	1911	1912	1913	1929	1931	1932†	1933	
May–Aug.	−0·03	−0·01	−0·01	−0·05	−0·13	−0·01	−0·05	*−0·04*
	1929							
Aug.–Nov.	−0·05							*−0·05*
Nov.–Feb.	No pairs of observations available							—

Half-yearly intervals

	1927/28			*Mean*
Nov.–Apr.	+0·04			*+0·04*
	1911	1929	1932	
Feb.–Aug.	+0·02	+0·06	0·00	*+0·03*
	1925	1927	1929	
May–Nov.	−0·04	+0·05	−0·06	*−0·02*
	1910/11	1926/27	1931/32	
Aug.–Feb.	+0·01	+0·07	+0·11	*+0·06*

Also

	1910/11	1911/12	1912/13	1913/14	1926/27	1931/32‡	1932/33	1933/34	*Mean*
Aug.–May	+0·06	0·00	+0·01	−0·03	+0·07	+0·11	+0·03	+0·05	*+0·04*

Temperature

Quarterly intervals

	1911	1927	1929*	1932				*Mean*	*Mean omitting 1932*
Feb.–May	−0·08	−0·13	−0·07	−0·61				*−0·22*	*−0·09*
	1911	1912	1913	1929	1931	1932†	1933		
May–Aug.	+0·06	+0·08	−0·12	+0·08	−0·09	+0·02	−0·01	*Nil*	*Nil*
	1929								
Aug.–Nov.	+0·18							*+0·18*	*+0·18*
Nov.–Feb.	No pairs of observations available							—	—

Half-yearly intervals

				Mean	*Mean omitting 1932*
	1927/28				
Nov.–Apr.	−0·17			*−0·17*	*−0·17*
	1911	1929	1932		
Feb.–Aug.	−0·02	+0·01	−0·59	*−0·20*	*Nil*
	1925	1927	1929		
May–Nov.	+0·13	+0·33	+0·26	*+0·24*	*+0·24*
	1910/11	1926/27	1931/32		
Aug.–Feb.	+0·04	−0·03	+0·68	*+0·23*	*Nil*

Also

	1910/11	1911/12	1912/13	1913/14	1926/27	1931/32‡	1932/33	1933/34	*Mean*
Aug.–May	−0·04	−0·06	−0·03	+0·06	−0·16	+0·07	+0·12	−0·03	*−0·01*

* 21 February–3 June. † 26 June (*Challenger* Station 1)–8 August.
‡ 17 August 1931–26 June 1932.

TABLE XXI. SEASONAL VARIATIONS AT STATION SS IN THE 200–400 M. WATER STRATUM

	Temperature	Salinity
Feb.–May	Average decrease of at least 0·09° C. Very marked decrease (0·6°) in 1932	Variable. Average increase of merely 0·02 ‰. In 1927, a year of strong cascading of shelf water, there was a decrease of 0·10 ‰. For 1930, probably a year of strong cascading, no observations are available
May–Aug.	Little change	Decrease in every year, average decrease 0·04 ± (S.D.) 0·04 ‰. (The statistical distribution is not 'normal'.)
May–Nov.	Average increase of 0·2°, mostly between August and November	Little regular change
Aug.–Feb.	Net slight overall tendency to increase; very strong warming (0·7°) in autumn of 1931–32	Average increase of about 0·06 ‰

N.B. Owing to the nature of the distribution of the observations in time, the positive and negative assessments cannot be expected exactly to cancel.

	Density
Feb.–May	Average increase of about 0·06 σ_t-unit
May–Aug.	Average decrease of about 0·03 σ_t-unit
Aug.–Nov.	Average decrease of about 0·03 σ_t-unit
Nov.–Feb.	Little change

Recent Warming up of the Upper layers at Station SS

For the twenty-nine sets of observations at and near station SS the departures from the mean temperature of the 200–400 m. stratum are presented in Table XXII. Positive departures are stressed by italic type. In the years 1910–14 and again from May 1925 to May 1927 the water was consistently colder than the average by 0·2° C. No records are available for the exceptionally warm autumn of 1921 (cf. Harvey, 1923).

During the summer of 1927 markedly warmer water arrived and remained with minor recessions until the end of the Irish observations in 1934.

When the position was next examined on 18–19 January 1950 by R.R.S. *William Scoresby*, the stratum was found to be 0·7° C. warmer as compared with 1910–14 and 1925 (cf. Helland-Hansen, 1949).

Smed (1949*a*,*b*, 1950) has found that there has been a warming up since about 1932 of the surface waters in the north-eastern North Atlantic in his areas I, H and L (between 55 and 67° N. lat. and between 10 and 20° W. long.), in area J (between 60 and 64° N. and between 0 and 10° W.), and in area K (between 58 and 60° N. and between 3 and 10° W.). It would seem from his reports that the marked warming up first appeared in the north about 1927 and that it is spreading towards the south and south-west. His findings seem to be compatible not with an increased transport of heat by the North Atlantic Drift but rather with reduced abstraction in the north of the heat transported. If this has been so, winter cascading from the more northern

shallow areas, such as the Rockall Table Mount, will have been affected and the rate of formation of the North Atlantic Deep water still farther north may have been reduced (see also Cooper, 1952*b*).

On the other side of the Atlantic, Lauzier (1950) has reported that from April to October 1949 the surface temperatures at St Andrews (mouth of the Bay of Fundy) and at Halifax (Nova Scotia) Lightvessel were much higher than usual, indeed the highest ever recorded.

TABLE XXII. WARMING UP OF UPPER WATERS (200–400 M.) AT STATION SS BETWEEN 1910 AND 1950, SHOWN BY DEPARTURES FROM MEAN TEMPERATURES

(Positive departures in italic type.)

Year	February	May	August	November	Period average
1910	—	—	−0·20	—	
1911	−0·16	−0·24	−0·18	—	
1912	—	−0·24	−0·16	—	
1913	—	−0·19	−0·31	—	
1914	—	−0·25	—	—	
Mean 1910–14	−0·16	−0·23	−0·21	—	−0·18
1924	—	−0·30	—	−0·17	
1926	—	—	0·00	—	
1927	−0·03	−0·16	—	—	
Mean 1925–May 1927	—	—	—	—	−0·13
1927	—	—	—	*+0·17*	
1928	—	0·00	—	—	
1929	*+0·20*	*+0·13*	*+0·11*	*+0·39*	
1930	—	—	—	—	
1931	—	*+0·02*	−0·07	—	
1932	*+0·48*	*+0·04*	*+0·02*	—	
1933	—	*+0·14*	*+0·13*	—	
1934	—	*+0·10*	—	—	
Mean November 1927–May 1934	*+0·34*	*+0·07*	*+0·08*	*+0·28*	*+0·19*
1950	*+0·52* (January)	—	—	—	(*+0·52*)

These events reflect the general warming up of the North Atlantic. One result is that the temperature-salinity relationships, epitomized in equations (1) and (2) (pp. 467 and 479) and drawn in Figs. 9 and 15, now refer to an age that is past. They need to be re-determined from fresh observations.

DISCUSSION

The purpose of this paper has been twofold: first, by achieving a better understanding of the exchanges of water with the Atlantic, to assist the preparation of papers to follow on the hydrography of the Celtic Sea and English Channel; and, secondly, to enable future investigations over the continental slope to be better directed to the solution of defined problems. It is a contribution to 'experimental oceanography'.

There is clearly a need for repeated observations at fixed points in deep water off the slope to keep track of the very considerable fluctuations which occur at all depths above 1500 m.

The theory of 'capsizing' water masses over the continental slope seems plausible. If capsizing can be shown to be dynamically sound and can be demonstrated by clear-cut observations, it provides a mechanism of great power for enriching the surface waters of the sea with deep nutrients.

It seems probable that, in general terms, winds of a given strength will prove very much more effective in producing extensive capsizing if preceding conditions have been optimal. Many variations of circumstances can be visualized. Thus, if strong winds have blown from between north and east for some time, as they did in February 1947, some degree of upwelling by the classical mechanism would occur. If then the wind veered quickly to the south, reaching gale force and producing severe capsizing while nutrient-rich water stood banked high against the slope, there would arise very favourable conditions for surface enrichment of a kind which would occur only a few times in a century.

It is necessary also to follow the conflict at 800–1000 m. depth between Gulf of Gibraltar water and cascade water from the north and to learn more of their properties. The Irish station SS, already worked twenty-seven times, is an obvious choice. It lies on the edge of the 'South Porcupine submarine indentation' which may act like an electrical choke, ironing out short-period fluctuations appearing in the water outside the indentation. On occasion, as on 14 May 1925 and 19 February 1927 (Cooper, 1952*a*, fig. 2), the compression of the temperature-salinity diagram suggests that vertical exchanges may become very large (cf. Atkins's determination (Table X) of inorganic phosphate at 860 m. at station SS on 19 February 1927, which was surprisingly low for such a depth). For purposes of comparison the T–S relationship found immediately south of the Celtic Sea at *Armauer Hansen* station 1914/6 (Figs. 8 and 9) and at *Armauer Hansen* station 1914/15 in the open Atlantic are included.

In such a submarine indentation, internal waves probably resonate strongly, causing great turbulence and vertical mixing and, by so doing, destroying themselves. Combined studies of cascading, capsizing, internal waves and resonance in this indentation will be necessary. Capsizing against either wall of the indentation should itself induce deep internal waves which would be expected to resonate strongly.

An additional Irish station has been worked three times, at 50° 00′ N., 13° 00′ W. The observations there have been consistent with those at station SS. It is in a strategic position north of the 'Sole submarine promontory' which seems sometimes to be a water parting.

Cascaded shelf-waters play an important part. It will be necessary to substantiate that the deeper cascade waters, do, in fact, come from the north,

probably from the Rockall Table Mount. A solution will require (i) a knowledge of the frequency of occurrence over the Rockall Table Mount, and over the other elevations of the sea-bed towards the east and north-east, of suitable water sufficiently heavy and in sufficient amount to cascade to the south and to undercut the main North Atlantic Drift; (ii) establishment of a descending current in late spring and summer along the continental slope west of the British Isles; (iii) determination of oxygen contents throughout the whole area, since waters from the Gulf of Gibraltar and the Atlantic to the south-west at around 1000 m. would be expected to have an oxygen content between 65 and 70 % saturated, whereas recently cascaded water should exceed 85 % saturated; (iv) a study of silicate distribution, which is likely to help; (v) a satisfactory account of the dynamics of a mid-water current gliding downhill towards the south with the continental slope on its left.

Cascading and capsizing are very different processes which may produce in our waters markedly similar distributions of salinity, temperature and oxygen. Often they may combine to give a large mass of water of composite origin. They should be distinguishable and the degree of admixture of the two waters or processes should be assessable in terms of the content of nutrients, especially silicate. Capsized water should be the richer.

Fraser (1950) states that the Scottish fisheries research vessels have found biological indications of two water masses approaching Faeroe from the south-west. One, the 'Lusitanian' stream, has travelled via the west coasts of Ireland and Scotland and will have been influenced by any vertical exchanges over and along the continental slope; the other, the Atlantic stream, travels farther west. The two streams, at least in the middle and late summer, are said to be very distinct but mix along the line of meeting. Such biological distinctions probably indicate chemical differences in the waters which may persist awhile. It would be desirable to know which of these waters bathes the Rockall Table Mount and other areas of formation in winter of cascaded water.

May one ask whether the 'Lusitanian' water may be identifiable with a 'capsized and cascaded water' similar to that at stations 6–8 of Fig. 11? Such water should exist all along the west European continental slope and for 75–150 miles to seaward. The 'Atlantic' water of the Scottish workers would then be identifiable with the 'North Atlantic Central' water of stations 9–15 and its winter-mixed surface skin.

The North Atlantic Drift carries warm-water plankton organisms ever northwards and eastwards into colder regions unsuitable for their reproduction. Any mechanism for returning part of the stock to the south should assist its survival. If therefore there are any organisms, not only animals but perhaps diatoms as resting spores, which can avail themselves of the deeper return current of cascade origin, their survival should be favoured. Diatom resting spores could only profit if they complete their travels by being brought

up to illuminated surface waters by some form of upwelling such as capsizing. Cascade water, formed as it is in winter, will start by being reasonably rich in nutrients and will become further enriched by lateral exchange or capsizing with richer deep North Atlantic Central or Gulf of Gibraltar water. Resting spores brought up in such water to illuminated levels would be able immediately to initiate rapid cell division. In their new home they would be considered to be more northern species. If this cyclical process can be firmly established as occurring it provides not only the nutrients required for growth but the seeds of life itself.

The mid-water cascade current will take time on its journey south. It will sink in the north mostly in February and March and will not reach its southern limit until late in the spring. Species of plants and animals which may be said to be characteristic of the waters around 58–60° N., 12–15° W., and would there start their seasonal reproductive cycle in, say, March, would not reach more southern waters until later in the spring.

Again, since the intensity of cascading will be related to air and sea temperatures in the more northern area, after warm 'northern' winters the 'seed' stock of northern species of phyto- and zooplankton abreast of the Celtic Sea should be poor, while after cold 'northern' winters it should be relatively rich. It should therefore be worth while to seek a correlation between abundance of 'more northern' species in May and June between 48 and 50° N. with air and sea temperatures in February and March between 58 and 60° N. Intensity of cascading should not be related so much to deviations of temperature from all-time means but to deviations from short-period average conditions. Therefore, such a correlation should be sought not in terms of all-time but in terms of immediately preceding decade means.

South of the Celtic Sea only one position has ever been exactly repeated, viz. 46° 28′ N. lat., 8° 01′ W. long. (*Dana* stations 1387 on 25 June 1922, and 4158 on 17 June 1930). Choice of standard stations will not be much restricted by history but will depend much more upon the position of submarine valleys and spurs in the neighbouring continental slope.

Summary

The properties of 'Mediterranean' water reaching the threshold of the Celtic Sea are outlined. This water may be recognized not only by its relatively high temperature and salinity but by an oxygen content between 65 and 69% saturated. The name 'Gulf of Gibraltar' water is preferred.

Due to admixture of nutrient-rich North Atlantic Central water, the Gulf of Gibraltar water in the neighbourhood of the Celtic Sea is fairly rich in nutrients, and the large 'anomaly of the nitrate-N–phosphate-P ratio found in its region of origin has largely disappeared.

The extension of the Gulf of Gibraltar water into the eastern North Atlantic

is very variable both in space and time and, at a given position, very large changes in temperature and salinity may occur in a few months.

The *Thor* investigations in 1906 revealed that the Gulf of Gibraltar water may be held into the right against the continental slope of the west European coast and not extend very far to seaward. Between 1000 and 2000 m. depth south of the Celtic Sea variations in phosphate-P content of at least 0·2 μg.-atom/l. seem to have occurred.

The properties and upper and lower limits of North Atlantic Central water in the area have been examined. Well away from the continental slope the upper limit of Central water, conforming to its T–S relation, and the lower limit of winter mixing have lain between 75 and 100 m. depth. Approaching the slope the apparent depth of vertical mixing becomes more than twice as great. This effect is attributed to cooled cascade water from the continental shelf which, by bringing about a state of labile equilibrium, assists mixing to a greater depth by wind and by processes such as capsizing of water masses peculiar to the continental slope.

Part of a survey of a section of the continental slope by H.M. surveying ship *Dalrymple* revealing a rugged topography is reproduced (Fig. 10).

It is possible to identify the several water masses in the vertical section worked south-west of the Celtic Sea in June 1914 by the Norwegian research vessel *Armauer Hansen* (Fig. 11), viz. (i) North Atlantic Deep water below approximately 2000 m.; (ii) between 1200 and 2000 m. water formed by mixing of Deep water and Gulf of Gibraltar water and conforming well to the T–S relation given as equation (1); (iii) between 800 and 1200 m. depth Gulf of Gibraltar water showing a salinity maximum and oxygen minimum, and warm; (iv) North Atlantic Central water conforming to equation (2), 700 m. thick at *Armauer Hansen* station 15 (Figs. 8 and 9) and thinning out towards the shelf which it did not reach; (v) an intermediate region of mixed Central and Gibraltar water; (vi–viii) three layers of cascaded waters lying against the continental slope, the uppermost one extending from the surface down to 400 m. depth and derived largely from the Celtic Sea and further mixed by capsizing processes, and two others at about 800 and at 1200 m. depth of northern origin: the Porcupine Bank and the Rockall Table Mount are tentatively suggested as the sources of these; and lastly (ix) at stations 10 and 11, 200 miles off the continental slope, a core of highly oxygenated water (86–94% saturated) and having temperature and salinity appropriate to the Celtic sea the preceding winter. This core is considered to be a cascade phenomenon whose understanding demands further knowledge of the topography and oceanography of the continental slope.

It is considered probable that these water masses of very different physical and biological histories will have acquired different contents of chemical micro-constituents. These may affect organisms for good or ill at sensitive stages in their life histories, e.g. development of diatom-resting spores,

fertilization and hatching of eggs and moulting of crustaceans. When 'Atlantic' water enters the Celtic Sea and English Channel, the particular kind needs to be identified.

On 18–19 January, 1950, R.R.S. *William Scoresby* worked four stations over the western continental slope of the Celtic Sea along the parallel 50° 34′ N. and on 11–12 May, R.R.S. *Discovery II* worked three over the southern slope in about 7° 40′ W. (Fig. 8). At no depth were the two sections closely related.

On the northern January section vertical mixing had extended to 250 m. and there was little horizontal difference in temperature or density. Total phosphorus and inorganic phosphate increased westward by 0·1 μg.-atom/l. in 30 miles. Along the southern section in May there was no relict isothermal, isopycnal layer from the winter.

The twenty-seven sets of observations made by the Irish Fisheries Service at their position 'SS', 50° 34′ N., 11° 17′ W., have been submitted to statistical examination. Mean temperatures, salinities and densities are set out in Table XV, together with standard deviations. The water there at 800–1000 m. depth and also at similar depths in the open Atlantic at 44° 36′ N., 20° 00′ W. shows a greater standard deviation and range of temperature and density than any other strata below 150 m. Currents there must be of the same order of magnitude as at 100 m. depth.

The conflict south-west of Ireland between Gulf of Gibraltar water and cascaded waters from the north is described. It is suggested, but not proved, that much of the northern cascaded water has been created over the Rockall Table Mount and flows south at about 5 miles a day. At station SS there is at 800–1000 m. depth a seasonal change in temperature with a range of about 0·5° C.

Immediately west of the British Isles in spring and summer geopotential topographies, derived from the distribution of density, suggesting surface currents to the north and north-east need to be interpreted with especial care. A mid-water descending current in the opposite direction and of considerable magnitude is always likely. The effect upon the survival of diatoms and of animal plankton of a cyclical process involving this mid-water return current is examined.

During 1927 as a whole, water movements around 800–1000 m. were on a scale larger than in any other year for which we have sufficient records.

At 200–400 m. depth the average seasonal changes in temperature were only one-fifth of those at 800–1000 m. Since 1927 the stratum of water between 200 and 400 m. has become warmer. In January 1950 it was 0·5° C. warmer than the mean of all observations. The relevance of these results to the widely held view that the Northern Hemisphere is warming up is discussed.

REFERENCES

ARMSTRONG, F. A. J., 1951. The determination of silicate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 149–60.

ATKINS, W. R. G., 1928. Seasonal variations in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *Journ. Mar. Biol. Assoc.*, Vol. 15, pp. 191–205.

BEAUGÉ, L., 1934. Entrée ouest de la Manche. *Carte* 2. *Haut fond du Président Théodore Tissier.* (*Carte préliminaire–Août 1934.*) Paris: Office des Pêches Maritimes.

BÔTO, R. G., 1945. Contribuïção para os estudos de oceanografia ao longo da costa de Portugal. Fosfatos e nitratos. *Trav. Stat. Biol. Maritime Lisbonne*, No. 49, 102 pp.

BRENNECKE, W., 1921. Die ozeanographischen Arbeiten der deutschen antarktischen Expedition 1911–1912. *Archiv. deutsch. Seewarte*, Bd. 39, pp. 1–216.

CONSEIL INTERNATIONAL POUR L'EXPLORATION DE LA MER. *Bulletins Hydrographiques*, published annually. Copenhagen. [Text references refer not to year of publication but to the year appearing as part of the title of each issue.]

COOPER, L. H. N., 1937. On the ratio of nitrogen to phosphorus in the sea. *Journ. Mar. Biol. Assoc.*, Vol. 22, pp. 177–82.

—— 1938*a*. Redefinition of the anomaly of the nitrate-phosphate ratio. *Journ. Mar. Biol. Assoc.*, Vol. 23, p. 179.

—— 1938*b*. Salt error in determinations of phosphate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. 23, pp. 171–8.

—— 1952*a*. Processes of enrichment of surface waters with nutrients due to strong winds blowing on to a continental slope. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 453–64.

—— 1952*b*. Factors affecting the distribution of silicate in the North Atlantic Ocean and the formation of North Atlantic deep water. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 511–26.

COOPER, L. H. N. & VAUX, DAVID, 1949. Cascading over the continental slope of water from the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 719–50.

DANA REPORT No. 12, 1937. *Hydrographical observations made during the 'Dana' Expedition* 1928–30. Copenhagen, Carlsberg Foundation. 46 pp.

FRASER, J. H., 1950. Plankton investigations from Scottish research vessels. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 6, pp. 91–5.

GAARDER, T., 1927. The cruises of the *Armauer Hansen*. No. 2. Die Sauerstoffverhältnisse im östlichen Teil des nordatlantischen Ozeans. *Geofys. Publ., Oslo*, Vol. 4, No. 3, 72 pp.

HARVEY, H. W., 1923. Hydrographic features of the water in the neighbourhood of Plymouth during the years 1921 and 1922. *Journ. Mar. Biol. Assoc.*, Vol. 13, pp. 225–35.

—— 1948. The estimation of phosphate and of total phosphorus in sea waters. *Journ. Mar. Biol. Assoc.*, Vol. 27, pp. 337–59.

HELLAND-HANSEN, B., 1930. Physical oceanography and meteorology. *Rep. Sci. Res. 'Michael Sars' North Atlantic Deep Sea Exped.* 1910, Vol. 1, 115 pp. (Pt. 1), 102 pp. (Pt. 2).

—— 1949. Remarks on some variations in atmosphere and sea. Glaciers and climate, geophysical and geomorphological essays dedicated to Hans W:son Ahlmann. *Geografiska Annaler*, Häfte 1–2, pp. 75–82.

HELLAND-HANSEN, B. & NANSEN, F., 1927. The cruises of the *Armauer Hansen*. No. 1. The eastern North Atlantic. *Geofys. Publ., Oslo*, Vol. 4, No. 2, 76 pp. and 71 pl.

JACOBSEN, J. P., 1929. Contribution to the hydrography of the North Atlantic. The Danish *Dana* Exped. 1920–22, Vol. 1, *Oceanogr. Rep. No.* 3, 98 pp. Copenhagen.

LAUZIER, L., 1950. Température des eaux de surface exceptionellement élevée en 1949. *Fisheries Res. Bd., Canada, Prog. Rep. Atlantic Coast Stations*, No. 51, p. 19.

NANSEN, F., 1912. Das Bodenwasser und die Abkühlung des Meeres. *Int. Rev. Ges. Hydrobiol. Hydrogr.*, Bd. 5, pp. 1–42.

NIELSEN, J. N., 1912. Hydrography of the Mediterranean and adjacent waters. *Rep. Danish Ocean. Exp.* 1908–1910, Vol. 1, pp. 77–191. Copenhagen.

SANDSTRÖM, J. W., 1918. The hydrodynamics of Canadian Atlantic waters. *Canadian Fisheries Expedition*, 1914–15, pp. 221–343. Ottawa.

SCHMIDT, J., 1912. Hydrographical observations. *Rep. Danish Ocean. Exp.* 1908–10, Vol. 1, pp. 53–75. Copenhagen.

SMED, J., 1949*a*. Monthly anomalies of the surface temperature in the sea round Iceland during the years 1876–1939 and 1945–1947. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 4, pp. 11–26.

—— 1949*b*. Monthly anomalies of the surface temperature in areas of the north-eastern North Atlantic during the years 1876–1939 and 1945–1948. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 5, pp. 11–15.

—— 1950. Monthly anomalies of the surface temperature in areas of the North Atlantic during the years 1876–1939 and 1945–1949. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 6, pp. 18–27.

STORROW, B., 1925. Fluctuations in fisheries. *Trans. Nat. Hist. Soc. Northumberland, Durham and Newcastle-upon-Tyne*, N.S., Vol. 6, pp. 182–200.

SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H., 1942. *The Oceans*. 1087 pp. New York.

TAIT, J. B., 1951. Oceanic influence in and around the North Sea. *Weather*, Vol. 6, No. 3, pp. 85–6.

THOMSEN, H., 1931. Nitrate and phosphate contents of Mediterranean water. *Rep. Danish Ocean. Exp.* 1908–1910, Vol. 3, No. 6, 14 pp. Copenhagen.

VALLAUX, C., 1936. The deep circulation in the Atlantic Ocean. *Hydrogr. Rev., Monaco*, Vol. 13, No. 2, pp. 32–45.

WILSON, D. P., 1951. A biological difference between natural sea waters. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 1–20.

APPENDIX

METHODS USED IN THE 1950 INVESTIGATIONS

The Nansen-Pettersson insulating water-bottle was used down to 400 m. at R.R.S. *William Scoresby* stations on 18–19 January and R.R.S. *Discovery II* stations on 11–12 May 1950, except at station WS962 (to 200 m.) and *Discovery II* station 2658 (to 150 m.). *Discovery* pattern reversing bottles were used at greater depths. All temperatures are appropriately corrected to give temperatures *in situ*. All salinities were determined by the Government Chemist.

The analyses of oxygen samples collected on R.R.S. *William Scoresby* were completed by Dr T. J. Hart and Mr R. I. Currie on 26 January in the ship's

laboratory whilst lying at Devonport. Analyses of inorganic phosphate were made by the present Plymouth procedure (Harvey, 1948) by Mr F. A. J. Armstrong between 21 and 23 January. Total phosphorus analyses were made on 24 January by him using Harvey's method.

All R.R.S. *Discovery II* samples were taken on to Malta whence they were sent back by sea. Unfortunately, they were delayed in transit and did not arrive at Plymouth until the end of July. The samples in glass bottles for analysis of salinity by the Government Chemist and in polythene bottles for silicate analyses by Armstrong's own method (1951) were in good condition. Analyses of the inorganic phosphate samples, preserved though they had been, were not attempted. Since the samples for total phosphorus analysis in baited polythene bottles had evidently stood upside down for some time and the accuracy which may be read into them has proved of much importance, it becomes necessary to quote Mr Armstrong's detailed comments on his analyses:

> The volume of each sample was measured before autoclaving. It should have been 69 ml. (67 ml. of sea water + 2 ml. reagents). In every case it was less. After autoclaving the volume was adjusted to 68 ml. by adding distilled water and the analysis completed.
>
> Fifty of the 59 samples showed deficiencies in volume of 2–8 ml., 8 of 9–14 ml. and one (Station 2655, 10 m.) of 25 ml. Deficient volume was assumed to be the result of evaporation or spillage and it seemed likely that both had occurred. Leakage of salt water from some bottles was evident because incrusted salt was seen around the stoppers and on the underside of the lid of the box. Loss by evaporation alone would not matter since it would be made up after autoclaving, during which evaporation occurs anyway.
>
> If the samples were homogeneous, spillage could be allowed for in calculation. The variable salinity of the samples, which might be expected to introduce small and variable 'salt errors' into the analyses, does not matter since salt errors are compensated by the 'subsequent addition of phosphate' technique of Harvey (1948, p. 351). Loss of sample can be allowed for by multiplying the first result found by the ratio unspilt volume/volume found, where 'unspilt volume' is the original volume of 69 ml. less that volume lost by evaporation. Since it was impracticable to find out what proportion of the losses in each sample was due to evaporation, it was assumed arbitrarily that each sample had lost 2 ml. in this way, and the unspilt volume was taken to be 67 ml.
>
> However, the samples were not homogeneous, since they contained a $Th(CO_3)_2$ suspension likely to occlude or adsorb phosphorus so that another unknown error, difficult to estimate, is involved. The results have therefore been given to the nearest 0·1 μg.-atom/l. The true value of a result reported as, say, 0·7 is believed to lie between 0·65 and 0·75.

FACTORS AFFECTING THE DISTRIBUTION OF SILICATE IN THE NORTH ATLANTIC OCEAN AND THE FORMATION OF NORTH ATLANTIC DEEP WATER

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(Text-figs. 1–2)

In the deep water of the eastern North Atlantic below 2000 m. the variations with depth of salinity, temperature, density, oxygen, phosphorus compounds and nitrate are quite small. By contrast the silicate content is doubled in a descent from 2000 to 4000 m.

The distinctive behaviour of silicate is revealed by diagrams (Fig. 1) relating it to salinity, temperature, density and total phosphorus at station 2659 worked by R.R.S. *Discovery II* on 12 May 1950 (Armstrong, 1951; Cooper 1952, Table IV). The temperature-salinity diagram (Cooper, 1952, fig. 15, to 1500 m. only) suggests that between 1200 and 2000 m. we have to deal with simple mixing of the mean Gulf of Gibraltar and North Atlantic Deep waters. If silicate concentration were subject only to mixing processes the curves in Fig. 1 between these depths would be straight lines. They are not—consequently it would seem that solution of either particulate silica or of aluminosilicates may be occurring. As yet, clear interpretation is not possible. At least five hypotheses may be erected to explain, in whole or in part, the observed distribution: (i) solution of bottom deposits; (ii) solution of 'clay' and of silica in suspension; (iii) concentration by vertical partition; (iv) tundra drainage; (v) sinking of surface water. These are examined in turn.

Solution of Bottom Deposits

Discovery station 2659 was near the continental slope, solution from which could have occurred. The results of Wattenberg (1937) and Koczy (1950), however, suggest that the converse process occurs, adsorption or chemical combination of silicate from the water into the material of the bottom or into hexactinellid sponges.

Solution of 'Clay' and of Silica in Suspension

The distribution may have come about by solution of minerals of terrigeneous origin. If this were so the content of aluminium should increase with depth in much the same way as does silicate, and a diagram relating silica in solution to aluminium in solution should approach a straight line.

The distribution may also have come about by re-solution of the skeletons of diatoms and radiolarians and the faeces of herbivores feeding on these.

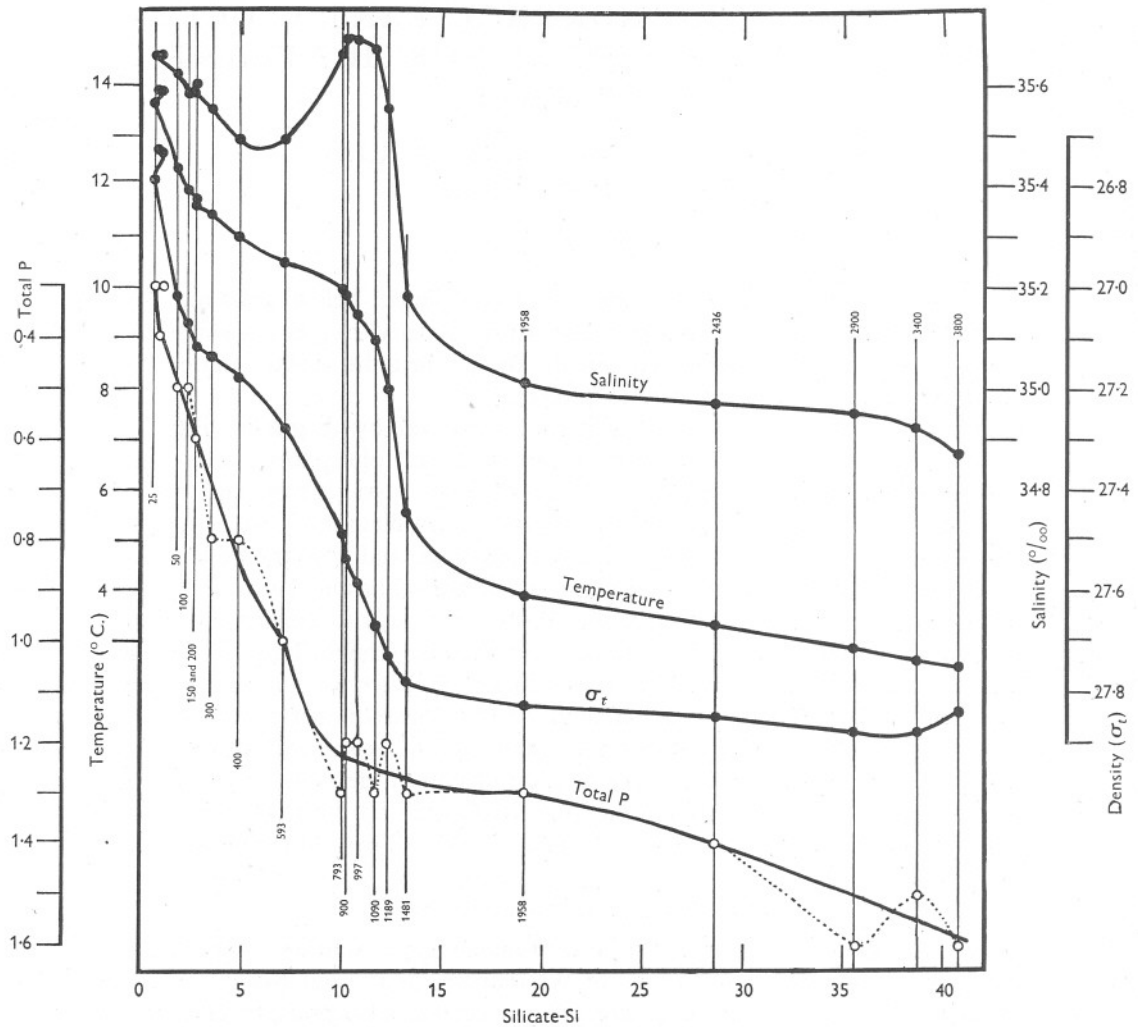

Fig. 1. Diagrams relating the vertical distribution of silicate to salinity, temperature, density, and total phosphorus at *Discovery II* station 2659 on 12 May 1950. Since the results for total phosphorus are less accurate than the rest, its curve has been smoothed. Silicate-silicon (Si) and total phosphorus (P) in μg.-atom/l. The figures against the thin vertical lines represent depths (in metres).

As the particles dissolve, whether they be of mineral or biological origin, they become smaller, sink more slowly, and expose to the action of the water a greater surface area relative to volume, which favours solution. Wattenberg (1937), who found a similar distribution of silicate in the neighbourhood of

the Cape Verde Islands, explained it in this way, whilst Clowes (1938) has produced cogent evidence for the process in the Antarctic. King (1938) stated that most of the reported figures for the solubility of silica in water vary between 700 and 2300 μg.-atom/l. Correns (1940) measured the variation with pH of the solubility of silica in terms of the fraction able to pass a membrane filter (Fig. 2). By interpolation at pH 8·15, the content of silica in solution was about 5 mg.-atom/l. Si. Natural sea water should never be saturated with silica.

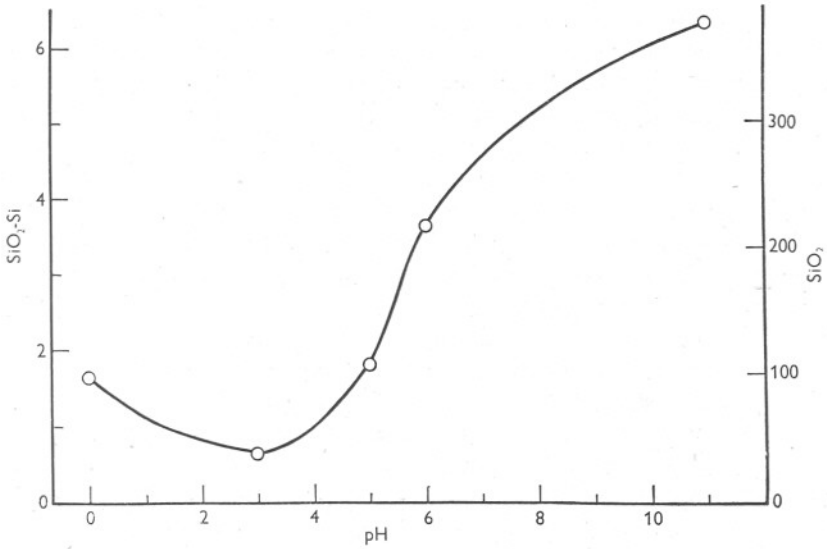

Fig. 2. Dependence of the solubility of silica (SiO_2) in water on pH (after Correns, 1940). Silica expressed as mg.-atom/l. silicon (left) and as mg./l. silica (right).

Hart (1934, pp. 11 and 185–6; 1942, pp. 322–39) has marshalled much evidence, circumstantial but strongly supporting the view that re-solution of diatomaceous silica is a speedy process in the sea. He examined (1942, p. 327 and private communication) the stomach contents of *Euphausia superba* and other planktonic animals, and found that the diatom species identifiable were those most strongly silicified, the same that remain recognizable in bottom deposits and in bird guano, such as *Fragilariopsis*, Discoidea (including *Thalassiosira* and also *Coscinodiscus* and *Actinocyclus* spp.), spines of the most robust of all chaetocerids, *Chaetoceros criophilum*, terminal spines of *Rhizosolenia* spp., etc. The more typically oceanic, exceedingly numerous but less strongly silicified forms, including most *Chaetoceros* species, are probably quite as important as food for the planktonic herbivores but are digested too thoroughly to be identified in the stomach contents. These less strongly silicified forms (p. 338) are also very rarely recognizable in the bottom deposits. It is therefore of interest that Wailes (1929) found that the silica

content of a collection consisting mostly of small species of *Chaetoceros* was only 40 %, whereas a collection mostly composed of large *Coscinodiscus* contained 75 % on the dry weight.

Again Hart (1942, p. 334) has discussed the removal of phosphate and silicate from Antarctic water by phytoplankton, largely diatoms. He considers that the same process of rapid re-solution of silica is going on there as was proposed for the English Channel (Cooper, 1933, p. 744). There the much lower production of phytoplankton computed from fall in silicate was attributed by the writer to the rapid return and immediate re-use of silica from the previous crop. It is suggestive that the shorter the time interval between sampling and re-sampling at the Antarctic stations the more nearly the crop of phytoplankton calculated from decrease in silicate approached that calculated from decrease in phosphate. Hart also pointed out (pp. 324–6) that in the northern zone of the Antarctic (i.e. immediately south of the Antarctic Convergence) as the silicate content of the upper waters decreases with the advance of spring so does the solenoid diatom *Corethron criophilum* change from a large strongly silicified spinose phase to a less strongly silicified, usually spineless, *inerme* phase.

There is evidence for the insolubility of the silica in diatoms, the result of direct experiment. Diatomaceous ooze is found on the floor of the oceans where the skeletons of strongly silicified species retain through geological ages the delicate markings of the living cell. According to Rogall (1939), the skeletons of marine and fresh-water diatoms consist of pure silicic acid (Kieselsaüre) shown by chemical analysis and X-ray crystallography. The preparation of most of the samples would have removed any organic material which would protect silica against solution. None the less, the recent, chemically untreated sample of the marine diatom *Coscinodiscus concinnus* gave X-ray photographs by the technique of Debye and Scherrer which showed no diffraction rings but only some scattering of X-radiation around the point of penetration of the main beam. This suggests that in geologically recent diatoms no 'crystallites' of significant size are present. In geologically older material annular scattering is to be seen, becoming fairly strong in Miocene diatomaceous earth. As diatomaceous earths age part of the 'sub-colloidal' silica becomes transformed by inner metamorphosis to a micro-crystalline crystal lattice which indicates progressive formation of an opal structure. Such a change would affect solubility.

Atkins and Miss F. A. Stanbury (Atkins, 1945) found evidence for the insolubility of diatom skeletons in sea water even at pH 8 and up to 10·6. Miss Stanbury's earlier observations to the contrary (1931) were based on an error of observation due to the difficulty of seeing nearly transparent diatom skeletons in sea water. Addition of safranin to the water allowed the uncoloured skeletons to be seen. Conger (1941) stated that although diatom shells present a great amount of thin surface to possible solution, the purity

of the hydrated silica (also Rogall, 1939) appears to render them resistant to such solution. Diatom shells, once formed, are said to be practically a permanent deposition or fixation of silica. Coupin (1922) studied the fresh-water diatom, *Nitzschia linearis*, cultured in Knop agar medium with various sources of silica. Washed sand, gelatinous silica, and alkaline silicates led to no increased growth, whereas in presence of kaolin, felspar and pure clay the cultures flourished. Atkins (1927) has shown the readiness with which soils and disintegrating rocks part with silicate to water; he concludes that solution of silicate most likely takes place from dispersed clay and that the rate of solution of diatom skeletons is too slow to matter. Consequently, he (1945) interprets Cooper's calculation of an apparently low phytoplankton crop from silicate consumption as due not to re-use of silica but to the production of autotrophic flagellates which require no silica and are more abundant than had been previously realized.

There is thus a direct conflict of much well-attested evidence. Is there an unrecognized factor which would allow this apparent conflict to be resolved? In this paper by 'dissolved silicate' we have meant no more than that form of dissolved hydrated silica sufficiently dispersed in sea water to react quantitatively with the standard reagents to form molybdosilicate. This presumably—but only presumably—is identical with the material which diatoms are able to withdraw from the sea to build their skeletons. Much has been written on the nature of 'dissolved silicate', but few clear unassailable conclusions have been drawn. One of the clearest expositions is that of Carman (1940). The metasilicate ion, SiO_3^{2-}, almost certainly does not exist. The simplest silicate ion is probably orthosilicate, SiO_4^{4-}, or more often $H_nSiO_4^{(4-n)-}$. In all silica compounds the central building bricks are SiO_4 tetrahedra linked through oxygen bonds. In vitreous silica, such as exists in colloidal silicates and in diatom skeletons, the tetrahedra are linked to produce a random three-dimensional network.

When sodium silicate is acidified, monosilicic acid is first formed. Molecular weight determinations by several workers have given values between 60 and 150. The lower figure would require that (mono)orthosilicic acid should be 60 % dissociated. The low-molecular silicic acid is believed to condense to long chains of polysilicic acid. The structure which results is heavily hydrated and holds fluid by capillarity and, no doubt, foreign ions also. Treadwell (1935) found that the molecular weight between 149 and 1015 increased at the rate of 22·2 per hour. Tourky (1939, 1942) found that the rate of increase depended upon pH; at pH 11·7 there is no polymerization, but this occurs at pH 10·85 and the rate of polymerization reaches a maximum between pH 6 and 7. The rate and extent fall to a minimum at pH 2·3 in a region much used for the development of yellow molybdosilicate for analytical purposes. In more strongly acid solutions polymerization again becomes more rapid and extensive. At pH 8·32, near that of sea water, 28 % of newly

formed silicic acid becomes in 1 hr. unable to pass an ultrafine membrane filter having a time constant of 200–300 min. Hurd & Merz (1946) found that the amount of silica capable of diffusing from a hydrosol through a membrane appears to approach a constant value. They explain this unexpected result as follows. The process of setting a silicic acid gel, whatever it may be, does not run entirely to completion but comprises a series of equilibria very much displaced towards the more complex side. Dialysis removes the simpler particles with a shift in the equilibrium towards the simpler materials. If correct this conclusion has great significance in oceanography if, instead of 'dialysis', we read 'removal of silica by diatoms'. A similar displacement of equilibrium would be achieved under the analytical conditions of determination of silicate in sea water (Hurd, 1938; Correns, 1940).

Tourky & Bangham (1936) recorded that nearly all the silica in Nile and Egyptian well waters and in dilute (20 μg.-atom/l. silicate-Si) Graham sols was held back by ultra-filters, but that sea water appears to exert a 'peptizing' action akin to that of alkali. Thus, known volumes of a dilute Graham sol of known silica content were added to silica-poor sea water, the quantities being such as to correspond to a silica-rich sea water. After addition of alkali, colorimetric determination returned the correct silicate content. Without addition of alkali 25–100 % of this was found, depending on the age of the solution when the molybdate reagent was added.

Kargin & Rabinovitch (1935) prepared a very pure SiO_2 sol by oxidizing silane, SiH_4, by ozone in water. This sol was electrochemically neutral, had a pH near to 7, no acidic properties and only a small quantity of compensating ions (*Gegenionen*) in the outer component of the double layer. Thus very pure hydrated silica dispersed in water is not an acid in the sense that hydrochloric acid, boric acid, or even phenol are acids.

Sols prepared by methods employing electrolytes—and these have been the subject of most investigations and correspond better to the process of solution of silica in sea water—seem always to retain ions of strong electrolytes either tightly bound as part of an electrical double layer or as components of interstitial fluids. The dissociation constants of so-called silicic acid derived from such systems are functions rather of these associated ions of strong electrolytes and vary much from experiment to experiment. Indeed it needs to be proved that orthosilicate ions can persist at the pH of natural sea water.

Carman (1940) described a method of hydration of colloidal silica which would set free hydrogen ions giving the surface of the colloid a negative charge, i.e. converting it into a large anion. The anionic character of such a colloid will depend on size, i.e. on the ratio of surface to volume. A solution of hydrated silica may contain aggregates or particles of every size ranging from an odd orthosilicate ion through $Si_3O_8^{4-}$ to a large diatom skeleton. Viewed in this way attempts to classify silicate in sea water, either in terms of ions all alike, or as all crystalloidal or all colloidal, become meaningless.

The practical problems are: (1) to establish what ranges of colloid particle size down to orthosilicate ion allow 'dissolved silicate' to react quickly to form molybdosilicate under analytical conditions; (2) what ranges are suitable for use by diatoms, radiolarians and sponges; and (3) how the solution or dispersion of large particles to smaller takes place.

Observations by Briscoe, Holt, Matthews & Sanderson (1937) and Kitto & Patterson (1942) are relevant. They established that freshly fractured surfaces of quartz and some mineral silicates are in a highly reactive state and readily yield 'soluble silica' on contact with water. In the sea much the commonest way of exposing fresh silica surfaces by fracturing will occur in the guts of herbivores which grind or triturate their food. During grinding the structure of the surface is disturbed and a layer of more irregular structure, possibly a Beilby layer, is formed. Such a Beilby layer, if formed, would increase with the amount of grinding to become many ångströms thick and would be likely to have a higher solubility than the underlying material. One may visualize the process of solution in the herbivore gut not as like the solution of sugar or common salt, but as one of mechanical attrition by which ever more reactive surfaces may become exposed and by which smaller pieces of colloidal silica, necessarily further hydrated by the process, may be torn from larger ones.

Dr T. J. Hart has made the following comment: 'At depths more than a few hundred metres below the photic zone herbivores cannot be feeding as such. Yet the bathypelagic fauna is very considerable. Obviously it cannot consist entirely of carnivores and their parasites. Detritus feeders ultimately dependent on the rain from above must here be the "key industry" forms. Hence my emphasis on the probability that most diatom skeletons pass through several stomachs on their way down.'

To sum up, the following assertions seem valid. (i) The phrase 'sea water saturated with silica or silicate' has little meaning. (ii) More silica or silicate could be 'dissolved' or held in sea water than is ever present in nature. (iii) Aluminium silicates or 'clay' are concerned in the silica system in sea water. (iv) Hydrated silica in equilibrium in sea water consists of particles of very varying size some of which can penetrate membrane filters and some of which cannot. (v) Aggregated hydrated silica is in the main electrochemically neutral and the acidic properties attributed to it are due to anions held in interstitial fluid, or to electrochemical charges on the surface, or to an electrical double layer arising from the distribution in space of SiO_4 tetrahedra and of unsatisfied valencies produced as the result of the process of hydration. Thus the term 'silicate' which suggests the anion of an acid or salt, whilst appropriate at $pH > 12$, is of doubtful validity at the pH of natural sea water: 'dispersed hydrated silica' or 'dispersed silica' may be more fitting terms than 'dissolved silicate'. (vi) If the equilibrium system is disturbed by removal of the simpler particles by dialysis in the laboratory

or by diatoms in the sea, more complex particles will slowly yield simpler ones in order to restore the equilibrium. (vii) Polymerization is least in the range of pH commonly used for the development of the yellow molybdosilicate complex in analytical practice. (viii) The chemical constitution of the silica in diatom skeletons is similar to that of hydrated silica dispersed in water. (ix) In spite of this, the skeletons of many but not all species of diatoms are resistant to solution and for all practical purposes are insoluble whilst intact. (x) This insolubility is difficult to understand unless the surfaces of the skeletons are in some way protected against solution by an organic skin. Such a skin has never been demonstrated by chemical or X-ray analysis. Since it would be sufficient to satisfy the residual valencies of the SiO_4 tetrahedra in the boundary surface more strongly than does water, a protective layer only a few molecules thick and undetectable chemically would suffice. Postulation of a siloxane bond $-\overset{|}{\underset{|}{Si}}-O-\overset{|}{\underset{|}{C}}-$, never yet found in nature,[1] would assist the formulation of such a protective coating. (xi) Freshly fractured surfaces of silica are highly reactive and soluble. (xii) The skeletons of diatoms, particularly thin fragile ones, are likely to be so fractured in the guts of herbivores browsing on them. Herbivores and detritus feeders are likely to be responsible for the greater part of the redispersion of hydrated silica frequently reported in the upper layers of sea. (xiii) In surface waters in which diatoms and radiolarians grow and are eaten a true equilibrium involving dissolved or dispersed hydrated silica may never be reached. (xiv) Sea water containing dispersed silica completely in equilibrium is likely to be found only in the ocean abyss. Only abyssal water may be suitable for a study of silica equilibria.

Confronted with the same body of evidence Atkins and the author have on some issues drawn opposed conclusions. The author's opinion is that the conflict is apparent and not real and arises from some condition of the intact diatom skeleton which is not understood. The conflicting lines of argument are presented to stimulate further study of the process of solution of siliceous matter in deep waters, especially in North Polar waters, the Norwegian Sea and the north-western North Atlantic.

[1] The following information has since been received by the Department of Scientific and Industrial Research in answer to their *Unanswered Question* 67: 'Is there any authentic case of organic silicon compounds having been isolated or detected in living organisms?' (1) T. Takeuchi (*Bull. Coll. Agric., Tokyo*, Vol. 7, pp. 929–31; *Chem. Abs.*, 1907, Vol. 1, p. 2620) reported detecting an organic silicon compound in hay. (2) E. Drechsel (*Chem. Zentrallblatt*, 1897, Vol. 2, p. 666) reported a substance $Si(OC_{34}H_{59}O)_4$ which appears to have been an ester of silicic acid. This compound was, it is understood, isolated from duck feathers and may originate in the oily gland at the base of the tail and be transferred to the feathers during preening. Thus the possible presence of Si—O—C linkages in diatoms may not be without precedent in other living organisms.

It remains for the future to show how great is the effect of solution of silica from siliceous matter compared with the processes to be described.

Concentration by Vertical Partition

The enormous concentration of silicate in Antarctic waters is much assisted by the vertical circulation (Clowes, 1938). The Antarctic surface water flows towards the north. The water goes on to sink at the Antarctic Convergence but much of the silicate remains behind. It has been removed by diatoms which get eaten by herbivores who need no silica. Siliceous faeces and dead broken frustules sink into the Intermediate Water beneath which, enriched in the writer's view by re-solution, returns to the Antarctic. In the North Atlantic there is a similar Intermediate Water (Wüst, 1936, p. 176). Comparatively it is rudimentary and its progress difficult to follow. The Polar front associated with it makes a seasonal migration of 500–1000 km. None the less, this Intermediate Water working against the Irminger Current above would seem capable of some degree of concentration of silicate. It needs to be shown whether this happens on a scale that matters, and whether the enriched water moves into the region where Nansen (1912) believed the North Atlantic bottom water may be formed in winter.

Tundra Drainage

The North Polar Sea receives much drainage from the tundra areas of Siberia, northern Canada and Alaska. Under a tundra climate the subsoil is permanently frozen. In summer this stops the normal downward percolation of subsurface water derived from thawing of the soil above and from precipitation (Flint, 1947, p. 459). As a result the thawed mantle becomes saturated with water and flows bodily downhill, a process known as 'solifluction'. Such a climate with hard freezing, shallow thawing, bad drainage, and much solifluction is likely to lead to rapid weathering and comminution of rock particles. Moreover, poor development of humus will hinder the development of a stable soil. Conditions should be very favourable for solution of silica and its transport by summer drainage into the surface waters of the North Polar Sea from which it may escape in the East Greenland Current. This in turn contributes to the mixing areas south-east and south-west of Greenland in which the North Atlantic deep water may be formed. Although the pure Polar water which escapes as the East Greenland Current is, according to Kiilerich (1945, p. 56), poor in nutrients, no silicate analyses have to the writer's knowledge ever been made on it. There is a strong probability that the silicate content will prove to be very high (at least 50 μg.-atom/l. SiO_2-Si). Thus it would seem that a full knowledge of the distribution of silicate in the North Polar Sea, in the East Greenland Current, the north-western Atlantic generally, and in the deeper water of the Norwegian Sea, will be needed for interpretation of deep-water results elsewhere.

Dr H. U. Sverdrup (private communication) has suggested that Antarctic waters should also receive much dispersed silica formed by comminution of rock beneath the very large glaciers of the Antarctic continent.

Sinking of Surface Water

Though Nansen's view (1912) that much of the bottom water of the North Atlantic is formed in an area south-east of Greenland around 59–62° N., 38–48° W., has gained wide currency, it has never been finally proved. The observations which he used were not his own and some of them may be suspect. In March 1933 and March 1935, the German research ship *Meteor* ran sections across the area (Defant, Böhnecke & Wattenberg, 1936). The densest surface water (temp. 4·07° C.; sal. 34·96‰; σ_t, 27·76) was found at station 79 (59° 38′ N., 4° 42·5′ W.), but water at least 1° colder and 0·10 σ_t-unit heavier was needed to provide satisfactory proof of Nansen's hypothesis. Defant (1936) had stated that a main objective of the *Meteor* cruises was to test Nansen's hypothesis but in the end he has nothing to say on the matter. He would seem to feel that the hypothesis remains unproven. Von Schubert (1935, pp. 35–7) examined the stability at *Meteor* station 76 (29 March 1933; 60° 56′ N., 41° 28′ W.). Down to 800 m. there was no obstacle to vertical mixing, but he also considers that the formation of bottom water there remains an open question.

The extent of formation of bottom water will depend upon the coldness of the winter. Smed (1947, 1948) has recently published monthly anomalies of the surface temperatures in areas of the North Atlantic from 1876 to 1939 (i.e. departures from Ryder's area monthly means for the years 1876–1915). Nansen's postulated region of formation of bottom water lies close to the point of union of Smed's areas B, C and D and mostly within areas B and D. The observations used by Nansen (1912, p. 25) were mostly collected in April 1906, which Smed's tables show to have been very cold (Table I), whereas the *Meteor* worked in years (March 1933 and March 1935) when the water temperatures were 0·5° above the long-term mean. It is therefore probable that temperatures in the late winter and early spring of 1906 were between 1 and 2° lower than in 1933 and 1935. In Table II the densities found by the *Meteor* have been adjusted for conditions 1 and 2° colder than in 1933. Thus, in 1906, the surface water may well have been heavy enough to sink right to the bottom of the Atlantic, and Nansen's conclusion for that year was correct, whereas in 1933 and also 1935 it could not have sunk much below 800 m. Only in 1907, 1918 and 1921 have comparable cold conditions recurred so that formation of North Atlantic bottom water south-east of Greenland may now have become a rare event.

Nansen (1912) showed quite clearly that in the years 1903 and 1910 cold heavy water from the Norwegian Sea flowed into the Eastern Basin of the North Atlantic over the sill of the Faeroe-Iceland ridge at about 64° N.,

13° W., a result substantiated in 1938 by the *Dana* (Cons. Perm. Int. Explor. Mer, 1944, p. 119, stations 5954–5957). He also definitely established a similar outflow over the Iceland-Greenland ridge into the Western Basin. Although he considered neither of these outflows adequate to account for the great volume of the cold bottom water of the Atlantic, that over the Faeroe-Iceland Ridge may be locally important for the hydrography of the waters bathing western Europe. The *Meteor*, on 21 March 1933, also found a small area of heavy water (temp. 3·66° C.; sal. 34·99‰; σ_t, 27·82) on the

TABLE I. MONTHLY ANOMALIES OF TEMPERATURE OF PART OF NORTH ATLANTIC

Departures from Ryder's 'area monthly means' for the years 1876–1915 of the sea surface temperature (° C.) in three areas south-east of Greenland in March and April in years studied by Nansen and by the *Meteor* expeditions; *n* is the number of observations averaged; from Smed (1947, 1948).

	Area B		Area C		Area D				
Latitude range...	55° N. to coast of Greenland		60–66° N.		55–60° N.			Arithmetic mean of all observations	
Longitude range...	40–50° W.		30–40° W.		30–40° W.		Mean of area means		
Mean anomalies	*n*	° C.	*n*	° C.	*n*	° C.	° C.	Σ*n*	° C.
March 1906	4	−0·7	6	+0·5	13	0·0	−0·1	23	0·0
April 1906	64	−1·1	2	−2·2	34	−1·3	−1·5	100	−1·2
March 1933	13	−0·1	5	+1·4	25	+0·7	+0·7	43	+0·5
April 1933	82	0·0	22	+1·0	53	+0·7	+0·6	157	+0·4
March 1935	19	+0·3	3	+0·9	15	+0·2	+0·5	37	+0·3
April 1935	76	+1·0	21	+0·1	29	+0·5	+0·5	126	+0·5

TABLE II. COMPUTED DENSITIES FOR APRIL 1906

Probable densities of the waters south-east of Greenland in April 1906 computed from *Meteor* observations in March 1933 and assuming that surface water temperatures were 1 or 2° C. colder.

Station no.	Latitude N.	Longitude W.	Observed temperature	Observed salinity	Actual σ_t	σ_t if temperature lowered by 1°	σ_t if temperature lowered by 2°
76	60° 56′	41° 28′	4·67	35·00	27·72	27·85	27·94
78	60° 12·5′	41° 52·5′	4·21	34·91	27·69	27·82	27·91
79	59° 38′	40° 42·5′	4·07	34·96	27·77	27·86	27·95

West Icelandic island shelf at 65° 17′ N., 25° 30′ W. heavy enough to cascade to a great depth. Jacobsen (1943), in his account of the water movements through the Faeroe-Shetland Channel, makes no mention of any outflow over that sill into the Atlantic, and no evidence for it was found by the *Explorer* in 1933 and 1935 (Cons. Perm. Int. Explor. Mer, 1934, p. 67; 1935, p. 69).

Smith, Soule & Olav Mosby (1937; see also Dunbar, 1951) suspect that the bottom water of the Labrador Sea is formed in winter in a restricted area of that sea centred on 60° N., 55° W., and discuss its rather complex

origin in so far as this can be surmised from summer observations. They point out that 'our deep water which evidently drains out of the Labrador Basin into the North Atlantic embraces what Wüst (1936) has designated as North Atlantic deep water'. Wüst himself (1936) also leaves the origin of the North Atlantic bottom water as unsolved. It would seem that only in one year in ten are temperatures low enough to produce water heavy enough to sink to the bottom of the Atlantic, and that attention would be better focused on the Labrador Sea rather than on the waters south-east of Greenland.

Since direct winter observations in these uncharitable waters are hard to come by, an alternative means of search for the origin of the North Atlantic bottom water should be welcome. This may well be provided by determinations of silicate by the quick and accurate method now available (Armstrong, 1951). For reasons already given, the postulated high silicate content of the fresh waters draining from the tundras should mark in turn the East Greenland Current, the Labrador Current and the waters of the Labrador Sea with distinctive contents of silicate. The deeper water of the Norwegian Sea may also acquire a high and characteristic content of silicate. In all these, except in surface water above the thermocline, content of silicate may be reasonably assessed in summer.

To enter the basin of the Eastern North Atlantic directly, heavy water from either south-east of Greenland or from the Labrador Sea would need to cross the mid-Atlantic Ridge in a region where its depth is about 3000 m. According to Wüst's charts (1936, Beilage LVI, LVII, LXXI and LXXII) the temperature there exceeds 2·9° (potential temperature 2·64°) and the salinity exceeds 34·96‰, whereas the water abreast of the English Channel between 3000 and 4000 m. has a lower temperature, 2·5–2·7° (potential temperature 2·15–2·45°) and a lower salinity of 34·90–34·92‰. There is no obvious passage north of 24° N. for bottom water from the north-western Atlantic to cross the Ridge into the Eastern Basin so that such water must needs approach Europe from the south. The water which the *Dana* observed entering the Atlantic from the Norwegian Sea across the Faeroe-Iceland Ridge in 1938 was cold enough but was 0·08‰ too saline. Consequently, the origin of the bottom water west of Europe is still uncertain.

The Antarctic bottom water extends well north of the Equator. Wüst (1936, Abl. 16) pictures it as extending to 40° N. in the Western Basin and to 25° N. in the Eastern. His conclusion is based largely on an apparent density inversion widely recorded below 4500 m. Since a true inversion is very unlikely, he attributes the phenomenon to a breakdown in Knudsen's equation, $S = 0{\cdot}030 \times 1{\cdot}8050\ Cl$, when applied to the bottom water of the Atlantic.

Sverdrup (1929, p. 129) had shown that the brine which becomes enclosed in sea-ice when it freezes retains relatively more chloride than other salts leaving the unfrozen water relatively deficient by about 0·02‰ Cl. The true

density of this water measured directly is about 0·03 σ-unit heavier than that computed from salinity and temperature by Knudsen's tables. When such water becomes admixed with Atlantic water to form North Atlantic deep water this anomalous property will become incorporated. The Antarctic bottom water arising more directly by a similar freezing-out process in the Weddell Sea (Deacon, 1937) would seem, according to Wüst, to have acquired an even greater chlorinity-density anomaly. The result is that in the deep water of large areas of the Atlantic, water of slightly greater computed density overlies lighter. When this occurs Wüst suggests that North Atlantic deep water overlies Antarctic bottom water.

There is abundant evidence that the Northern Hemisphere is warming up (*inter alia*, Helland-Hansen, 1949; Defant & Helland-Hansen, 1939; Cooper, 1952, p. 501), a state of affairs which in the area south-east and south-west of Greenland in winter should slow down the rate of formation of the North Atlantic deep water. Less should be sinking to the ocean abyss than in years past. Much less is known about any similar warming up in the Antarctic and Southern Oceans, but the huge reserves of ice there should slow down the process. Consequently, in a struggle between North Atlantic and Antarctic bottom waters, victory would be expected to go to the Antarctic water. There should to-day be a marked tendency for Antarctic bottom water to spread northwards in the Atlantic and to fill the Eastern basin to a greater depth. At *Discovery II* station 2659 the water at 3800 m. (salinity 35·87 ‰, computed density σ_t 27·84, computed potential density σ 27·87) is apparently lighter than the water at 3400 m. by 0·03 σ_t -unit. Error in any single result is always likely but, at least, the need is indicated for fresh deep observations in the Eastern North Atlantic. Since the presence of Antarctic water is in question, determinations of silicate may be of much value.

Locally down to 1200 m. near the continental slope of the eastern North Atlantic the distribution of silicate will be affected by cascading in winter and by capsizing of water masses, processes which are under investigation.

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Summary

The distribution of silicate at the deep *Discovery II* station No. 2659 west of Ushant between 1200 and 2000 m. cannot be attributed to simple mixing of 'Gulf of Gibraltar' water and North Atlantic Deep water as can the distribution of some other constituents. Moreover, between 2000 and 4000 m. the concentration of silicate is doubled. Five hypotheses have been examined which may bear on the distribution of silicate.

The chemistry of silicate dispersed in water has been examined with respect to the possible solution of aluminosilicates and of intact and fractured diatom skeletons in sea water. Conclusions have been summarized.

Solution of silicate from, and removal by, the sea bottom and concentration within the sea by vertical partition are severally discussed.

Reasons are presented for believing that drainage from the tundras of the Northern Hemisphere should yield very large amounts of silicate to the North Polar Sea. From this initial hypothesis further oceanographical deductions have been drawn.

The evidence for the formation of North Atlantic Bottom Water at the sea surface south-east of Greenland, first proposed by Nansen, has been re-examined in relation to the movement of dissolved silicate. It is suggested that in the cold spring of 1906, from which year Nansen drew most of his data, his conclusion was probably sound, but that in most years sufficiently cold surface conditions are not attained.

The probable effect of the warming up of the Northern Hemisphere in recent years on the deep circulation of the Atlantic is reviewed.

It is suggested that the great variations which occur in the concentration of silicate in the sea should be of use in interpreting the nature and movements of the major ocean water masses.

REFERENCES

ARMSTRONG, F. A. J., 1951. The determination of silicate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 149–60.

ATKINS, W. R. G., 1927. The soluble silicate content of soils. *Sci. Proc. Roy. Dublin Soc.*, Vol. 18, pp. 433–6.

——1945. Autotrophic flagellates as the major constituent of the oceanic phytoplankton. *Nature*, Vol. 156, pp. 446–7.

BRISCOE, H. V. A., HOLT, P. F., MATTHEWS, J. W. & SANDERSON, P. M., 1937. Some new characteristic properties of certain industrial dusts. *Nature*, Vol. 139, pp. 753–4.

CARMAN, P. C., 1940. Constitution of colloidal silica. *Trans. Faraday Soc.*, Vol. 36, pp. 964–73.

CLOWES, A. J., 1938. Phosphate and silicate in the Southern Ocean. *Discovery Reports*, Vol. 19, pp. 1–120.

CONGER, P. S., 1941. Fixation of silica by diatoms. *A Symposium on Hydrobiology*, pp. 395–6. University of Wisconsin.

CONS. PERM. INT. EXPLOR. MER, 1934, 1935. Température et salinité de l'Atlantique. *Bull. Hydrogr.*, Ann. 1933, pp. 39–85; Ann. 1934, pp. 39–90.

—— 1944. Observations hydrographiques de l'Expedition Internationale du 'Gulfstream' 1938. *Bull. Hydrogr.*, Ann. 1938 et 1939, pp. 113–37.

COOPER, L. H. N., 1933. Chemical constituents of biological importance in the English Channel, November 1930 to January 1932. Parts I and II. *Journ. Mar. Biol. Assoc.*, Vol. 18, pp. 677–728, 729–53.

—— 1952. The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 465–510.

CORRENS, C. W., 1940. Über die Löslichkeit von Kieselsäure in schwach sauren und alkalischen Lösungen. *Chemie der Erde*, Bd. 13, pp. 92–6.

COUPIN, H., 1922. Sur l'origine de la carapace silicieuse des Diatomées. *C.R. Acad. Sci., Paris*, T. 175, pp. 1226–9.

DEACON, G. E. R., 1937. The hydrology of the Southern Ocean. *Discovery Reports*, Vol. 15, pp. 1–124.

DEFANT, A., 1936. Bericht über die ozeanographischen Untersuchungen des Vermessungsschiffes 'Meteor' in der Dänemarkstrasse und in der Irmingersee. III. *Sitzb. Preuss. Akad. Wiss., Phys.-Math. Kl.*, Bd. 19, pp. 1–13.

DEFANT, A., BÖHNECKE, G. & WATTENBERG, H., 1936. Die ozeanographischen Arbeiten des Vermessungsschiffes 'Meteor' in der Dänemarkstrasse und Irmingersee während der Fischereischutzfahrten 1929, 1930, 1933, und 1935. I. Teil. Plan und Reiseberichte, Die Tiefenkarte, Das Beobachtungs-material. *Veröff. Inst. Meereskunde, A. Geogr.-naturwiss. Reihe*, Heft 32.

DEFANT, A. & HELLAND-HANSEN, B., 1939. Bericht über die ozeanographischen Untersuchungen im zentralen und östlichen Teil des nordatlantischen Ozeans im Frühsommer 1938. *Abh. Preuss. Akad. Wiss., Phys-math. Kl.*, Jahrg. 1939, Nr. 5.

DUNBAR, M. J., 1951. Eastern Arctic waters. *Fish. Res. Board, Canada*, Bull. No. 88, pp. 1–131.

FLINT, R. F., 1947. *Glacial Geology and the Pleistocene Epoch*. 589 pp. New York.

HART, T. J., 1934. On the phytoplankton of the south-west Atlantic and the Bellingshausen Sea, 1929–31. *Discovery Reports*, Vol. 8, pp. 1–268.

—— 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports*, Vol. 21, pp. 261–356.

HELLAND-HANSEN, B., 1949. Remarks on some variations in atmosphere and sea. Glaciers and Climate, geophysical and geomorphological essays dedicated to Hans W:son Ahlmann. *Geografiska Annaler*, Häfte 1–2, pp. 75–82.

HURD, C. B., 1938. Theories of the mechanism of setting of silicic acid gels. *Chem. Rev.*, Vol. 22, pp. 403–22.

HURD, C. B. & MERZ, P. L., 1946. Studies on silicic acid gels. XIV. Dialysis of silica hydrosol and hydrogel. *Journ. Amer. Chem. Soc.*, Vol. 68, pp. 61–4.

JACOBSEN, J. P., 1943. The Atlantic Current through the Faeroe-Shetland Channel. *Cons. Int. Explor. Mer, Rapp. Proc.-Verb.*, Vol. 112, pp. 1–47.

KARGIN, V. A. & RABINOVITCH, A. J., 1935. Some electrochemical properties of colloidal silica. *Trans. Faraday Soc.*, Vol. 31, pp. 284–97.

KIILERICH, A., 1945. On the hydrography of the Greenland Sea. *Medd. om Grønland*, Bd. 144, Nr. 2, Appendix No. 2, pp. 1–63.

KING, E. J., 1938. The solubility of silica. *Lancet*, 28 May, p. 1236.

KITTO, P. H. & PATTERSON, H. S., 1942. The rate of solution of particles of quartz and certain silicates. *Journ. Industr. Hyg.*, Vol. 24, pp. 59–74.

KOCZY, F. F., 1950. Die bodennahen Wasserschichten der Tiefsee. *Naturwissenschaften*, Jahrg. 37, Heft 15, p. 360.

NANSEN, F., 1912. Das Bodenwasser und die Abkühlung des Meeres. *Int. Rev. ges. Hydrobiol. Hydrogr.*, Bd. 5, pp. 1–42.

ROGALL, E., 1939. Über den Feinbau der Kieselmembran der Diatomeen. *Planta*, Bd. 29, pp. 279–91.

SCHUBERT, O. VON, 1935. Quantitative Untersuchungen zur Statik und Dynamik des Atlantischen Ozeans. I. Die Stabilitätverhältnisse. *Wiss. Ergebn. deutsch. atlant. Exped. 'Meteor' 1925–1927*, Bd. 6, Teil 2, pp. 1–54.

SMED, J., 1947. Monthly anomalies of the surface temperature in the sea round South Greenland during the years 1876–1939. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 2, pp. 17–22.

—— 1948. Monthly anomalies of the surface temperature in some areas of the north-western North Atlantic in 1876–1939 and 1945–1946. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 3, pp. 12–24.

SMITH, E. H., SOULE, F. M. & MOSBY, OLAV, 1937. The *Marion* and *General Greene* Expeditions to Davis Strait and Labrador Sea under direction of the United States Coast Guard 1928–1931–1933–1934–1935. Scientific Results. Part 2. Physical Oceanography. *U.S. Treasury Dept., Coast Guard, Bull.*, No. 19, 259 pp, also as *Woods Hole Coll. Reprint*, 1937, Part II.

STANBURY, F. A., 1931. The effect of light of different intensities, reduced selectively and non-selectively, upon the rate of growth of *Nitzschia closterium*. *Journ. Mar. Biol. Assoc.*, Vol. 17, pp. 633–53.

SVERDRUP, H. U., 1929. The waters on the North Siberian Shelf. *Norwegian North Polar Exped. with the 'Maud' 1918–1925, Sci. Res.*, Vol. 4.

TOURKY, A. R., 1939. Zum Mechanismus der Aggregation der Kieselsäure aus Natriumsilikatlösungen. *Zeits. anorg. allgem. Chem.*, Bd. 240, pp. 198–216.

—— 1942. The heat of coagulation of silica and its bearing on the structure of silica gels. *Chem. & Ind.*, 1942, p. 254.

TOURKY, A. R. & BANGHAM, D. H., 1936. Colloidal silica in natural waters and the 'silicomolybdate' colour test. *Nature*, Vol. 138, pp. 587–8.

TREADWELL, W. D., 1935. Polymerisation phenomena of silicic acid. *Trans. Faraday Soc.*, Vol. 31, pp. 297–304.

WAILES, G. H., 1929. Plant life in the open sea. *Museum and Art Notes, Vancouver*, Vol. 4, pp. 20–8.

WATTENBERG, H., 1937. Die chemischen Arbeiten auf der '*Meteor*'-Fahrt Februar-Mai 1937. Beiheft zum September Heft der *Ann. Hydr. Marit. Meteorol.*, pp. 17–22.

WÜST, G., 1936. Schichtung und Zirkulation des atlantischen Ozeans, das Bodenwasser und die Stratosphäre. *Wiss. Ergebn. deutsch. atlantisch. Exped. 'Meteor' 1925–1927*, Bd. 6, Teil 1, 288 pp. and Atlas.

ON THE BIOLOGY OF *CALANUS FINMARCHICUS*. VII. FACTORS AFFECTING EGG PRODUCTION

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(Plate I and Text-figs. 1–5)

Comparatively little is known about the factors affecting egg-laying in *Calanus*. Deductions from work in the field have been made by Nicholls (1933*a*, *b*) and Marshall, Nicholls & Orr (1934), and experimental work in the laboratory has been done by Raymont & Gross (1942).

Egg-laying in *Calanus*

The anatomy of the reproductive system has been described in detail by Lowe (1935). In the female there is a pair of diverticula extending from the proximal end of the oviduct into the head region, and into this the developing eggs pass. Each diverticulum has a dorsal and a ventral channel, and the eggs pass from the dorsal into the ventral channel and then into the oviduct proper. The oviduct rises from the forward end of the ovary and crosses the body laterally and ventrally so that a short part of it can be clearly seen.

The state of development of the eggs can be seen in the living *Calanus*, and four stages have been described by Marshall *et al.* (1934); these are, early, medium (Pl. I A), mature and spent. It has been found convenient to make a further division between the medium and the mature, namely the semi-ripe. In the immature female the ovary is small and in the oviduct there is only one row of small eggs. As the ovary enlarges the two diverticula also enlarge and become filled with eggs. In the medium state the dorsal channels of the diverticula are filled with enlarging eggs, and the eggs in the oviducts also increase in size and number. The diverticula gradually fill up until the whole of the space in the head is full of enlarging eggs; this may be called the semi-ripe stage. In the mature female (Pl. I B) the most ventral rows of eggs are larger than those in the rest of the diverticula, and similar large eggs are also seen in the oviducts which have now developed secondary pockets projecting towards the body wall (Lowe, 1935). Before laying (sometimes as much as 48 hr. before) these large eggs swell still further, become granular in appearance and turn slightly orange-pink in colour. Just before laying the pink colour usually deepens, the nucleus disappears and the eggs are then squeezed out through the genital aperture as a string of roughly pear-shaped masses which separate and round off within a minute or two (Pl. I D–F).

Raymont & Gross (1942) state that 'the ova which were extremely small in the narrow oviduct were seen to swell almost instantaneously after extrusion to form oval or slightly irregular shaped eggs of very much greater volume; in fact each egg attained a volume greater than that of all the 30–40 eggs inside the oviduct, obviously by a rapid imbibition of water'. Lowndes (1943) also states that whereas the diameter of the largest eggs in the oviducts is 61·5 μ, the diameter of eggs 18 hr. after extrusion is 171 μ. Pl. I C, however, shows the oviduct in a ripe *Calanus* with large eggs almost ready for spawning, and it will be seen that they are much the same size as those being laid (Pl. I D). Several other stages in egg-laying are also shown. In a ripe female the pressure in the diverticula and oviducts causes the eggs to assume an irregular shape, often almost square in side view, and it is impossible to measure the volume accurately. Approximate measurements made on about a dozen eggs from several ripe females gave a volume very much the same as the shed eggs. Thus 5 eggs from a single ripe female had volumes ranging from $1{\cdot}12 \times 10^6$ to $1{\cdot}45 \times 10^6 \mu^3$, whereas the same batch of eggs, when measured after they had been laid about half an hour later, had an average volume of $1{\cdot}59 \times 10^6 \mu^3$ (diameter 145 μ). It is probable that Lowndes was measuring unripe eggs. The size he gives (171 μ diameter) is that of *C. helgolandicus*, which is the predominant form at Plymouth (Russell, 1951). The process of laying a batch of eggs which may consist of anything up to 150 (though usually 20–60) occupies quite a short time—usually under a quarter of an hour and sometimes only a few minutes. In the laboratory a batch of eggs was usually found in one clump which indicates that the *Calanus* remains passive during the process. After laying, the appearance of the *Calanus* may go back to the semi-ripe state again if all the large eggs have been extruded.

Occasionally eggs were laid which were abnormal. Sometimes they went opaque at once, sometimes they appeared to have no membrane and at a touch collapsed into a viscous drop of protoplasm; sometimes they extruded part of their substance as a very small droplet. These small spheres were observed by Raymont & Gross (1942), who took them for newly laid eggs. Occasionally, also, in a batch of eggs one will be twice or three times as large as the rest. These large eggs may begin to develop but never hatch. J. P. Harding's observations (personal communication) suggest that they are diploid or polyploid eggs. After *Calanus* has been kept in the laboratory for some time the laying of abnormal eggs becomes more frequent.

A number of females were found in which the reproductive organs were in the same state as in the ordinary Stage V. Occasionally a Stage V is seen with a large ovary and well-developed eggs in the diverticula, but as a rule the gonad is very small, no diverticula are visible and the genital ducts are thin cords with no eggs in them. Some of these very immature females may have been newly moulted, but this category also contains the infertile, the

parasitized and the abnormal. They are often characterized by an unusually marked development of red pigment at the posterior end of the cephalothorax. Thirty-eight of them were kept and fed to see if they would eventually produce eggs, but most of them died without doing so. In some the ovaries became obviously abnormal and in several a nematode became visible in the body cavity after a few days. Twelve reached maturity and laid eggs, one in 7 days, two in 9, one each in 15 and 16, two in 17, one each in 18 and 19 and three in 20 days.

In view of Rees's (1949) discovery that two forms of *Calanus* were present in the North Sea, those in our hauls in the Clyde sea area were examined. It was found that there were usually a few *helgolandicus*, but the proportion was never more than 5–10 %. In the course of egg-laying experiments it was observed that some females were laying eggs decidedly larger than the

TABLE I. SIZE OF EGGS IN *CALANUS FINMARCHICUS* AND *C. HELGOLANDICUS*

finmarchicus		*helgolandicus*	
Size (μ)	No. of eggs	Size (μ)	No. of eggs
138–142	2	159–163	0
142–146	13	163–168	1
146–151	8	168–172	10
151–155	2	172–176	10
155–159	0	176–181	3
		181–185	1

majority, and on examination these females were found to be *helgolandicus*. The difference in size extends also to the nauplius. The result of a measurement of 25 of each type of egg laid on 14 March 1950 is shown in Table I. There is a certain variation in size even in the eggs laid by *finmarchicus*, but there is usually a clear difference between the two types. Occasionally, however, eggs of intermediate size were seen and these were laid by *finmarchicus*. No experiments on interbreeding were made, but Rees has suggested that it may take place and if so an intermediate size of egg might be one result. Of 683 females of the over-wintering stock laying eggs in our experiments 4·1 % were *helgolandicus*. No *helgolandicus* were seen among the first generation females.

The *Calanus* for experiment were usually obtained in the afternoon off Garroch Head at a depth of 50–100 m. in a coarse silk tow-net. They were sorted shortly after capture and the selected females kept singly in small crystallizing dishes of 25 ml. capacity. The volume of water used was about 20 ml. They were usually kept in ultra-filtered water or ultra-filtered water with culture added. The sea water was collected off Keppel Pier and filtered through a 'Gradocol' membrane of average pore diameter 0·9 μ. *Calanus* kept in this without addition were considered to be starved. The medium was changed every second day and in these conditions the *Calanus* lived well

and if suitably fed, sometimes for months. After a long time, those kept in culture tended to develop surface growths in the form of a dense mat of minute unidentified organisms, probably largely bacterial. Sometimes the growth would envelop the whole of the cephalothorax and the *Calanus* might live like this for some weeks, although it would become very sluggish. Only healthy specimens were used but, when the required type was rare, rigorous selection was not possible and specimens therefore often lacked caudal furcae, or the tips of their antennae, and sometimes lacked spines or even joints on some of the pleopods. They lived well in spite of these injuries and, indeed, it is surprising how much a *Calanus* will endure.

When set up in small dishes in the evening practically all the 'mature' *Calanus* had laid by the next morning (see p. 536), although Harding (Harding, Marshall & Orr, 1951) observed that few mature females fixed during the day contained completely ripe eggs. His criterion of ripeness was the reaching of the full metaphase of the first reduction division, which is the stage reached

TABLE II. DIURNAL EGG PRODUCTION 19–20 MARCH 1951. TOW-NETTING TAKEN 4 P.M., 19 MARCH. 104 *CALANUS*

Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch	Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch
19	0	0	—	4	14	583	41·6
20	0	0	—	5	4*	120	40·0
21	0	0	—	6	2	33	16·5
22	0	0	—	7	1	28	28·0
23	1	36	36·0	9	2	70	35·0
24	2	79	40·0	12	0	0	—
1	24*	817	37·1	15	0	0	—
2	27*	1165	44·8	18	0	0	—
3	20	911	43·4	21	1	15	15·0

* One laid whose eggs were not counted.
Numbers below 5 not included in average.

when the eggs are laid. It was therefore decided to examine *Calanus* hourly to see if there was a restricted time for egg-laying. One hundred and four ripe female *Calanus* picked out from a tow-netting taken at 4 p.m. off Garroch Head between 50 and 100 m. (with 75 fathoms of warp out) were set up about 6 p.m. each in a separate dish of ultra-filtered sea water. They were kept in a cool aquarium and examined at hourly intervals throughout the night. No attempt was made to keep them entirely in the dark. The production of eggs is shown in Table II. Only three had spawned by midnight, 68% spawned between 12 midnight and 3 a.m. and most of the remainder before 4 o'clock. Of the total only five did not lay. The number of eggs laid per *Calanus* was remarkably constant, the average being about 40.

These rather surprising results might have been caused by the disturbance of capture and examination or else, since they were caught at a considerable depth, by the sudden decrease in pressure. Another tow-netting was there-

fore taken at the same place but slightly nearer the surface (with only 50 fathoms of warp out) at 4 a.m., fifty ripe females were picked out into separate dishes and these were examined every 3 hr. Although a smaller total number of eggs was laid and the peak of production was not so marked, spawning again took place mainly during the early morning (Table III). Thirteen of the fifty did not lay. The smaller number of eggs laid may be caused by the longer period of starvation in ultra-filtered water. It will be shown later (see Table VI) that starvation may have a marked effect on egg production even as early as the second day.

Each *Calanus* was discarded after it had laid unless the number of eggs was very small. Several laid small numbers in consecutive hours (e.g. 6+8+10 and 5+18), but one laid 28 and 34 with an interval of 18 hr. between. The great majority, however, are unlikely to have laid again before the following night.

TABLE III. DIURNAL EGG PRODUCTION 20–21 MARCH 1951. TOW-NETTING TAKEN 4 A.M., 20 MARCH. FIFTY *CALANUS*

Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch	Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch
9	2	103	51·5	3	9	275	30·0
12	2	49	24·5	6	12	304	30·7
15	2	33	16·5	9	3	143	35·8
18	0	0	—	12	1	58	58·0
21	2	94	47·0	15	0	0	—
24	4	137	39·3				

Numbers below 5 not included in the average.

In an experiment in February 1950 on the feeding of *Calanus* throughout 24 hr., six out of ten unselected females laid as follows: one between midnight and 2 a.m., four between 2 and 4 a.m. and one between 4 and 6 a.m., thus confirming the more detailed experiments of 1951. *Mesopodopsis* and *Squilla* have also been found to lay only during the night (Nair, 1939, 1941).

In the Clyde sea area *Calanus* of the first generation are found close to the surface in May (Marshall *et al.*, 1934), and since this change of habit may make a difference in their egg-laying behaviour a similar experiment was done on 30 April to 1 May 1951 when the first generation had reached maturity. The results are shown in Table IV, and it will be seen that in contrast to the over-wintering stock this generation laid throughout the 24 hr. Some *Calanus* are found also in deep water at this time, and the experiment was repeated using fifty ripe females from deep water (below 50 m.) and fifty from the top 2 m. Both lots behaved in the same way, laying throughout the 24 hr.

Another difference between the winter and the first-generation females is that far more (29%) of the May females laid second batches of eggs within 24 hr. and five even laid a third batch. The average number of eggs laid in the first batch was 61·3, in the second 41·7, and in the third 28·0. In the majority

the second batch was laid within 10–15 hr. after the first. This difference may have been caused by the fact that during May the sea was very rich in diatoms.

In 1950, to find the total number of eggs which can be produced by a female, those carrying spermatophores (which, since fertilization takes place soon after moulting, may be assumed not to have laid any eggs) were kept in separate dishes in a refrigerator at about 5° C., fed regularly and examined daily. In all of them the spermatophore was lost after the first day or two. One or two laid also within the first day or two, and, since females normally take a week or two to mature the eggs, these must have been fertilized late when the eggs were almost mature. Most remained for 1 or 2 weeks without laying. This in itself

TABLE IV. DIURNAL EGG PRODUCTION 30 APRIL–1 MAY 1951. TOW-NETTING TAKEN 11 A.M. NINETY-NINE *CALANUS*

Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch	Time (hr. G.M.T.)	No. of *Calanus* laying	Total egg production	Av. no. eggs/batch
15	15	916	61·1	3	0	0	—
16	6	387	64·5	4	0	0	—
17	1	78	78·0	5	4	307	76·8
18	14	881	62·9	6	2	93	46·5
19	6	373	62·2	7	0	0	—
20	6	430	71·7	9	4	240	60·0
21	8	512	64·0	10	3	144	63·0
22	6	406	67·7	11	3	211	70·3
23	5	340	68·0	13	2	129	62·5
24	2	69	34·5	14	2	118	59·0
1	3	162	54·0	15	0	0	—
2	2	109	54·5	16	0	0	—

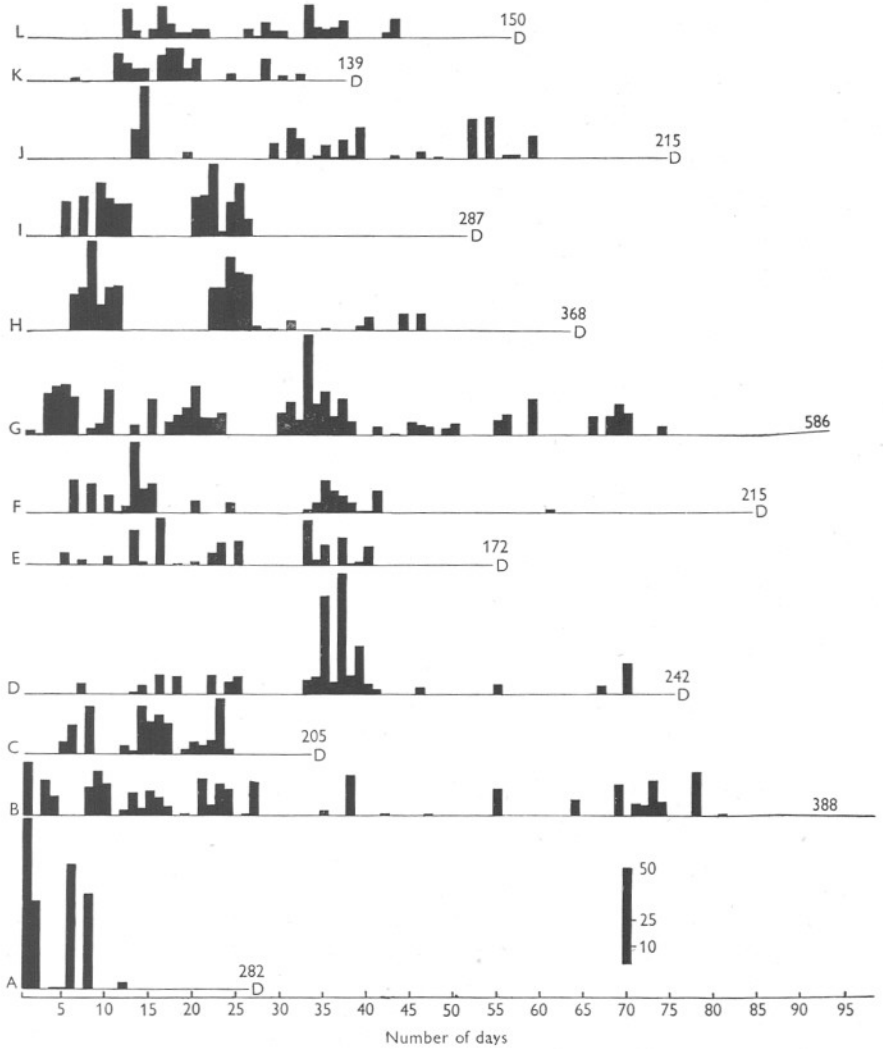
Numbers under 5 not included in the average.

was a disadvantage, for conditions in the laboratory were presumably not so healthy as in the sea. From June onwards, therefore, to avoid delay in egg production, they were kept in an aquarium room at a temperature of about 16° C.

The results given by those which laid most are shown in Text-fig. 1. The majority laid several hundred eggs over periods up to 80 days. The most prolific was brought in on 16 June, laid 586 eggs over a period of 74 days and was still alive on the 93rd day. From the diagram it is readily seen that egg production often takes place in a series of bursts lasting about a week. These bursts tend to occur at intervals of about 2 weeks and it seemed possible that they might be related to the phases of the moon. In some of the *Calanus* the egg-laying periods do seem to begin 2 or 3 days after new and full moon, but in others no relation can be made out. The number laid each day varies from 1 up to about 70, but after about the 40th day the numbers both of eggs and of days on which laying occurs decrease. The eggs were usually kept for a day or two and, although at the beginning they were all normal and produced healthy nauplii, as the experiment went on the number of abnormal or unhealthy eggs increased. However, eggs produced after as much as 68 days

in the laboratory did hatch, showing that one fertilization is enough for the whole period of egg production by a female.

It is of course impossible to say how far this pattern is natural for the sea. In the laboratory they had a continuous ample supply of food, whereas in the

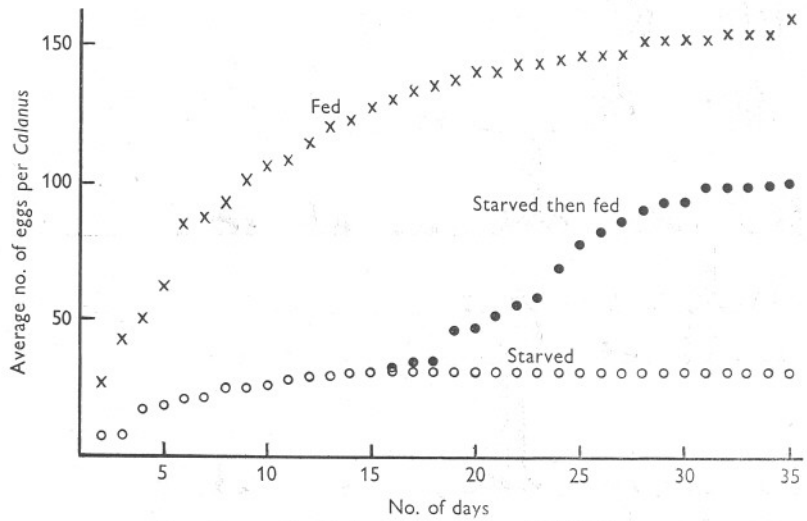


Text-fig. 1. Total number of eggs laid by individual *Calanus*. A: 5. v. 50; B: 13. vi. 50; C–F: 15. vi. 50; G: 16. vi. 50; H, I: 27. vi. 50; J: 7. vii. 50; K, L: 26. vii. 50.

sea the amount would be much less and probably sporadic (see, however, p. 543). In the sea, on the other hand, *Calanus* has many enemies at each stage, and few females will survive to lay all their eggs.

The Effect of Food on Egg-laying

Many workers have discussed the connexion between maxima of phytoplankton and zooplankton. Marshall *et al.* (1934) suggested that broods of *C. finmarchicus* depended for their survival on the presence of diatoms at the time the young brood was growing up. Wimpenny (1937) concluded that phytoplankton-rich water served as a breeding and nursery ground, although adults apparently avoided it. Ussing (1938) showed that in East Greenland, where there is only one diatom increase in the year, copepod reproduction was entirely dependent on it. More recently Wiborg (1940) found a possible connexion between spawning of *Calanus* and an abundant phytoplankton.



Text-fig. 2. Egg-laying in starved and fed *Calanus*.

During 1950 and 1951, when females were laying eggs freely, it was thought of interest to see whether they would lay better when fed than when starved. A number (thirty-two) of female *Calanus* were taken from the sea at the end of April 1950, put singly into the usual small dishes and examined daily for egg production. To avoid the effect of fluctuating temperature they were kept in a refrigerator at about 5° C. Half were starved by keeping them in ultra-filtered sea water and half were kept in ultra-filtered sea water enriched by *Chlamydomonas*. The experiment lasted for 35 days, but after 15 days the starved *Calanus* were divided into two lots; seven of them were now fed and the remaining six continued starved. After the 30th day conditions deteriorated rapidly, and the majority of the *Calanus* died. At the end only four survived in the fed, four in the starved then fed, and two in those starved all the time. The results are given in Text-fig. 2, where the total number of eggs laid per living *Calanus* is shown. There was a large production of eggs on the first and

second days, and for reasons stated later (p. 536) these have been ignored in the calculations. Thereafter the production of eggs by the fed was always greater than that by the starved; indeed after a week few of the starved were laying at all. The production of eggs in the fed *Calanus* fell away considerably after 2 weeks, and after the 25th day only two of them were still laying. The average number of eggs produced per fed *Calanus* (ignoring the first 2 days) was 109·8. In the starved *Calanus* it was 23·7, and only one egg was produced after the division into two batches on the 15th day. On the other hand, the starved *Calanus* which were given food produced a total of 92·6 eggs per *Calanus* of which 69·0 were laid after they were fed. Thus, in spite of the deteriorating conditions, feeding the starved *Calanus* resulted in an egg production not much below that of those fed all the time. It looks as if the eggs had been retained until feeding conditions were favourable.

A similar experiment lasting 36 days and giving similar results was done at the same time, keeping however three *Calanus* in each of twenty larger dishes which held about 50 ml. of water. In this the average number of eggs per *Calanus* was: in the fed 106·5; in the starved 20·1 (only three per *Calanus* were laid after the 15th day when the starved were divided into two lots as before); in the starved and then fed, 17·1 before and 40·2 after feeding. The condition of the gonads was examined at the end of this experiment. In the fed the majority still had large eggs in the oviducts, although in one or two the ducts had shrunk. In the starved all had shrunken oviducts, but in those starved then fed all except one had large eggs.

These two experiments were made with females which may or may not have laid before they were caught. One or two indeed, which did not lay during the experiment, may already have completed their egg-laying, and this may account for the smaller total numbers laid when compared with the females of Text-fig. 1.

One interesting fact is that even the starved *Calanus* retained fat up to the end of the experiment. Most *Calanus* have a store of fat (Lowe, 1935) in a sac which lies along the gut. Sometimes, especially in Stage V, this is a large bolster-like mass, sometimes only a small globule restricted to the hind end of the gut. Female *Calanus* on the whole carry less fat than Stage V, that in the anterior part of the sac usually disappearing gradually as the eggs develop. When mature, however, and under starvation conditions, the fat evidently does not go towards making more eggs but is retained by the animal.

The effect on egg-laying of food in general and of different kinds of food was investigated. The following organisms were used: *Coscinodiscus centralis* Ehrenberg, *Lauderia borealis* Gran, *Skeletonema costatum* (Greville), *Rhizosolenia delicatula* Cleve, *Ditylum brightwelli* (West.), *Chlamydomonas* sp. (Dr Parke's *Chlamydomonas* I), *Hemiselmis rufescens* Parke, *Dicrateria inornata* Parke, *Syracosphaera carterae* Braarud, *Gymnodinium* sp., *Peridinium trochoideum* (Stein) Lemm., and *Chlorella stigmatophora* Butcher.

As a standard food a culture of *Chlamydomonas* was used; some animals were also starved in ultra-filtered sea water.

In January and part of February 1951 the females obtained were almost all immature or medium stage and these were used for feeding experiments. Apart from a few specimens (which were probably wrongly diagnosed as immature) most of the immature when fed did not lay until about the 4th day, after which egg production gradually increased. The starved laid no eggs at all.

In a typical experiment lasting from 9 to 16 February the egg production of twenty immature *Calanus* was 17, 0, 0, 69, 144, 141, 179 on successive days, whereas twenty starved produced no eggs over the same period.

A number of experiments were also done about the same time on medium-stage and semi-ripe *Calanus*. These probably included quite a range of degrees of ripeness. Usually one or two laid eggs on the first day, and the number of eggs and of laying females increased from then on. In a typical experiment lasting for 7 days the egg production by twenty fed *Calanus* on successive days was 26, 72, 149, 193, 178, 155 and 66, a total of 839. In twenty starved it was 26, 17, 2, 19, 13, 1, 14, a total of 92.

From the middle of February onwards, ripe females became more abundant and were used for a long series of experiments using different kinds of food.

On the morning after an experiment had been set up there was always a large number of eggs in nearly all the dishes whether the *Calanus* had been fed or not. Apparently the shock of capture and examination stimulates a ripe female to lay. The first day's results are therefore not taken into account in the calculations of the average numbers produced with different foods. The great majority of the *Calanus* in the experiments did lay some eggs, and those which were given suitable food both laid more often and produced more eggs than the starved. Some of the cultures used as food were as good as *Chlamydomonas*, and in others the *Calanus* produced no more eggs than when starved. The organisms are of different size and no attempt was made to equate the volume of food given, but the concentration was always very much richer than anything the *Calanus* would find under natural conditions.

Table V shows a typical experiment comparing the eggs produced by *Calanus* fed on *Chlamydomonas*, *Hemiselmis*, *Syracosphaera* and *Ditylum* with starved *Calanus*. It is apparent that (omitting egg production on the first day) *Ditylum*, *Chlamydomonas* and *Syracosphaera* are all effective foods, whereas giving *Hemiselmis* is little better than starvation. In it they produced fewer faecal pellets than with *Chlamydomonas*. With the starved *Calanus* only one or two faecal pellets were produced and these were very small and almost transparent. With *Chlamydomonas* they were well compacted and dark, with *Ditylum* (as with all diatoms tested) and with *Syracosphaera* they were larger and paler.

It will be seen that there are individual variations in the *Calanus* and that with suitable food some lay every day and some most days. Raymont & Gross (1942) assumed that when a *Calanus* laid on two successive days, one period of egg-laying had been interrupted. Table V and Text-fig. 1 show, however, that with suitable food laying on several days running is quite normal (see also p. 532). The batches laid on succeeding days are often quite large but

TABLE V. EGG PRODUCTION IN INDIVIDUAL *CALANUS* USING DIFFERENT FOODS. 22–29 MARCH 1951

(Experiments run simultaneously with fifteen animals in most.)

		Calanus															
Day	Food	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	Total
1	*Chlamydomonas*	25	72	17	16	26	3	22	14	17	10*	0	30	63	0	41	356
2		36	0	0	0	1	31	0	28	2	17*	0	0	1	0	24	140
3		40	0	31	29	0	35	19	30	0	4*	88	6	44	27	26	379
4		56	51	0	0	36	1	0	16	0	13*	0	7	0	19	0	199
5		19	44	24	0	1	0	23	8	0	0*	32	1	0	0	20	172
6		10	0	8	30	4	1	25	18	0	3*	0	50	0	18	17	184
7		9	0	18	0	M.	0	1	0	0	0*	0	0	20	0	17	65
	Total	195	167	98	75	68	71	90	114	19	47	120	94	128	64	145	1495
1	*Hemiselmis*	32	25	32	80	51	10	12	27	30	74	0	2	41	39	—	455
2		0	1	0	0	0	1	1	0	0	0	0	0	1	2	—	6
3		0	0	0	0	0	0	15	0	0	0	0	0	0	0	—	15
4		0	0	0	0	0	0	0	4	11	0	0	0	0	5	—	20
5		30	1	0	15	24	4	0	0	0	0	D.	0	0	0	—	74
6		0	D.	0	0	0	0	7	0	0	0	—	D.	0	9	—	16
7		0	—	2	0	0	0	0	0	0	0	—	—	0	0	—	2
	Total	62	27	34	95	75	15	35	31	41	74	0	2	42	55	—	588
1	*Syracosphaera*	13	19	0	0	12	39	31	0	19	28	29	0	0	34	53	277
2		36	41	0	22	26	0	1	38	36	10	27	0	34	0	0	271
3		26	20	0	0	19	30	45	0	32	50	0	39	0	37	58	356
4		0	0	11	0	0	0	0	30	0	1	27	0	19	0	0	88
5		0	0	1	0	0	33	0	0	23	13	0	0	0	0	0	70
6		45	23	0	D.	0	0	0	6	24	15	0	0	D.	33	40	186
7		0	10	0	—	0	33	0	1	0	0	0	1	—	0	0	45
	Total	120	113	12	22	57	135	77	75	134	117	83	40	53	104	151	1293
1	*Ditylum*	23	0	27	24	24	19*	3	51	23	28	26*	12	23	19	26	328
2		36	0	31	32	23	30*	10	0	23	2	26*	42	32	34	8	329
3		15	0	20	43	0	29*	1	21	34	41	29*	25	23	26	40	347
4		33	7	0	0	0	K.	0	0	22	31	0*	0	0	16	0	109
5		27	0	23	21	19	—	M.	1	2	16	14*	0	18	21	19	181
6		22	34	18	37	23	—	7	42	50	27	12*	16	14	35	29	366
7		2	6	7	7	1	—	M.	39	1	6	14*	4	0	2	1	90
	Total	158	47	126	164	90	78	21	154	155	151	121	99	110	163	123	1750
1	Starved	32	50	26	43	38	43	11	8	—	—	—	—	—	—	—	251
2		0	0	0	0	0	0	0	28	—	—	—	—	—	—	—	28
3		0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0
4		0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0
5		0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0
6		0	D.	3	0	0	0	D.	0	—	—	—	—	—	—	—	3
7		0	—	0	0	3	0	—	0	—	—	—	—	—	—	—	3
	Total	32	50	29	43	41	43	11	36	—	—	—	—	—	—	—	285

* *helgolandicus*. M. = moribund; D. = dead; K. = killed.

occasionally a small number appears, often only one or two. A number of eggs ripen together in the oviduct, but possibly for some reason they are not all laid at once and the few remaining are extruded later. For this reason numbers under five are omitted in calculating the number per batch.

Table VI shows the summarized results of all feeding experiments.

In a culture of *Chlorella* as rich as the *Chlamydomonas* used, the egg production was extremely low, even lower than in the starved. The faecal pellets

Table VI. Comparison of the Effect of Different Foods on Egg Production

Date begun	No. of *Calanus*	Food	Total no. of eggs laid on day							Omitting first day			
			1	2	3	4	5	6	7	No. laying	Total no. of eggs	Eggs per batch*	Eggs per *Calanus* per day
29. i. 51	11	*Chlamydomonas*	49	28	140	76	157	—	—	9	401	20·4	9·1
	8	Starved	146	4	0	17	9	—	—	3	30	12·5	0·9
21. ii. 51	20	*Chlamydomonas*	245	66	189	203	304	77	—	18	839	21·4	8·8
	20	Starved	266	32	17	15	0	0	—	6	64	12·4	0·8
27. ii. 51	15	*Chlamydomonas*	312	174	375	214	177	105	138	14	1183	23·0	15·4
	15	*Coscinodiscus*	258	17	74	35	26	53	56	13	261	11·5	3·0
	15	*Skeletonema*	217	142	177	97	231	113	27	14	787	19·5	9·4
	15	Starved	236	32	3	0	11	31	7	9	84	8·9	1·0
6. iii. 51	15	*Chlamydomonas*	169†	406	358	230	70	82	—	14	1146	29·0	16·4
	15	*Peridinium*	331†	132	313	86	213	111	—	15	865	24·8	11·5
	15	*Rhizosolenia*	514	195	98	51	69	50	—	12	463	22·6	6·6
	8	Starved	63†	49	32	0	0	1	—	5	81	15·4	2·3
12. iii. 51	15	*Chlamydomonas*	581	204	555	309	279	142	77	15	1566	30·5	17·4
	15	*Dicrateria*	547	16	1	102	37	26	18	11	200	16·8	2·5
	15	*Chlorella*	639	63	1	0	0	5	2	7	71	15·3	0·8
	15	Indian Ink	359	48	38	42	4	14	12	11	158	16·3	1·8
	8	Starved	208	50	3	2	28	0	22	6	105	19·8	2·2
22. iii. 51	15	*Chlamydomonas*	356	140	379	199	172	184	65	15	1139	26·6	12·8
	13	*Hemiselmis*	455	6	15	20	74	16	2	10	133	14·5	1·7
	15	*Syracosphaera*	277	271	356	88	70	186	45	15	1016	28·9	11·8
	15	*Ditylum*	328	329	347	109	181	366	90	15	1422	24·2	16·7
	8	Starved	251	28	0	0	0	3	3	2	34	28·0	0·8
23. iv. 51	13	*Chlamydomonas*	311	479	310	204	337	141	78	13	1549	32·1	20·7
	15	*Lauderia*	581	477	103	105	207	437	450	15	1779	33·4	21·2
	15	*Gymnodinium*	417	224	346	224	256	540	384	15	1974	29·9	21·9
	11	Starved	209	35	59	32	39	0	17	7	182	16·2	2·8

* Numbers below 5 omitted.

† Those of *Chlamydomonas* and 'starved' and three of those with *Peridinium* had been in the laboratory overnight and had probably laid their first batch of eggs.

consisted of a mass of *Chlorella* cells apparently unchanged. *Dicrateria* and, as already mentioned, *Hemiselmis* were both used but neither was a good food. The coccolithophore *Syracosphaera* was readily taken and egg production was high. This was true also of the dinoflagellate *Peridinium trochoideum*. The five diatom species used all gave a positive result, although some were apparently better than others. Production in *Coscinodiscus*, for instance, was only a little higher than in the starved, but the cells were large and lay almost entirely on the bottom of the dish where they may not have been so readily available. Only *Peridinium trochoideum*, *Gymnodinium*, *Syracosphaera*, *Ditylum* and *Lauderia* were as good as *Chlamydomonas*, although *Skeletonema* (whose cells were mostly on the bottom) was nearly as good.

One inert substance was used, a very dilute suspension of Indian ink. With this the *Calanus* produced faeces, but the egg production was no higher than in the starved. Thus egg-laying is not caused by the mere passage of material through the gut. In order to test whether the high pH value or some other factor accompanying a phytoplankton increase had any effect, female *Calanus* were kept in sea water whose pH value had been raised to about 8·2, and also in sea water to which cell-free filtrate from a rich *Chlamydomonas* culture had been added. Neither showed any effect on egg production.

The results show that even although they may be freely taken into the gut, not all the organisms available in the sea are of equal value for egg production. If, as seems probable, the food taken is used in the formation of the eggs laid, then its metabolism must be very rapid. The experiments suggest that egg production by ripe *Calanus* can be used to test the nutritive value of different food organisms. It is a simpler and quicker method than feeding copepodites through one or more moults, during which development may also be affected by factors other than food.

An attempt was made to measure the relation between increase in food and increase in egg production. The *Calanus* were kept in *Chlamydomonas* cultures varying in concentration from 0 to about 250 cells/mm.^{3} and the medium changed every other day. The results are shown in Table VII and Text-figs. 3 and 4. With concentrations as low as 7–8 cells/mm.^{3}, the egg production is practically the same as with the starved *Calanus*. It then increases rapidly with increase in food up to about 40 cells/mm.^{3}, after which the curve flattens off. Although in the richer concentrations some of the *Chlamydomonas* cells sank to the bottom and were thus less available, it may be concluded that beyond a certain point more food will not lead to greater egg production. If a *Chlamydomonas* cell is considered to be of equal food value to a *Skeletonema* cell (being of about equal size), the lowest figures which gave an increase in egg production are less than those of a normal spring diatom increase in the Clyde sea area.

Some experiments in the spring of 1950 had suggested that the presence of food might act as a trigger to set off egg-laying. This was not confirmed in

TABLE VII. EFFECT ON EGG PRODUCTION OF FEEDING WITH INCREASING CONCENTRATION OF CULTURE. 3–10 MAY 1951

No. of *Calanus*	Strength of culture (cells/mm.^{3})	Total no. of eggs laid per *Calanus* up to day						Omitting first day		
		2	3	4	5	6	7	No. laying	No. of eggs per batch*	Eggs per *Calanus* per day
15	200–250	38·3	74·2	95·7	108·5	117·0	119·4	14	34·0	21·2
15	70–80	38·7	61·9	83·5	93·1	98·9	106·5	15	29·5	18·7
15	34–40	36·0	61·5	71·2	82·4	87·1	88·7	14	32·2	15·1
15	14–16	23·5	31·4	37·8	39·5	40·8	42·2	15	25·0	7·2
15	7–8	13·9	19·8	21·7	24·1	25·9	26·4	15	18·5	4·6
15	0	12·9	19·6	19·7	21·4	21·4	21·5	10	28·2	3·6

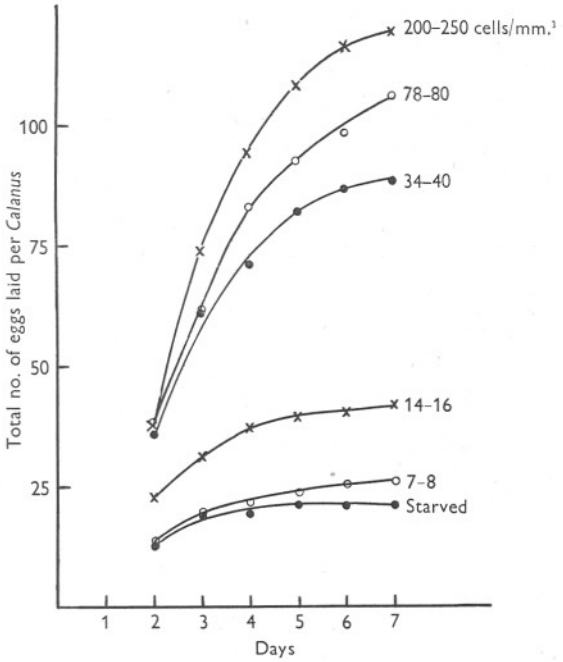
* Numbers below 5 omitted.

TABLE IX. EGG PRODUCTION OF RIPE FEMALES KEPT IN UNFILTERED SEA WATER, 1951

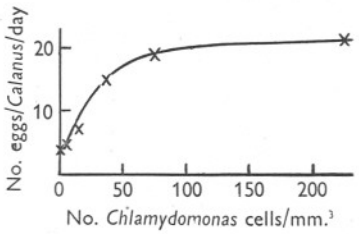
Date begun	No. of *Calanus*	Total no. of eggs laid on day							Omitting first day			
		1	2	3	4	5	6	7	No. laying	Total no.	Eggs per batch*	Eggs per *Calanus* per day
21. ii. 51	20	270	7	2	33	20	7	—	7	69	20·0	0·7
27. ii. 51	15	273	14	1	0	0	8	0	8	23	8·0	0·3
6. iii. 51	15	366	156	63	31	10	5	—	14	265	20·6	3·6
12. iii. 51	15	499	31	82	25	12	8	25	9	183	17·8	2·2
22. iii. 51	13	367	1	19	0	44	11	3	5	78	18·5	1·1
23. iv. 51	15	512	77	62	160	44	66	72	14	481	17·7	5·7
3. v. 51:												
1st week	14	681	156	552	214	187	138	111	14	1358	31·3	16·2
2nd week	14	61	84	274	317	259	91	194	13	1280	24·7	13·9
3rd week	11	117	82	157	27	51	25	47	10	506	25·5	6·9
Three weeks	—	—	—	—	—	—	—	—	—	3144	27·4	12·6

* Numbers below 5 omitted.
In the experiment beginning on 3 May the first day is not omitted in the calculations for the second and third week.

1951: the shock of capture and examination seems to be enough. The presence or absence of food has no effect on the number of eggs or the number of females laying immediately after capture.



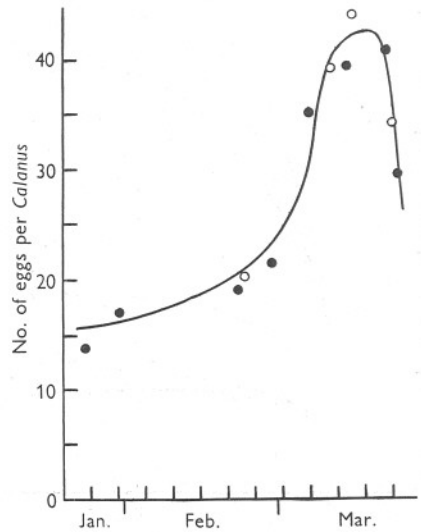
Text-fig. 3. Effect on egg production of feeding *Calanus* on *Chlamydomonas* cultures of different concentrations.



Text-fig. 4. Average number of eggs laid per day by *Calanus* fed on *Chlamydomonas* cultures of different concentrations.

The average number of eggs laid by a 'ripe' *Calanus* on the first night after being brought into the laboratory increased from January to March, as is shown in Text-fig. 5 and Table VIII. The increase was at first slow, but in both 1950 and 1951 there was a steep rise in March and a subsequent fall. In 1950 the maximum number (44·4) on 14 March can be related to a normal increase of *Skeletonema*, which by then had reached a figure of 340 cells/ml.

In 1951 the maximum egg number (41) was not quite so high and corresponded to a much smaller increase of *Chaetoceros* and *Coscinodiscus*. After this the number laid per batch fell and it is possible that this is because the females were now laying in the sea. *Calanus* eggs were scarce in the sea on 2 March, there were a few on 14 March and considerable numbers were present on 20 March. The results suggest that until the middle of March the female is enlarging the eggs gradually but not necessarily laying them in the sea.



Text-fig. 5. Number of eggs per batch produced by *Calanus* during the spring. ○, 1950; ●, 1951.

TABLE VIII. AVERAGE NUMBER OF EGGS IN FIRST LAY OF RIPE *CALANUS*

(Numbers under 5 omitted.)

Date	No. of *Calanus*	Average no. of eggs	Date	No. of *Calanus*	Average no. of eggs
22. ii. 50	5	20·4	21. ii. 51	41	19·0
10. iii. 50	25	39·2	27. ii. 51	60	21·4
14. iii. 50	46	44·1	6. iii. 51	29	35·2
21. iii. 50	16	34·3	13. iii. 51	69	39·4
24. i. 51	7	13·9	20. iii. 51	94	41·0
30. i. 51	11	17·1	22. iii. 51	69	29·6

When the first generation reaches maturity the average number of eggs per batch rises again, and on 30 April–1 May was 64·2.

During the experiments on different foods a number of ripe females was also kept in unfiltered sea water in the hope of finding out whether the sea during the spring diatom increase would become a medium as effective as the cultures used. Unfortunately the spring of 1951 was quite abnormal, and the enormous numbers of *Skeletonema* which usually appear in March did not come until May. Instead there was about the middle of March a much smaller

increase in the numbers of *Chaetoceros* and *Coscinodiscus* and this was apparently sufficient to let the breeding of *Calanus* go on as usual.

In the laboratory the number of eggs laid in sea water (Table IX) was very low in February, rose a little in March and April but did not equal the cultures used until the first-generation females were laying during the *Skeletonema* increase in May. Until May the low numbers may have been caused partly by the small volume in which the *Calanus* were kept — 20 ml. changed every second day. Gauld (1951) has shown that a Stage V *Calanus* can filter an average of about 70 ml. per day.

In May, therefore, fourteen *Calanus* were kept each in 50 ml. of water which was changed daily, and in the 21 days during which they were kept the egg production per *Calanus* varied from 187 to 422. Towards the end of the 3 weeks egg production fell off considerably, although diatoms were still numerous in the sea water. In spite of this the females when examined on the 21st day mostly contained a number of large eggs apparently ready to lay. One of them is shown in Pl. Ic. The egg production per *Calanus* per day was 16·2 for the first week and 12·6 for the whole time, thus approaching the production by *Calanus* kept in *Chlamydomonas* culture.

The high egg production in these females (nine of the 11 surviving laid over 250 eggs in the 21 days) shows that the figures given for the spermatophore-bearing females (Text-fig. 1) may well be equalled or exceeded by *Calanus* in the sea.

Discussion

It is interesting to consider the relation of these results to events in the sea.

When the over-wintering stock of Stage V comes to moult in the beginning of the year it does so with a good store of fat, in spite of having spent several months in diatom-poor water. It may be that the *Calanus* can find more food in winter than is supposed, or that its metabolism in winter is lower than during the rest of the year. That a lowered metabolism in winter may be an important factor is indicated by the results of several experiments comparing the food taken in by Stage V and female *Calanus* in the same culture of *Chlamydomonas*. On 10 January, judging from the number of faecal pellets produced, the Stage V were eating less than half the amount that the females were. The experiment was repeated with the same results on 23 January and on 13 March; by 9 April, however, the new generation had appeared and Stage V was eating as much as, or more than, the females.

In 1950 the over-wintering Stage V *Calanus* began to moult in the end of December, and by the middle of February 1951 most of the population consisted of adult females. On 1 February 53% of the females were immature and only 4% ripe, but the proportion of ripe increased gradually until on 5 March 1% was immature and 94% were ripe. *Calanus* eggs were scarce in the sea on 2 March, but considerable numbers of both eggs and nauplii were

present on 20 March and the new generation grew up during the rest of March and April. Adult females of the new brood appeared on 12 April as immature and gradually replaced the over-wintering stock.

Nicholls (1933*a*) estimated from field work that a female after moulting takes about a month before the eggs are ready to lay. The egg-laying experiments, however, have shown that the time taken will depend very much on the food present in the sea. When given a plentiful supply an 'immature' female can lay eggs in 4 or 5 days and a 'semi-ripe' one in 2 or 3, but the experiments with the females carrying spermatophores indicate that they do not often lay within a week after fertilization. The time taken from moulting up to this stage is uncertain and must depend partly on the stage of maturity at moult. The results with very immature females (p. 529) indicate a lapse of 2–3 weeks, but the fact that the proportion of immature females found in tow-nettings is low makes it more likely that the time is usually shorter. The fluctuating food conditions in the sea make it certain that the period from moulting to maturity will be longer than in the laboratory, and the dates given above for the increase in ripe females from 4 to 94 % confirm Nicholls's estimate of about a month. The experiments also indicate that the life of a female may be considerably longer than has been hitherto supposed, for besides the 4 weeks or so taken to mature it may live at least another month laying successive batches of eggs.

The facts that the number of enlarging eggs in the female (judging from the numbers laid per batch) increases over a period of some weeks, and that during that time the eggs are scarce in the plankton indicate that the female does not need to lay eggs once they have matured but can retain them until the conditions are favourable. Unless food is present *Calanus* will lay only a few eggs in the sea; a large egg production will occur only with a diatom increase lasting some time. The actual stimulus to egg-laying and to the completion of the first maturation division which immediately precedes it is unknown. Food does not act as the immediate stimulus, but when available it seems to be rapidly digested and used for egg production.

The production of viable eggs after as much as 68 days by an isolated female *Calanus* is interesting in that it shows that a single fertilization is sufficient. In the sea males reach their peak of abundance before females and the percentage of females bearing spermatophores is highest early in the development of a generation. Only on rare occasions do the majority of females bear spermatophores. This is understandable when we remember that the spermatophore is carried for only 1 or 2 days, after which it drops off. When females are caught in the sea they are almost invariably fertilized, that is, the spermathecae are dark in colour and full of sperm. A few females were found with empty spermathecae, and some of these were kept in a dish with males but fertilization did not take place. Males do not live in captivity so well as females and copulation was never seen.

The maximum total number of eggs laid by a single female (586) is much above the only previous estimate, over 112, which is that of Raymont & Gross (1942). However, their *Calanus* may have laid before their observations began.

Not all feeding experiments resulted in egg production. With the possible exception of *Coscinodiscus* all the diatoms tried gave positive results. Other organisms were also successful, but perhaps more surprising is the complete failure of *Hemiselmis* and *Chlorella*. *Chlorella* is known to be difficult to attack because of its cellulose membrane, but on the same grounds it might have been expected that *Chlamydomonas*, which in fact gave very good results, would be difficult to digest. Raymont & Gross (1942) found that *Nitzschia closterium* var. *minutissima* and *Chaetoceros pseudocrinitus* as well as several flagellates were eaten, although the *Calanus* survived better with the diatoms. The present observations extend and amplify their findings.

Nicholls (1933*b*) suggested that *Calanus* spawns at night, since eggs and young stages are always found above 30 m., and this has now been confirmed for the over-wintering generation. The eggs are heavier than sea water, and the rate of sinking is given by Gross & Raymont (1942) as 36 m. in 24 hr. Since the minimum time of hatching is about 24 hr. the greatest depth at which the eggs will be found should be about 36 m. In the results of Nicholls (1933*a*) and of Marshall *et al.* (1934) the vertical hauls were divided at 30 and 10 m. respectively. When summed over the year the number of nauplii above and below 10 m. was approximately the same, but very few were found below 30 m. The young copepodites do not show diurnal vertical migration (Nicholls, 1933*b*) and are confined to the surface layer so that the nauplii must swim up towards the surface. Since females show a marked diurnal vertical migration, the fact that the eggs are laid during the night ensures that they will be laid fairly near the surface. The first generation, which becomes adult towards the end of April and in May, is found near the surface during the day and lays throughout the 24 hr. However, those females of the first generation which live in deep water also lay throughout the 24 hr., and this is more difficult to understand. For if nauplii hatch below 50 m. they will have a much longer way to swim up to the surface layers.

The suggestion that successive broods of *Calanus* depend on outbursts of diatom growth is supported by the evidence given here of the dependence of egg-laying on food. Although the experimental results show that food and egg-laying are closely connected, it does not follow that a food which will induce egg-laying will also be suitable for the feeding and development of the nauplii and early copepodite stages. Some preliminary work has shown, however, that even as large a diatom as *Coscinodiscus centralis* can be broken up and ingested by Copepodite Stage II, and that *Peridinium trochoideum* ($25 \times 19\,\mu$) can be eaten by at least Nauplius VI.

The production of broods by some of the smaller copepods also seems to

depend on diatom outbursts (Marshall, 1949), and it may therefore be expected that these will show a similar effect of feeding on egg-laying.

We have pleasure in acknowledging the help given throughout the work by the staff of the Marine Station. We are very grateful to Dr Mary Parke of the Plymouth Laboratory for sending us cultures of all the organisms used.

Summary

A description is given of female *Calanus* at different stages of maturity and of the process of egg-laying.

It has been observed that the eggs of the two forms of *Calanus* differ in size, those of *helgolandicus* being larger than those of *finmarchicus*. The former was scarce, about 4%, in the over-wintering stock.

The females of the over-wintering stock of *Calanus* lay their eggs early in the morning, mainly between midnight and 3 a.m.; those of the first generation, which come to maturity in May, lay throughout the 24 hr.

The total egg production of individual females kept in the laboratory and fed has been found. The maximum was 586 eggs. Egg-laying may be spread over as much as 74 days and tends to occur in a series of bursts, each burst lasting for about a week. A single fertilization is enough for the whole of the egg-laying.

Egg production is largely dependent on the food available. When females are starved egg-laying ceases, but if they are fed again egg production begins too and is eventually not much less than in *Calanus* fed continuously.

A number of different cultures of diatoms and flagellates were tested as food, but it was found that not all of them resulted in egg production. All diatoms tested were successful. Inorganic material or a change in the reaction of the medium had no effect on egg production.

Calanus when kept in natural sea water produced only small numbers of eggs unless the water was rich in diatoms.

When brought into the laboratory ripe *Calanus* usually lay eggs overnight. The number thus laid was low in January and February and increased rapidly in March to a maximum of about 40 per batch. With the first-generation females much higher numbers were obtained.

The relation of these results to events in the sea is discussed. It is suggested that even when ripe a female *Calanus* can defer egg-laying until a suitable food supply is available. The spawning of *Calanus* in the sea should therefore coincide with diatom increases.

REFERENCES

GAULD, D. T., 1951. The grazing rate of planktonic copepods. *Journ. Mar. Biol. Assoc.*, Vol. 29, pp. 695–706.

GROSS, F. & RAYMONT, J. E. G., 1942. The specific gravity of *Calanus finmarchicus*. *Proc. Roy. Soc. Edinb.*, B, Vol. 61, pp. 288–96.

HARDING, J. P., MARSHALL, S. M. & ORR, A. P., 1951. Time of egg-laying in the planktonic copepod *Calanus*. *Nature*, Vol. 167, p. 953.

LOWE, E., 1935. On the anatomy of a marine copepod *Calanus finmarchicus* (Gunnerus). *Trans. Roy. Soc. Edinb.*, Vol. 58, pp. 561–603.

LOWNDES, A. G., 1943. Some applications of the displacement method of weighing living aquatic organisms. *Proc. Zool. Soc. Lond.*, Vol. 113A, pp. 28–43.

MARSHALL, S. M., 1949. On the biology of the small copepods in Loch Striven. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 45–122.

MARSHALL, S. M., NICHOLLS, A. G. & ORR, A. P., 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933 and their relation to the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. 19, pp. 793–828.

NAIR, K. B., 1939. The reproduction, oogenesis and development of *Mesopodopsis orientalis* Tatt. *Proc. Indian Acad. Sci.*, B, Vol. 9, pp. 209–19.

—— 1941. On the embryology of *Squilla*. *Proc. Indian Acad. Sci.*, B, Vol. 14, pp. 543–76.

NICHOLLS, A. G., 1933*a*. On the biology of *Calanus finmarchicus*. I. Reproduction and seasonal distribution in the Clyde sea-area during 1932. *Journ. Mar. Biol. Assoc.*, Vol. 19, pp. 83–110.

—— 1933*b*. On the biology of *Calanus finmarchicus*. III. Vertical distribution and diurnal migration in the Clyde sea-area. *Journ. Mar. Biol. Assoc.*, Vol. 19, pp. 139–64.

RAYMONT, J. E. G. & GROSS, F., 1942. On the feeding and breeding of *Calanus finmarchicus* under laboratory conditions. *Proc. Roy. Soc. Edinb.* B, Vol. 61, pp. 267–87.

REES, C. B., 1949. The distribution of *Calanus finmarchicus* (Gunn.) and its two forms in the North Sea, 1938–39. *Hull Bull. Mar. Ecol.*, Vol. 2, pp. 215–75.

RUSSELL, F. S., 1951. A re-examination of *Calanus* collected off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 313–14.

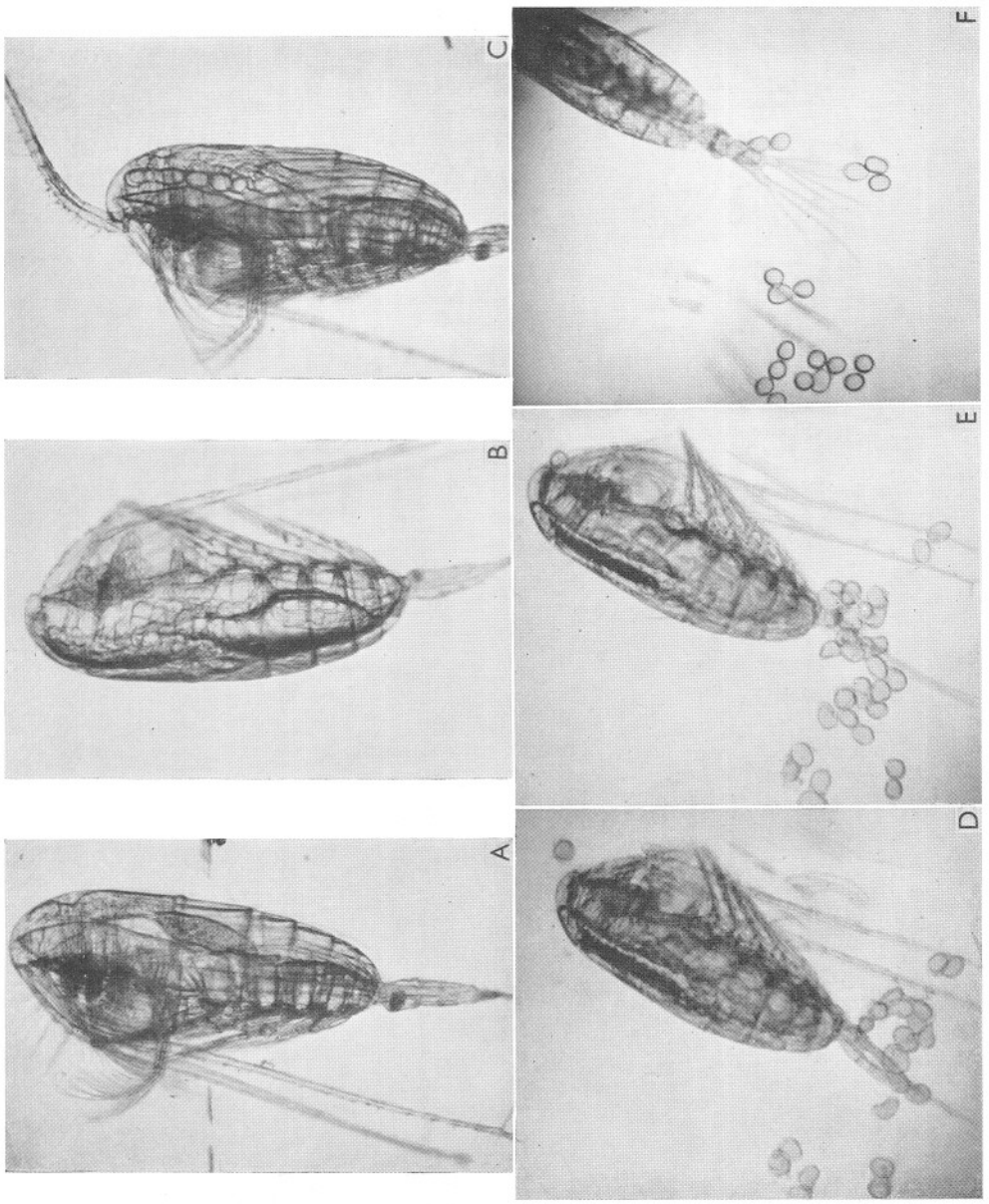
USSING, H. H., 1938. The biology of some important plankton animals in the fjords of East Greenland. *Medd. om Grønland*, Bd. 100, pp. 1–108.

WIBORG, K. F., 1940. The production of zooplankton in the Oslo fjord in 1933–1934 with special reference to the copepods. *Hvalrådets Skrifter*, No. 21, 85 pp.

WIMPENNY, R. S., 1937. The distribution, breeding and feeding of some important plankton organisms of the south-west North Sea in 1934. Part I. *Fish Invest.*, Ser. II, Vol. 15, No. 3, pp. 1–53.

EXPLANATION OF PLATE I

A. Female *Calanus* with ovary in medium state. The diverticula from the genital ducts fill only part of the head end. B. Female *Calanus* with ovary in ripe state. Large eggs are seen filling the diverticula in the head end and along the course of the oviducts. C. Female *Calanus* with ovary in ripe state. This *Calanus* has already laid many eggs and they are not so crowded as in B, but one row of large eggs is visible. D. *Calanus* in the process of laying eggs which have not yet begun to round off. E. The same *Calanus* slightly later. The same groups of eggs can be traced and the earlier laid are rounding off. F. A later stage in egg-laying. Some of the eggs are now spherical.



Figs. A–F.

CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L. III. AGE AND GROWTH

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(Plate I and Text-figs. 1–4)

Introduction

The first serious attempt to determine the age and growth rate of the common mackerel (*Scomber scombrus* L.) appears to have been made by Captain Atwood in 1856 (quoted by Brown Goode, 1884, p. 116) in the Massachusetts Bay area of northern North America. Small fish caught by Atwood in October of that year measuring $6\frac{1}{2}$–7 in. in length (16·5–17·5 cm.) he believed to be the young of the year (i.e. they belonged to the O-group). Mackerel belonging to this group he calls 'spikes'. 'Blinks', 'tinkers' and 'second size' fish he assigns to the I-, II- and III-year age groups respectively, but unfortunately gives no data as to the sizes of those categories, merely stating that everyone well acquainted with mackerel makes the same groupings 'as there seems to be a line of demarkation between the different kinds which stands out prominently'. Sixteen years later, on 27 July 1872, Malm (1877, p. 409) observed large numbers of small mackerel close inshore in the Gullmarfjord near Christineberg. Several tons of those mackerel were enclosed in a seine, but only ten specimens were retained as all the others escaped through the meshes. These ten fish ranged in length from 67 to 100 mm. and Malm surmised their age to be 13 months. Collett (1880, p. 18) stated that on the coast of Norway 1-year-old mackerel are 'fingerlang'. To fish of 20 cm., taken at the end of August, he ascribed (without supporting data) an age of 2 years, with sexual maturity supervening at 3 years at an unspecified length. Marion (1889, p. 86) studied the same species of mackerel in the Mediterranean. In catches obtained at Nice between 2 and 9 May 1888 he found small individuals from 6 to 11 cm. in length, which he considered to be derived from eggs spawned during the preceding January to March, the range of size being attributed to a spread of spawning activity over those 3 months. In the Gulf of Marseilles, too, at the end of May, Marion obtained mackerel of 11 cm. which he considered to be the young of the year. At the end of the year fish of 15–18 cm. were common. Still later, at the beginning of February, both at Marseilles and farther west, Marion noted the presence of mackerel measuring 20–24 cm.

These he considered to be derived from the previous year's spawning—i.e. they were the survivors of the brood that in May, 9 months earlier, were 6–11 cm. long.

Along the shores of the Mediterranean mixed fish fry is a readily marketable commodity which commonly includes mackerel. On certain dates in 1891 Gourret (1891, p. 57) recorded the following quantities and sizes landed by a small shore fishery near Marseilles:

	kg.	cm.
17–23 April	70	4–8·5
10–13 May	30	2–3
11, 12, 14, 17 May	31	3–4
23, 26 May	6	3–5
29, 31 May	25	3–6

The April fry Gourret believed to be derived from the earliest spawning of that year, perhaps in January. The various May fry he ascribed to spawning in February (5–6 cm.); March (4–5 cm.) and even April (2–3 cm.).

In 1892 (pp. 232–3) and again in 1896 (p. 314) Cunningham expressed the belief that mackerel of from 22·2 to 23·5 cm. in length, caught on 10 June, must be more or less exactly 1 year old. Others taken on 23 June having a length range of 29·5–32·8 cm. he regarded as precisely 2 years old. Still others of 16–21 cm., taken in November, were assumed to be 16 months old. This discrepancy Cunningham attributed to individual variation in size, but was greatly perplexed by a single specimen of 13·8 cm. taken in September 'which could not have reached that length in 2 or 3 months and must have been an unusually small specimen at 14 months'. Cunningham's age estimations were based on the erroneous belief that in all the mackerel of the region spawning is 'approximately simultaneous', proceeds very rapidly when once begun, and is limited definitely to one short period of the year extending from about the beginning of June to mid-July (Cunningham, 1889, p. 25; 1896, p. 313: cf. Steven, 1949, p. 565).

Matthias Dunn (1893, pp. 4–5) expressed the firm opinion that in the western end of the English Channel young mackerel 5–6 in. long (12·7–15·2 cm.) at the end of August, are derived from that year's spring spawning. According to Dunn, these small fish stayed inshore for a further 2 months or so, growing meanwhile at the rate of about $1\frac{1}{4}$ in. (3·2 cm.) per month. By about the end of October when $7\frac{1}{2}$–$8\frac{1}{2}$ in. long (19–21·6 cm.) they disappeared from Dunn's ken until about the beginning of the following June, by which time they had attained a length of from 9 to 11 in. (22·9–27·9 cm.). Ehrenbaum (1923, p. 21) records that Knut Dahl caught 311 specimens of small mackerel ranging in length from 6 to 9 cm. in a seine net on 19 July 1905. This total was made up as follows:

Length (cm.)	6	7	8	9	(mean 7·8)
No. of fish	5	102	162	42	

Ehrenbaum considers all these fish to have been in their first year of life. Young mackerel of similar sizes have also been taken in small numbers, by other observers elsewhere from time to time without their ages having been determined or surmised. These various records are collected by Ehrenbaum (1923, pp. 12–26), who reaches the conclusion that, in general, the growth of the mackerel (*Scomber scombrus*) during the first year of life 'does not seem to amount to much over 10 cm.' (p. 22). Towards the end of their second summer Ehrenbaum considers the average length to be 20–22 cm., and 27–28 cm. in the third summer (p. 39).

Nilsson (1914, pp. 1–59) was the first investigator to make any real attempt to determine the age and growth rate of mackerel after the first year of life. Age determination in this fish is a matter of great difficulty. No bone has been found which reveals distinctive growth markings either with or without special treatment. Visible and readable markings are present on certain scales, but there is great difficulty in collecting them. They are so small as to be easily rubbed off and transferred from one fish to another in all samples collected by ordinary methods. For scales to be used reliably mackerel must be caught individually, e.g. by hook and line, and each fish kept by itself in a separate container—conditions that cannot easily be met if adequate numbers are to be dealt with. Otoliths are less clearly marked, but with practice readings can be obtained from a high proportion of them in the younger year classes—up to about 6 years. In my experience otoliths from older fish are seldom readable.

Nilsson (1914, p. 20) used scale readings checked against a few otolith determinations for age assessment of 208 specimens. From this somewhat scanty material he gives the following lengths reached by mackerel at the end of each year of growth up to and including 6-year-old fish (lengths measured to tip of tail):

End of 1 year	Maximum recorded length	22·9 cm.
„ 2 years	23·5–30·6 cm.	
„ 3 years	31·1–33·9 cm.	
„ 4 years	34·4–36·1 cm.	
„ 5 years	36·7–38·5 cm.	
„ 6 years	39·1–40·3 cm.	
„ 7 years	40·9–?	

Nilsson's findings are in agreement, therefore, with those who ascribe to the mackerel a growth of 20 cm. or more in the first year of life, as against those who consider fish of this size to be at or near the end of their second year of life.

This divergence of opinion as to the growth rate of the mackerel, at any rate in its early years, has persisted. As late as 1939 Le Gall (p. 14) gives the

following figures based on length frequencies (not given) and the distribution throughout the year of mackerel shoals comprising fish of different sizes.

End of 1 year	8–11 cm.
„ 2 years	18–21 cm.
„ 3 years	26–28 cm.
„ 4 years	30–32 cm.
„ 5 years	35 cm.

At the same time, Steven and Corbin (1939, p. 18) made considerably different tentative assessments of age and growth rate based on scale and otolith readings. These were:

End of 1 year	?
„ 2 years	Up to 27 cm.
„ 3 years	„ 31·5 cm.
„ 4 years	„ 33·5 cm.
„ 5 years	„ 35·0 cm.
„ 6 years	„ 35·5 cm.
„ 7 years	„ 36·0 cm.

According to Sette (1943, p. 154), on the American side of the North Atlantic the fry of the common mackerel reach a length of about 50 mm. in about 70 days after hatching—i.e. by about the end of July for the majority of them. Subsequently, Sette (1950, p. 312) states, without supporting data, that these July fingerlings reach a length of 8 in. (i.e. just over 20 cm.) by September; and that they range, in their second year of life, from 25 cm. in early summer to 32 cm. by fall.

Recently, Le Gall (1950) has repeated his 1938 figures concerning age and growth of mackerel, again without supporting data, but with the accompanying remark that 'la présence, en quantités parfois très abondantes de la mi-Juin à la fin de Septembre, de jeunes maqueraux de 7 à 11 centimètres, confirment l'opinion que nous avons deja émise sur la croissance de ce poisson'.

The two schools of thought on mackerel growth are at variance mainly in their conclusions concerning rate of growth in the first year of life, one school placing the first year's increment at 10 cm., or a little over, while the second attributes a length of 20 cm. or more at the end of the first year. Ehrenbaum, of the first school, supports his view by saying that the mackerel is hardly likely to grow faster than cod and haddock, which at the end of their first summer measure only about 14 cm. (1923, p. 23).

Striking confirmation of rapid growth by mackerel in their first year of life has recently been provided by Dannevig (1947, p. 93; 1948, p. 219), who has been able to make direct observations on the growth of young mackerel in his fish-hatchery basins at Flødevigen, Norway. On 6 August 1939, a number of young mackerel, 8 cm. in length, appeared in the leads between the basins

and the lobster hatchery. One was caught and placed in an aquarium where there were large quantities of small Crustacea, and throve remarkably. Later it could be provided with only dead food which did not agree with it, and it died on 1 September being then 10·5 cm. long. The fish had grown 2·5 cm. in 25 days. Later, on 14 September, about twenty small mackerel were observed in the oyster basins. Their lengths were approximately 15 cm. The basins had been emptied in the spring and those small mackerel must have entered as eggs contained in the water pumped into the basin in May–June of the same year. Dannevig states that young fish could not have passed through the centrifugal pump and lived. He is therefore in no doubt that those mackerel were young fish of the current year and that they had reached a length of 15 cm. in about 4 months. This agrees closely with Dunn's figures of 12·7–15·2 cm. length at the end of August in the English Channel. There can be now no doubt that mackerel may reach a length of 20 cm. or more in the course of their first year of life.

Methods

Investigations by the present author into the life history and biology of mackerel in the English Channel and Celtic Sea have included researches into ages and growth rates. Otoliths have been collected from a total of 8422 fishes, of which 6261 (74·3%) have been readable and 2161 (25·7 %), mainly in the higher length groups, have been unreadable. In addition, scales from 1364 fish were collected, but scale reading was discontinued when it was found that a sufficient proportion of otoliths could be read to give reasonably satisfactory results.

The otoliths were collected from each fish by cutting transversely through the head behind the eye at a point immediately in front of the small cavities in which the otoliths lie. There are two otoliths on each side, but the smaller one is useless for age determination. After the cut is made the brain is removed from the remaining posterior part of the cranium. The large otoliths can then be removed, one at a time, by probing for them with a weakly-sprung sharp-pointed forceps. At first this may present some difficulty, but with a little practice the operation becomes both simple and speedy.

As thus obtained, each otolith is covered with soft tissues that must be completely removed before drying. This cannot conveniently be done immediately, as too much time would be taken up in disposing of the sample of fish. The otoliths are therefore stored under water until they can be cleaned. This is best done by making shallow holes in a block of hard, close-grained wood about 9 in. square. One hundred such holes, preferably $\frac{5}{8}$ in. in diameter and $\frac{3}{16}$ in. deep, can conveniently be made in such a block. They should be arranged in regular rows of 10 × 10. Above the uppermost hole in each vertical row the numerals 1–10 are clearly marked. The whole upper surface of the

block, including the shallow holes, should then be painted black with a waterproof paint that will retain the water with which the holes have to be filled. A specially made block of black plastic material would be even more suitable. On removal from the fish the otoliths are placed in the appropriate hole which is filled with water to keep them wet.

As soon as possible after the sample has been dealt with the otoliths must be divested of all soft tissues adhering to them and placed in numbered containers. Envelopes are unsuitable as the otoliths are so small and brittle that they become lodged in the corners, are hard to see, and often get broken. The best method is to glue small cardboard pillboxes by their bottoms on a square piece of cardboard—100 boxes arranged in rows of 10 × 10 to each piece of board.

To clean the otoliths two pieces of cane about 3 mm. in diameter and 15 cm. long are used. Before use each piece is sharply pointed at one end and the points worked gently backwards and forwards on a piece of glass. This breaks up the single fine point and releases the fibres so that a tiny brush of just the right stiffness is formed. With two brushes thus prepared the otoliths can be easily and completely cleaned in water in a solid watch-glass, preferably of black glass, under the low power of a dissecting microscope.

Mackerel scales are very small and easily rubbed off. Special precautions had therefore to be taken to ensure that the scales removed from a fish really belonged to it. Nilsson's method of using hooked fish for scale-reading purposes was therefore adopted. Each fish, on removal from the water carefully suspended from its hook so as not to touch anything, was lowered tail first into a clean, grease-proof paper bag. Both bag and fish were then held firmly in the left hand while the hook was removed. By adopting this method, very few scales actually became dislodged from the fish, and any that were rubbed off were inside that fish's own bag.

For age determination, scales from the anterior part of the body just below and slightly behind the pectoral fin have invariably been used. A scraping in this position is made with a scalpel and the small mass of scales so collected is washed off into a small specimen tube ($1\frac{1}{2} \times \frac{1}{2}$ in.) almost filled with clean water. The tube is then corked. Groups of 100 tubes are used, fitted into a 10 × 10 arrangement of holes in a block of wood, the holes smaller and deeper than those made for the reception of otoliths.

The scales are collected and stored in tubes because they are too small to be removed individually with a pair of forceps, followed by dipping in water, cleaning between the thumb and first finger of the left hand, and mounting on a microscope slide—as can be done with herring and pilchard scales, for example. In their tubes they can be left for an indefinite period before eventual cleaning and mounting. If left for more than a few days the contents of the tube will smell strongly, but this does no harm; indeed it is an advantage because the scales are more easily cleaned after the organic matter covering

them has decomposed. In a normal scraping anything up to 500 scales may be present. From amongst these at least three scales should be selected for mounting. In most samples, scales of many shapes and sizes will be found of which only a few will be readable. Most kinds are well illustrated by Nilsson (1914, plate I, figs. 1–13). The clearest and most consistent zoning and ringing are found on those shaped as in Nilsson's figs. 8 and 11. At least three scales of this type should be looked for amongst the mass of others, and removed to a second watch-glass. There they must be cleaned, in water, under a binocular dissecting microscope, using brushes made from pieces of cane in the way described above. Three such scales are shown in Pl. I, figs. 1–3.

Age and Growth

In this investigation scales from each of 1364 fish were mounted on microscope slides previously smeared very lightly with prepared egg albumen. All these scales were separately 'read', and it was found that in 1343 out of the 1364 fish (98·5 %) the readings of all three scales were in agreement. In the remainder, the three scale readings did not all agree. This degree of discordance is not excessive and gives good grounds for assuming that the readings are reliable. Even more confidence can be placed in them when comparison is made with otolith readings from the same fishes. Omitting those fishes that gave discordant scale readings, it is found that in only fifteen out of a total of 1343 individuals (1·1 %) did the scale readings differ from those of the otoliths. Difficulty in reading the otoliths can very easily account for this discrepancy. These results are shown in detail in Table I.

In consequence of this satisfactory agreement between scale and otolith readings, the collection of scales was discontinued and only otoliths were taken from later samples. In this connexion it must be emphasized that a high proportion of otoliths were rejected as unreadable. Included in this group are all otoliths whose readings were to any appreciable extent doubtful. It is believed to be better to reject completely a doubtful reading than to include it in any group to which it 'probably' belongs.

In the mackerel there are two otoliths on each side—a larger and a smaller one. The latter, flat and somewhat irregularly crescent-shaped in outline, is generally almost completely transparent and never exhibits readable 'ringing' and 'zoning' (Nilsson, 1914, plate I, fig. 16). The larger otolith is thickest and widest at its posterior end, tapering towards its anterior end where it terminates in two points of unequal length. Nilsson (p. 23) states that this otolith 'can at times have fairly distinct annual rings, especially on the longer of the two points'. In the present investigations reliable readings have been more easily obtained at the blunt posterior end of the otolith.[1] While it is true that

[1] In Nilsson's own figures (plate I) the markings are clearest at the blunt ends of the otoliths shown.

markings are often most distinct on the longer point, secondary markings are often so much in evidence that interpretation is difficult or impossible.

Reading is best carried out in a solid watch-glass made of jet-black glass. The otoliths are viewed under water or alcohol by direct illumination.[1] Thus examined, the central part of the otolith shows up as opaque chalky white. In fish of more than 1 year the dense central portion is surrounded by a dark, narrow 'ring'. With increasing age further zones and rings are formed (see Pl. I, figs. 4–6).

TABLE I

Serial no. of sample	Total fish	No. of fish with discordant scale readings	All scales in agreement but differing from otoliths	Percentage of fish with all scales and otoliths in agreement
13A	100	6	1	93
15	61	4	1	92
24	96	0	0	100
29	93	0	0	100
31	71	0	5	93
32	99	0	0	100
37	13	0	2	85
39	49	0	0	100
41	100	10	1	89
44	20	0	0	100
45	40	0	0	100
46	50	0	0	100
47	41	0	0	100
48	39	0	0	100
49	51	0	0	100
50	40	0	0	100
52	58	0	1	98
54	45	0	0	100
55	48	0	2	96
56	50	0	0	100
57	100	0	2	98
58	100	1	0	99
Total	1364	21	15	97·4

The central zone is first laid down. This is followed by the first ring which, although formed in winter, does not generally become clearly defined until late spring or early summer when the new season's zone, now forming outside it, serves to show it up. This applies also to all the dark transparent winter rings that are laid down in subsequent years.

Unlike a ring, a zone is recognizable while growing, long before the next ring is laid down demarking its final limit. Thus a 2-zoned fish is one in which a fully developed central zone is surrounded by a fully formed ring, and a second zone, the latter being either partly formed or completed.

New zones, narrow and obviously of recent origin, begin to show up in late spring and early summer. Thus a fish in its second year, caught say in September, will have a distinct second zone clearly noticeable. Its otolith reading will therefore be '2 zones 1 ring', recorded as '2–1'. The same fish

[1] Otoliths that have been stored dry for a long time float in water; alcohol must then be used.

will continue to have a reading of '2–1' until next May or June when a third zone, newly forming, will show up the second winter ring. Readings of '1–1', '2–2', '3–3' have therefore seldom been made; for by the time that the new zone has shown up the immediately preceding winter ring clearly, it has become itself recognizable and must be recorded. It will be convenient, therefore, to discuss otolith readings in terms of zone numbers. An otolith with two zones will obviously have a winter ring between them; a three-zoned otolith will have two intervening rings; and so on.

Since new growth begins about May and continues rapidly throughout the summer and autumn, distinction must be made between fish caught at or near the beginning of the growing season and those caught at or near the end of it. In the early part of the year, before the new seasons's growth has got well under way, a fish whose otoliths record two zones will have completed 2 full years' growth, and really should read '2 zones–2 rings'. By the time the second ring becomes definitely recognizable, the third zone will also be showing up and that fish becomes '3–2'. In late summer and autumn, a fish recording two zones is really aged only 1+; i.e. the second full year's growth is not completed: similarly a three-zoned fish will be 2+, and so on.

Otoliths from a total of 8422 fish, obtained over the years 1936–40 and 1948, have been examined. Of these, readings have been possible from 6261 fish, and 2161 (25·7 %), mainly from individuals over 6 years of age, have been unreadable.

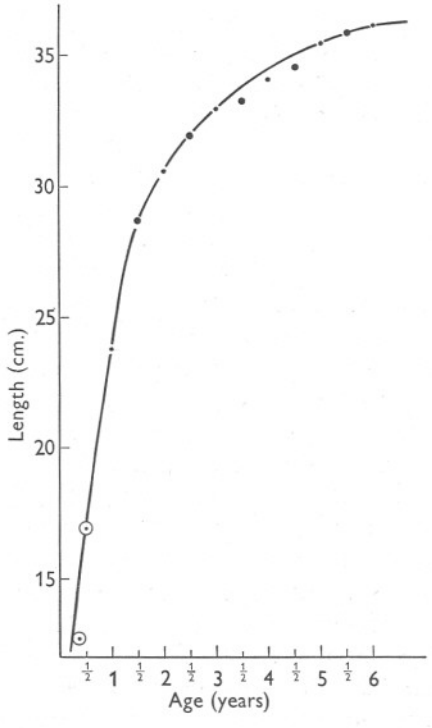
It has been found convenient to group the 6261 fish that gave otolith readings into two groups, 'A' and 'B', the former having 1 September and the latter 1 May as their 'approximate mean date' of capture. Fish included in group A, having the same otolith reading as those of group B, will therefore have a lesser mean length than the latter by the amount of growth that has taken place in the 8 months September to April inclusive.

The mean lengths measured to the nearest centimetre below and suitably corrected, obtained for fishes of different zone readings grouped in this way are given in Table II.

In Text-fig. 1 the lengths of the May fish are plotted against the numbers of otolith zones which, at that time of year, represent fairly exactly the numbers of completed years of growth. A curve has been fitted empirically to those points. The lengths of the September fish can be plotted on the same graph. On inspection it is found that if, in doing so, the number of years' growth recorded in column 2 of Table II as 1+, 2+, ..., be taken to read $1\frac{1}{2}$, $2\frac{1}{2}$, ..., then the points (large on the graph) conform remarkably closely to the curve already drawn for the May fish. This means that September fish with (n) zones on their otoliths have completed ($n-\frac{1}{2}$) annual increments of growth; that is to say, that half the total growth increment for the year is completed during the 4 months of May–August inclusive, while the other half is spread over the months September–April inclusive.

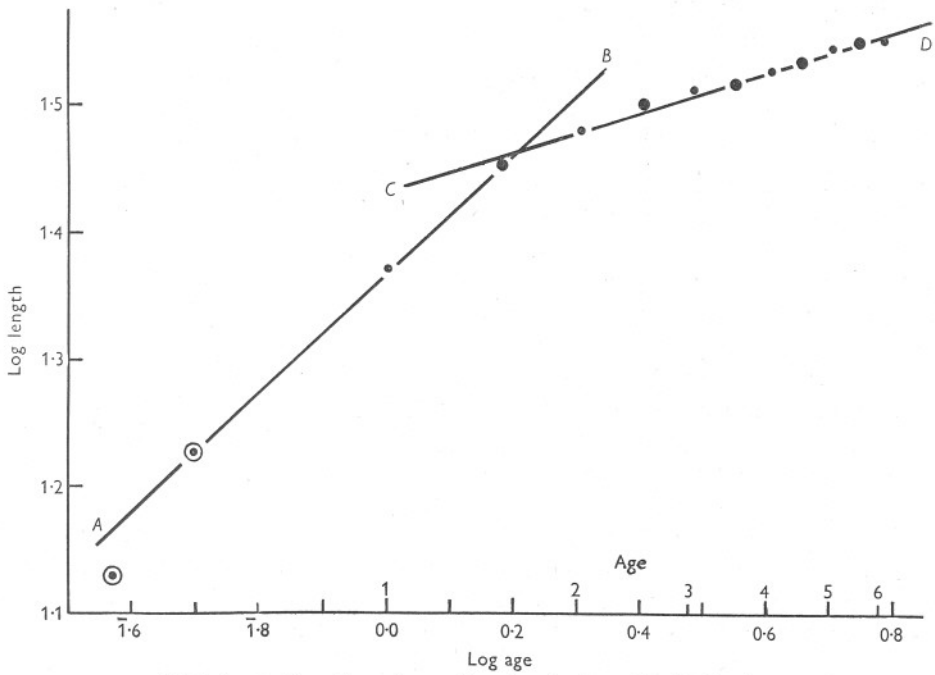
TABLE II. MEAN LENGTHS OF FISH OF DIFFERENT ZONE READINGS (UP TO 6) IN SEPTEMBER AND MAY

	Mean date, *c.* 1 September		Mean date, *c.* 1 May	
No. of zones on otoliths	No. of years' growth	Mean length	No. of years' growth	Mean length
1	<1	—	No records	
	—	—	1	23·8
2	1+	28·7	—	—
	—	—	2	30·6
3	2+	32·1	—	—
	—	—	3	33·0
4	3+	33·3	—	—
	—	—	4	34·1
5	4+	34·6	—	—
	—	—	5	35·5
6	5+	35·9	—	—
	—	—	6	36·2



Text-fig. 1. Growth of mackerel up to 6 years.

Small mackerel of less than 15 cm. in length are seldom caught in this area. Occasionally, however, they put in an appearance in shallow water (Steven, 1948, p. 536). Ford (unpublished data) obtained a few small mackerel in Plymouth Sound in August 1926 having a mean length of 15·3 cm.; and again in August 1927 he caught about fifty similar fish in a sprat seine having a mean length of 13·6 cm. (range 12·5–15·2 cm.). In 1937 very large numbers of small mackerel appeared in and around Newlyn harbour, in Cornwall, and in the first days of August the present writer caught 273 of them having a mean length of 12·7 cm. (range 8·0–16·4 cm.). At the end of the same month



Text-fig. 2. Length and age of mackerel—logarithmic plotting.

84 more small fish were taken having a mean length of 16·9 cm. (range 14·0–17·9 cm.). Assuming that half a full year's growth takes place, on the average, in May–August inclusive, the fish caught in the first week of August 1937 may be assumed to have made about three-eighths of a full year's growth. The small fish taken at the end of the month would have completed approximately half a year's growth. These points are also plotted (in circles) on the graph in Text-fig. 1 and appear to conform to the curve derived from plotting the age-length relationships of older fish.

In Text-fig. 2 the same age-length data are plotted on a double logarithmic scale. When this is done it is found that for fish of 2 years and upwards the points fall on or near the straight line *CD* and that those appertaining to

younger fish fall on or near another straight line AB, with the exception of the early August fish which do not quite conform. On the assumption that they have grown about three-eighths of their full year's increment, the mean length of these fish should have been 14·6 cm. to fall on the line AB, a figure that lies well within the length range of the 273 fish from which the mean was derived and may be accepted as being in reasonable agreement for all practical purposes. On the other hand, an adjustment of 3 weeks in their assumed age is all that is necessary to obtain agreement.

There can be little doubt therefore that in the young fish up to about 2 years of age the growth gradient conformed to that indicated by the line AB, which provides the expression

$$L \propto A^{0\cdot49}, \text{ i.e. } A \propto L^{2\cdot06},$$

where L = length in cm., and A = age in years.

In older fish the growth gradient conformed to that indicated by the line CD, which provides the expression

$$L \propto A^{0\cdot15}, \text{ i.e. } A \propto L^{6\cdot65}.$$

The two lines AB and CD intersect at a point representing the logarithms of length 29·3 cm. (limits 28·6–29·5) and age 1·6 years.

It seems likely that this point of discontinuity in the growth gradient represents the approximate length and age at which the onset of active sexual development takes place in the majority of individuals, i.e. that the onset of sexual maturity takes place at a length of about 29 cm. in the second year of life. This means that fish hatched in the spring of any year will begin to 'fill up' in the late autumn of the following year and will spawn for the first time during the subsequent spawning season when approximately 2 full years of age. This is in agreement with Nilsson's statement (1914, p. 41) that 'maturity is reached at the age of 2 years' if by this is meant that the fish arrive at first spawning when they are approximately 2 full years old. Confirmation of these results has been obtained from simultaneous observations on gonad development. Le Gall (1950, p. 71) also states that the onset of first maturity takes place at or over a length of 26–28 cm., but ascribes an age of 3 years to such fish.

Onset of Sexual Maturity

Data bearing on the onset of sexual maturity in the mackerel of this region have been obtained by examination of 9334 fish in which sex and gonad condition have been determined. The determinations were made by naked-eye observation. Young individuals in which the sex could not be decided by this means have been recorded as immature fish. The later stages of development

of the sexual organs have been classified according to a scheme similar to that used internationally for the herring and other clupeoids (see Jensen, 1950, p. 6), but suitably modified for the somewhat special characteristics exhibited by the mackerel.

Stage O. Immature juveniles. Sex not ascertainable by naked-eye examination.

Stage I. Virgin individuals. Sexual organs very small but sex ascertainable by naked eye. Ovaries rich wine colour and very slender torpedo shape; individual eggs indistinguishable. Testes much paler in colour than the ovaries; also thinner and more blade-like.

Stage II. Maturing virgins (maiden fish) and recovering spents. In virgin fish the ovaries are slightly larger now than in stage I and individual eggs begin to be distinguishable. Testes also enlarging; paler in colour than ovaries. In recovering spents, at this stage, both ovaries and testes are also quite small but flabbier than in virgin fish and generally somewhat bloodshot.

Stage III. Sexual organs considerably larger and occupying about half of the ventral cavity. Differences between virgin fish and recovering spents now scarcely distinguishable.

Stage IV. Sexual organs still growing. Ovaries becoming a pronounced orange-yellow colour with conspicuous opaque eggs. Testes becoming a clear creamy or milky colour.

Stage V. Sexual organs now filling ventral cavity. In the ovary superficial blood-vessels have become large and conspicuous. No transparent eggs. Testes assuming a fairly uniform milky whiteness.

Stage VI. *Testes*—large, firm and clean milky white. Small amount of ripe milt can be expelled from them on slight pressure.

Ovaries. In the female stage VI has been subdivided into two stages:

Stage (♀) VI A. Ripe translucent eggs scattered throughout unripe eggs giving rise to a 'plum pudding' appearance (see Steven, 1949, p. 565 and plate I). No ripe eggs free in the lumen.

Stage (♀) VI B. Ripe eggs present in the lumen of the ovary which generally must be opened to find them. Externally, the ovary may appear to be in stage V or VI A, but the presence of ripe eggs free in the lumen indicates that one or more batches of eggs have already been spawned. After several batches have been shed the ovary becomes progressively more flabby and bloodshot, especially posteriorly.

Stage VII. *Spent fish.* Ovaries slack with only residual eggs. Very bloodshot. Testes also small, flabby and bloodshot.

A stage VIII as used for herring (Jensen, 1950, p. 6) has not been separately distinguished.

The 9334 fish examined for sex comprised 995 immature juveniles whose sex was not evident from naked-eye observation. The remainder comprised 4031 males and 4308 females. Of these 803 males and 681 females were in maturity stage I—i.e. were virgin fish in which signs of rapid gonad development towards ripening are still absent though the sex is determinable by naked-eye observation. Some females whose lengths ranged from 22 to 28 cm. had ovaries of quite small size that nevertheless exhibited a typically shotten appearance, but which, after the most careful examination, always failed to reveal any residual ripe eggs in the lumen. The explanation appears

to be that, in those fish, the gonads had progressed a considerable way towards ripeness and then assumed a spent appearance without any ripe eggs having been actually produced and shed. Similar precocity was detectable also in some males over a length range of 24–28 cm. Since these fish—designated 'false stage VII'—had not spawned, they have been grouped with stages O and I as maiden fish which had not yet reached first maturity.

In Table III the total numbers of fish at the various stages of gonad development have been entered against the length in cm. From this table it will be seen that all fish under 18 cm. in total length were in those stages of immaturity in which the sex was not determinable by naked-eye examination. Fishes in this stage were not uncommon up to a length of 22 cm. after which their numbers diminished and they were almost totally absent in all sizes exceeding 29 cm. Fishes in stage I begin to appear in small numbers at lengths of from 18 to 20 cm. and remain common up to lengths of just over 30 cm. Fishes at stage II, which includes maiden fish with gonads in the very early stages of active ripening, and recovering spents in which the gonads have gone far towards resuming their original appearance in maiden fish, begin to appear at 21 cm. and become plentiful at lengths of 27 cm. and upwards. The later stages, up to and including stage VI, do not appear in any numbers until lengths of 30 cm. and upwards are reached. The table further reveals that spent fish may be at times noticeable in the catches at smaller sizes than fully ripe fish. There are probably two explanations for such apparently anomalous occurrences: (i) that fish in a state of precocious maturity and giving a false appearance of 'spentness' have been mistaken for true spents; and (ii) that, by some vagaries of the fisheries or of sampling, spent fish on occasion were obtained for examination from schools of smallish fish from which no samples were collected when they were in the spawning state.

In further reference to Table III it will be seen that the immature fish of stages O and I and precocious stage VII are chiefly confined to fish of less than 29 cm. in total length—i.e. they are grouped on the left of the line *AB* drawn through the table—and that stages III–VII are comprised mainly of fish of 30 cm. and upwards, i.e. they are grouped on the right of the line *AB*. Stage II may be regarded as a transition phase in which the ripening process is actively beginning but has not yet reached the state of very rapid gonad development associated with stage III onwards.

This grouping of the fish in Table III on either side of a line falling between lengths of 29 cm. and 30 cm. agrees well with the figure of 29·3 cm. as the point of discontinuity in the curve of growth derived from plotting log length against log age. There can be little doubt, therefore, that the change in the growth gradient in respect of the age-length relationship is very closely associated with the onset of first sexual maturity. This is further borne out by the fact that if the percentage of fish exhibiting gonad stages II–VII inclusive (Table III) is plotted against length, the derived sigmoid curve

TABLE III. LENGTH DISTRIBUTION OF THE VARIOUS REPRODUCTIVE STAGES

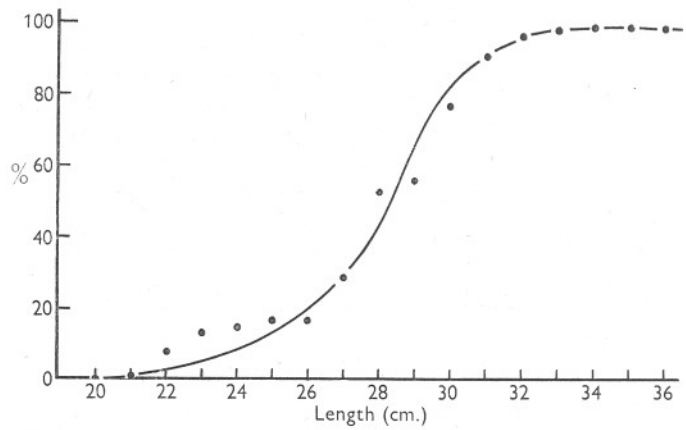
Length of fish (in cm.)

State of sexual organs		< 18	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	Totals
O:		339	75	88	98	120	122	62	19	19	18	13	9	9	2	1	1	—	—	—	—	—	—	—	—	—	995
I:	♂♂	—	1	1	3	14	37	52	40	31	67	97	124	179	98	38	15	5	1	—	—	—	—	—	—	—	803
	♀♀	—	*1*	*14*	—	*42*	*87*	*63*	*20*	*46*	*92*	*99*	*99*	*72*	*27*	*9*	*7*	*2*	*1*	—	—	—	—	—	—	—	*681*
False VII:	♂♂	—	—	—	—	—	—	—	2	3	14	20	9	—	—	—	—	—	—	—	—	—	—	—	—	—	48
	♀♀	—	—	—	—	—	*1*	*2*	*2*	*1*	*2*	*12*	*8*	—	—	—	—	—	—	—	—	—	—	—	—	—	*28*
II:	♂♂	—	—	—	—	1	1	1	—	2	5	9	23	38	51	61	52	34	29	20	10	11	2	2	1	—	353
	♀♀	—	—	—	—	*2*	*21*	*27*	*15*	*17*	*28*	*58*	*145*	*174*	*129*	*64*	*41*	*35*	*35*	*23*	*17*	*7*	*5*	*2*	*1*	—	*846*
III:	♂♂	—	—	—	—	—	—	—	—	—	—	1	—	1	5	7	31	26	25	13	22	5	4	—	—	—	140
	♀♀	—	—	—	—	—	—	—	—	—	—	—	*2*	*4*	*10*	*20*	*52*	*89*	*101*	*101*	*60*	*48*	*11*	*5*	*3*	*1*	*507*
IV:	♂♂	—	—	—	—	—	—	—	—	—	—	—	—	2	5	6	20	29	44	46	39	24	6	13	—	—	234
	♀♀	—	—	—	—	—	—	—	—	*1*	—	—	—	—	*2*	*11*	*38*	*33*	*59*	*69*	*82*	*64*	*34*	*8*	*1*	*1*	*403*
V:	♂♂	—	—	—	—	—	—	—	—	1	—	—	—	2	6	12	34	78	85	87	83	46	12	4	4	1	455
	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	—	*5*	*12*	*43*	*60*	*71*	*82*	*62*	*40*	*25*	*10*	*4*	—	*414*
VI:	♂♂	—	—	—	—	—	—	—	—	—	—	2	1	7	61	106	169	231	191	186	149	69	36	13	—	1	1222
VI A:	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	—	*4*	*10*	*19*	*27*	*42*	*29*	*20*	*15*	*7*	*2*	—	—	*175*
VI B:	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	*2*	*13*	*35*	*72*	*88*	*87*	*70*	*46*	*34*	*23*	*5*	*3*	*2*	*480*
VII:	♂♂	—	—	—	—	—	—	—	—	1	6	17	61	53	64	96	101	131	96	78	46	19	5	1	1	—	776
	♀♀	—	—	—	—	—	—	—	—	*1*	*1*	*10*	*50*	*79*	*80*	*72*	*83*	*95*	*107*	*82*	*68*	*29*	*14*	*2*	*1*	—	*774*
Total fish		339	77	103	101	179	269	207	98	123	233	338	531	622	562	560	778	963	974	886	704	411	184	67	19	6	9334
Total: O, I, False VII		339	77	103	101	176	247	179	83	100	193	241	249	260	127	48	23	7	2	—	—	—	—	—	—	—	
Total II–VII		—	—	—	—	3	22	28	15	23	40	97	282	362	435	512	755	956	972	886	704	411	184	67	19	6	
Percentage II–VII in total fish		*0·0*	*0·0*	*0·0*	*0·0*	*1·68*	*8·18*	*13·53*	*15·31*	*18·69*	*18·45*	*28·70*	*53·11*	*58·20*	*77·40*	*91·43*	*97·04*	*99·27*	*99·79*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	

has its point of inflexion at a length of 28·8 cm. (limits 28·4–29·2) (Text-fig. 3).

Weight-Length Relationship

Weights to the nearest gram of a number of fish covering the whole range of available lengths have been determined. For this purpose fish under 20 cm. in length are arranged in ½ cm. size-groups, measured to the nearest ½ cm. below. Fish over 20 cm. are placed in 1 cm. size-groups, measured to the nearest cm. below. A correction of half a group unit has been added to all mean lengths. The weight-length data so obtained are shown in Table IV. When plotted logarithmically (Text-fig. 4) a definite discontinuity is manifest in the weight-length relationship at 27·9 cm. mean length (with rather wide limits of *c.* 25·7–31·6) and 135 g. mean weight.

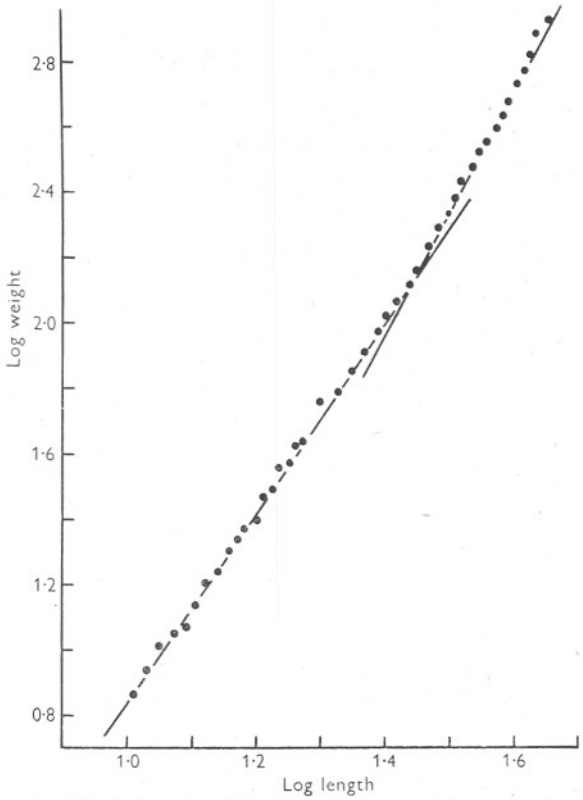


Text-fig. 3. Percentage of all fish examined showing gonad stages II–VII inclusive: in centimetre length-groups.

From 28 cm. down to 10 cm. (the smallest fish weighed) the weight-length relationship is expressed by $W \propto L^{2\cdot86}$. From 28 cm. upwards the weight increases much more rapidly in relation to length and conforms to the expression $W \propto L^{3\cdot54}$. This applies only to fish in the early part of the year when they have recovered from the spent condition and are again actively ripening; comparative figures for newly spent fish have not been obtained.

A change in the weight-length relationship of growing fish appears to manifest itself at a slightly earlier stage than the change in the length-age relationship, but the difference is doubtfully significant, and anyhow the two critical mean lengths are sufficiently close to suggest that both changes may be initiated simultaneously at the onset of first sexual maturity.

Age determination by direct methods has not been possible beyond 6 years. Further researches and improved techniques may increase the range of direct readings—from otoliths, scales or other body structures—by a few years;



Text-fig. 4. Weight-length relationship of mackerel: logarithmic plotting.

Table IV. Weight-length Relationship

Length group (cm.)	No. of fish	Mean weight (g.)	Length group (cm.)	No. of fish	Mean weight (g.)	σ
10·25	7	7	21·5	11	62	4·7
10·75	10	9	22·5	17	72	6·8
11·25	22	10	23·5	25	81	7·8
11·75	21	11	24·5	33	95	8·0
12·25	32	12	25·5	26	105	12·9
12·75	32	14	26·5	18	115	8·6
13·25	38	16	27·5	26	129	9·3
13·75	25	17	28·5	39	146	17·0
14·25	26	20	29·5	49	169	12·0
14·75	32	22	30·5	49	194	14·3
15·25	20	24	31·5	54	217	16·2
15·75	10	25	32·5	60	241	17·7
16·25	14	30	33·5	72	271	23·6
16·75	12	31	34·5	96	300	25·0
17·25	2	37	35·5	77	331	31·7
17·75	5	37	36·5	100	354	35·9
18·25	1	42	37·5	88	392	44·5
18·75	3	43	38·5	67	430	47·0
19·25	—	—	39·5	43	481	34·4
19·75	—	—	40·5	24	542	55·8
20·5	6	58	41·5	8	584	29·1
			42·5	6	669	24·3
			43·4*	3	782	—
			46·1†	1	851	—

Specimens up to 20 cm. in length were weighed all together in their length groups and the mean obtained by a single calculation: σ was therefore not obtained.

* Actual mean (without correction) of fish measured to nearest mm.

† Actual measurement to nearest mm.

but such determinations are unlikely in the foreseeable future to cover the entire life span. It is worth while, therefore, to use the data already available to calculate approximate theoretical mean lengths and mean weights attained by fish in each year of life until a length of 43 cm. is reached—this being the maximum length recorded in this investigation, except for a single fish of 46·1 cm. total length weighing 851 g.

TABLE V. LENGTH AND WEIGHT OF MACKEREL AT DIFFERENT AGES UP TO 20 YEARS: UP TO 6 YEARS FROM DIRECT OBSERVATION, THENCE BY CALCULATION

Age (years) ...	1	2	3	4	5	6	7	8	9	10
Approximate mean length (cm.)	23·8	30·6	33·0	34·1	35·5	36·2	37·1	37·8	38·5	39·1
Approximate mean weight (g.)	80	188	247	278	322	345	381	410	436	462
Age (years) ...	11	12	13	14	15	16	17	18	19	20
Approximate mean length (cm.)	39·7	40·2	40·7	41·1	41·5	41·9	42·3	42·7	43·0	43·4
Approximate mean weight (g.)	486	509	532	553	574	594	614	633	651	669

According to these calculations the single 46·1 cm. fish obtained during these investigations would be 30 years old and should weigh approximately 832 g.

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The investigations described here and in Parts I and II benefited very greatly from abundant help and advice freely given by many persons. Chief amongst them was Skipper B. Moore of the Lowestoft steam drifter 'B.T.B.' (L.T. 1153), who took a keen interest in the work from its inception and on two occasions put his ship at my disposal for special cruises. Other drifter skippers who helped in various ways were E. W. J. Capps (L.T. 89, *Present Friends*), J. R. Capps (L.T. 240, *Justified*), W. A. Capps (L.T. 145, *Silver Prince*), F. Darkins (L.T. 244, *Justifier*), H. Darkins (L.T. 730, *Implacable*), R. Green (Y.H. 497, *Young John*), A. W. Jackson (L.T. 172, *True Reward*), W. G. Jenner (L.T. 89, *Present Friends*), W. C. Julings (L.T. 277, *Oak Apple*), T. Lane (Y.H. 105, *Wydale*), H. Muttett (L.T. 730, *Implacable*), S. Spilling (Y.H. 711, *Harry and Leonard*), W. Thompson, senr. (L.T. 756, *Buckler*), W. Thompson, jun. (L.T. 1217, *Golden Chance*), L. Tooke (L.T. 256, *Welcome Home*), A. R. J. Warner (Y.H. 471, *Ocean Swell*), A. W. Wilkinson (Y.H. 141, *Playmates*), E. J. H. Tallop (L.T. 711, *Lord Fisher*) and Skipper W. H. E. Nicholls of the steam trawler *Elk* (M. 36).

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Summary

Owing to the difficulty of age-determination in mackerel, the age and growth rate of these fish had not previously been satisfactorily determined.

Two schools of thought arose, one attributing a length of little over 10 cm. at the end of the first year of life, while the other ascribed lengths of up to about 25 cm. to 1-year-old fish.

The present investigation supports the second school. Direct age-readings from scales and otoliths have been made of fish up to 6 years of age, and the probable sizes at greater ages have been calculated.

There appears to be a critical change in growth characteristics at a mean length of about 29 cm., coinciding with the first ripening of the genital products.

REFERENCES

Brown Goode, G., 1884. Materials for a history of the mackerel fishery. I. Natural history. *U.S. Comm. Fish and Fisheries, Commissioner's Report for* 1881, pp. 91–138.

Collett, R., 1880. Meddelelser om Norges Fiske i Aarene 1875–78. *Forh. Vidensk.-Selsk., Christiania*, Aar 1879, No. 1, 107 pp.

Cunningham, J. T., 1889. Studies of the reproduction and development of teleostean fishes occurring in the neighbourhood of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. 1, pp. 10–54.

—— 1892. On the rate of growth of some sea fishes, and the age and size at which they begin to breed. *Journ. Mar. Biol. Assoc.*, Vol. 2, pp. 222–64.

—— 1896. *The Natural History of the Marketable Marine Fishes of the British Islands.* 375 pp. London.

Dunn, Matthias, 1893. The mackerel. *Rep. Roy. Cornwall Polytechnic Soc.*, 1893, pp. 1–15.

Dannevig, Alf., 1947. Hvor hurtig vokser makrellyngelen? *Naturen*, Årgang 71, Nr. 3, Mars 1947, pp. 92–4.

—— 1948. Spawning and growth of young mackerel on the Norwegian Skagerak coast. *Journ. Cons. Int. Explor. Mer*, Vol. 15, pp. 218–20.

Ehrenbaum, E., 1923. The mackerel. Spawning—larval and post-larval forms—age groups—food—enemies. *Cons. Int. Explor. Mer, Rapp. Proc.-Verb.*, Vol. 30, 39 pp.

Gourret, M. Paul, 1891. La pêche des mugelières, à Marseille, en 1891. *Ann. Mus. Hist. Nat. Marseille, Trav. Zool. Appliquée*, T. 4, S. 1, année 3, pp. 54–67.

Le Gall, J., 1939. Quelques résultats des recherches faites sur la biologie du maquereau de l'Atlantique. *Cons. Int. Explor. Mer, Rapp. Proc.-Verb.*, Vol. 111 (*Rapp. Atlantique* 1937–38), pp. 13–14.

—— 1950. Maquereau (*Scomber scombrus* Linné). Observations faites en 1949 sur sa biologie. *Cons. Int. Explor. Mer, Ann. Biol.*, Vol. 6, pp. 70–1.

JENSEN, AAGE J. C., 1950. Changes in the quality of the herring in the course of the year and from year to year. *Rept. Danish Biol. Stn*, No. 51, pp. 3–17.

MALM, A. W., 1877. *Göteborg och Bohusläns fauna, Ryggradsdjuren*. Göteborg.

MARION, M. A.-F., 1889. Remarques relatives au maquereau des côtes Mediterranéennes. *Ann. Mus. Hist. Nat. Marseille, Trav. Zool. Appliquée*, T. 3, S. 1, année 1, pp. 83–7.

NILSSON, D., 1914. A contribution to the biology of the mackerel. *Cons. Int. Explor. Mer, Publ. Circon.*, No. 69, 59 pp.

SETTE, OSCAR ELTON, 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. I. Early life history, including the growth, drift, and mortality of the egg and larval populations. *Bull. Fish & Wildlife Service, U.S. Dept. Interior*, Vol. 50, pp. 149–237 (Fishery Bulletin No. 38).

—— 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. II. Migrations and habits. *Bull. Fish. & Wildlife Service, U.S. Dept. Interior*, Vol. 51, pp. 249–358 (Fishery Bulletin No. 49).

STEVEN, G. A., 1948. Contributions to the biology of the mackerel, *Scomber scombrus* L. Mackerel migrations in the English Channel and Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 27, pp. 517–39.

—— 1949. Contributions to the biology of the mackerel, *Scomber scombrus* L. II. A study of the fishery in the south-west of England, with special reference to spawning, feeding and 'fishermen's signs'. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 555–81.

STEVEN, G. A. & CORBIN, P. G., 1939. Mackerel investigation at Plymouth. Preliminary report. *Cons. Int. Explor. Mer, Rapp. Proc-Verb.*, Vol. 111 (*Rapp. Atlantique* 1937–38), pp. 15–18.

EXPLANATION OF PLATE I

Fig. 1. Mackerel scale showing one ring and two zones: × 55. From a fish 28 cm. in length, 9 October 1936.

Fig. 2. Mackerel scale showing two rings and three zones: × 44·3. From a fish 33 cm. in length, 8 June 1937.

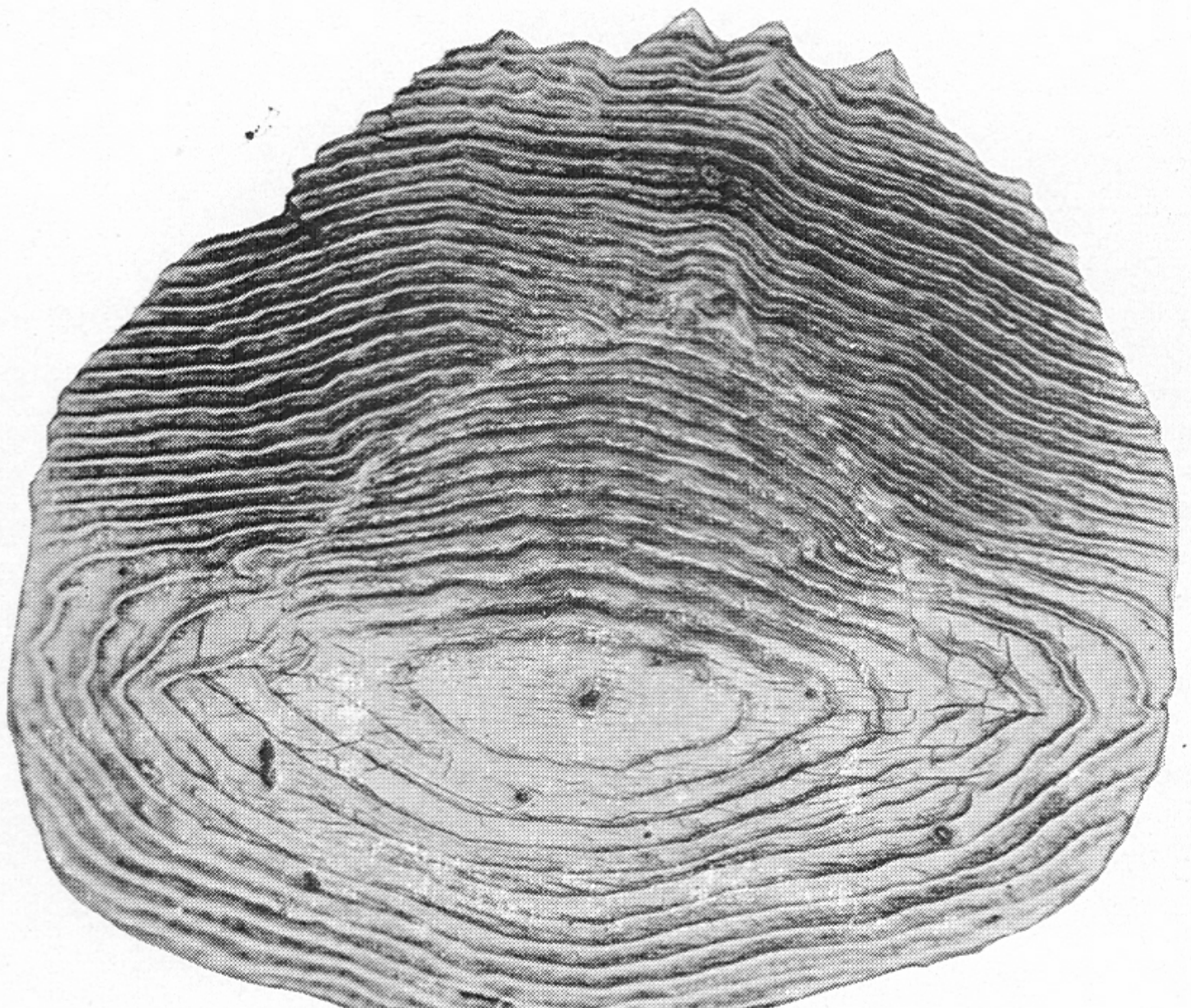
Fig. 3. Mackerel scale showing three rings and four zones: × 48·5. From a fish 34 cm. in length, 24 September 1936.

Fig. 4. Otolith showing one ring and two zones: × 12·8. From a fish 29 cm. in length, 22 September 1936.

Fig. 5. Otolith showing two rings and three zones: × 12·4. From a fish 33 cm. in length, 23 July 1936.

Fig. 6. Otolith showing three rings and four zones: × 12·05. From a fish 34 cm. in length, 22 September 1936.

The illustrations in this plate are all from un-retouched photographs.



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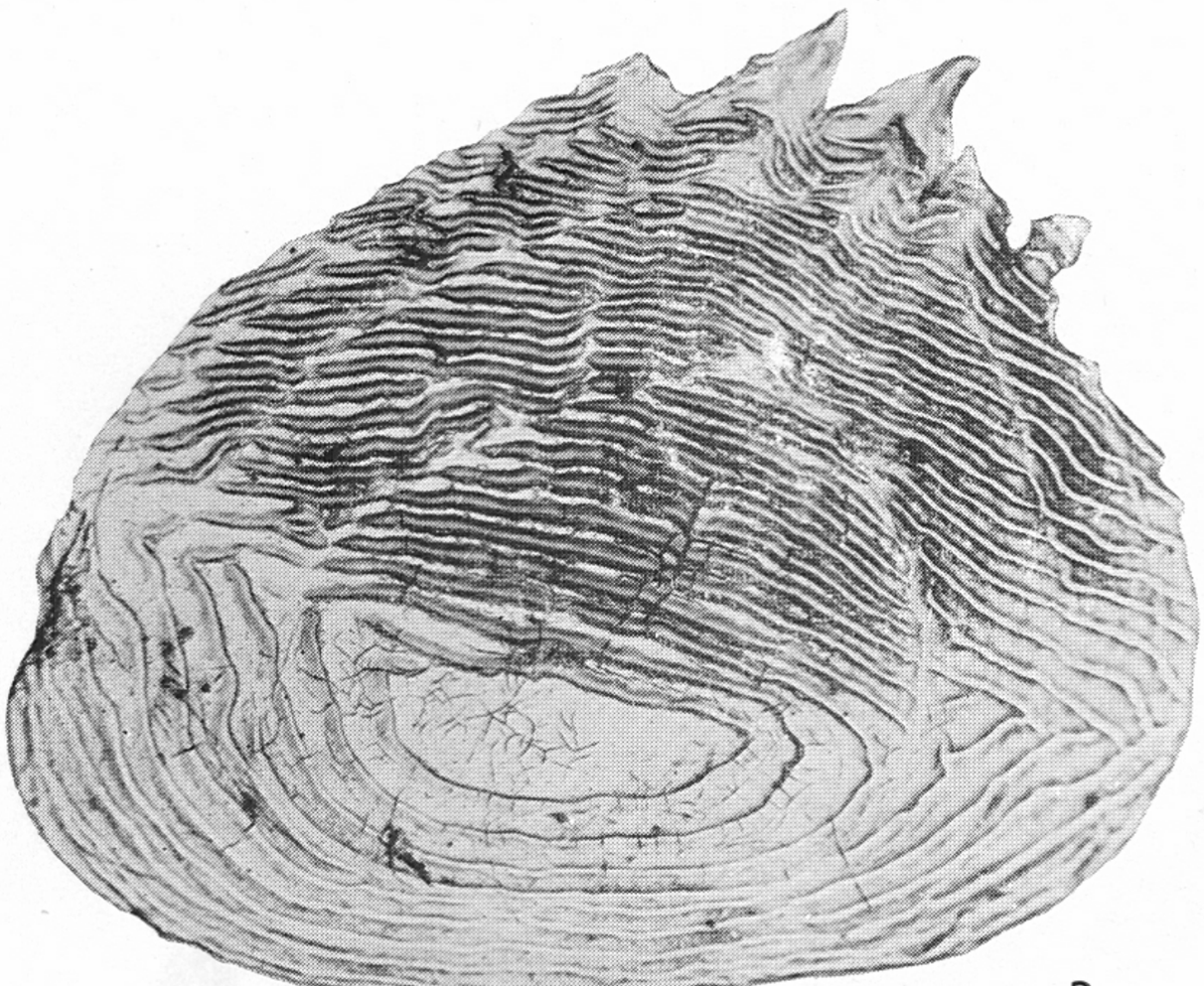

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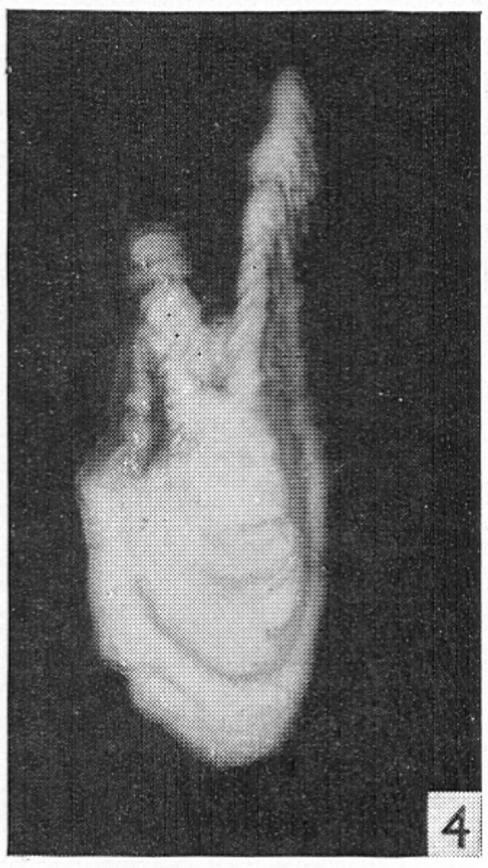

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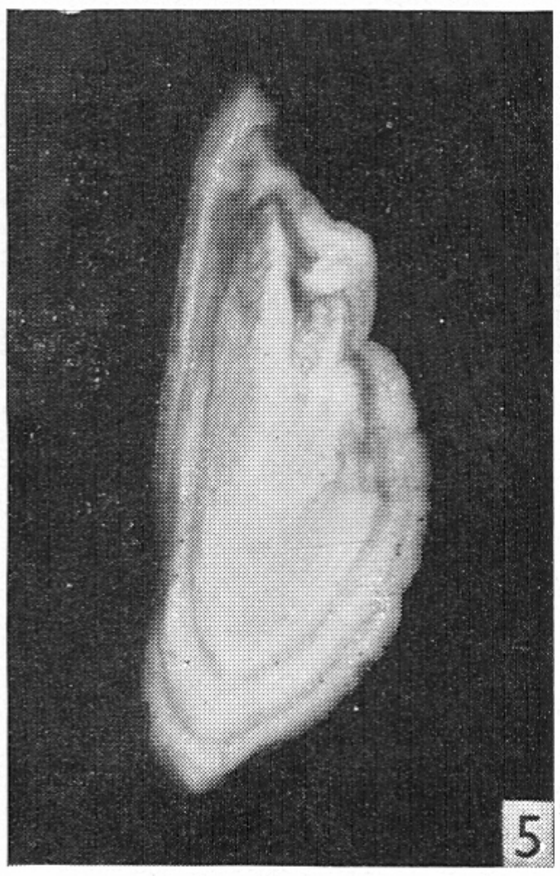

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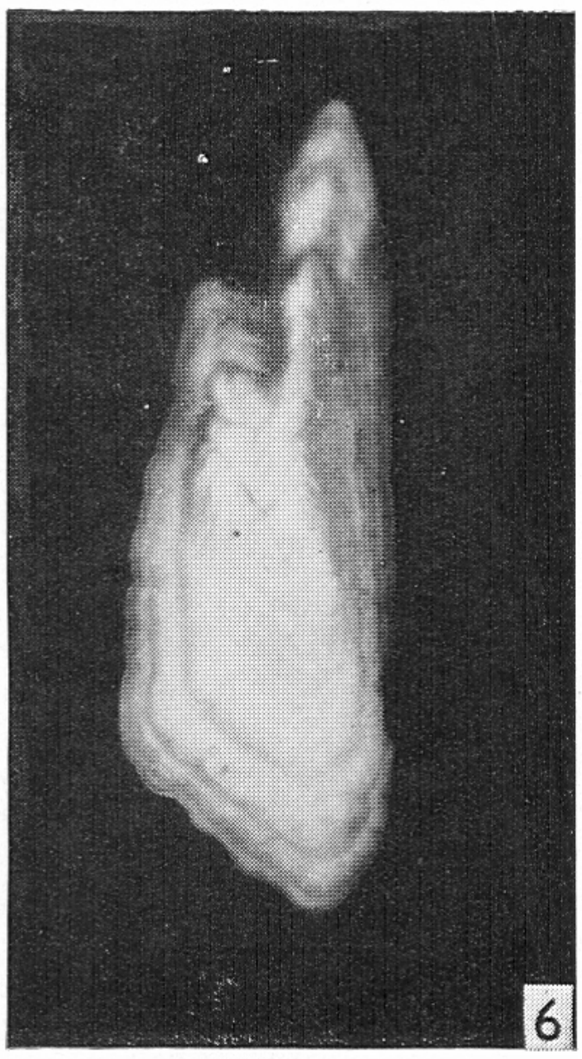

6

THE BIOLOGY OF *ASTERIAS RUBENS* L. III. CAROTENOID PIGMENTS IN THE INTEGUMENT

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

In the Plymouth area there is often a marked and consistent difference in coloration of starfishes (*Asterias rubens*) from different populations. Starfish from populations to the south of Plymouth Breakwater are red-brown or occasionally pale yellow-brown in colour, whereas those from a population living well within Plymouth Sound have been found to be consistently bright red or brick red in colour (Vevers, 1949). In the present work analysis has been made of the integumentary carotenoids of dark red-brown *A. rubens* taken from the trawling grounds between Plymouth Breakwater and the Eddystone.

The asteroids are usually richly coloured, and investigation of a number of species has shown the almost universal occurrence of carotenoid pigments in the integument. In addition to the carotenoids, MacMunn (1886), working at the Plymouth Laboratory, extracted a porphyrin pigment which he identified as haematoporphyrin from the integument of *A. rubens*. It is now known that haematoporphyrin does not occur in nature, and a re-examination of the porphyrin pigments of this species is in course of preparation (Kennedy & Vevers).

Cuénot (1887) observed that the integument of starfishes consists of three distinct layers: the internal epithelium, which lines the general body cavity and which is not concerned with the external pigmentation of the animal, a median conjunctive layer, in the outer part of which the calcareous plates are deposited, and an external epithelium of tall, elongated cells, covered by a cuticle, through which the cilia protrude. The external epithelial cells with the cuticle make up the epidermis. The majority of the epidermal cells are narrow and columnar, with their inner ends resting on a basement membrane which divides the epidermis from the median conjunctive layer (Ludwig & Hamann, 1899). Scattered among these more generalized epidermal cells are two types of more specialized cells, the mucus gland cells, which are particularly frequent in *A. rubens*, and the mulberry cells, first described by Cuénot (1887) and of unknown function.

Ludwig & Hamann (1899) stated that, in general, the integumentary pigments of starfishes are deposited in the epidermal layer. Cuénot (1887) found that in *Echinaster sepositus* a red pigment was deposited in the epidermis, and in the present work it was found that most of the carotenoid pigment of the integument is contained in the unspecialized columnar epithelial cells. There are no special chromatophores.

Carotenoid Pigments in the Integument

Abeloos (1926) observed that the carotenoids in the integument of *Asterias rubens* were sometimes present in the form of complexes produced by the conjugation of a carotenoid with a protein radical. Lönnberg (1931, 1933, 1934) extracted carotenoids from a large number of marine invertebrates, including *A. rubens*. In most he was able to partition the crude extracts into an epiphase (in petroleum ether) and a hypophase (in 90 % methanol). He did not, however, use any chromatographic adsorption technique for the separation of the pigments, and in general his results only indicated that at least one and probably two carotenoid pigments were present in the integument of *A. rubens*.

Von Euler & Hellström (1934) isolated a carotenoid acid from the aboral integument of *A. rubens*, which they named 'Asterinsäure'. Karrer and Rübel (Karrer & Jucker, 1948, p. 351) subsequently obtained a yield of astacene from this species, and Karrer & Jucker (1948, p. 351) now consider that 'Asterinsäure' is probably identical with astacene (or astaxanthin).

Experimental

In the present work on the separation of the integumentary carotenoids only dark red-brown specimens of *A. rubens* were used. For analysis by Methods 1 and 2, aboral integument was finely chopped and ground up with dry acid-washed silver sand (the sand was washed with HCl, and then with three changes of water before being dried). The integument was then extracted with successive portions of acetone, until no further colour appeared in the extract. Petroleum ether (b.p. 40–60° C.) was added to the acetone extract, and the volume of the whole extract was doubled by addition of distilled water. After gentle shaking, the pigment passed from the acetone-water fraction to the petroleum ether, which was dried by shaking with anhydrous sodium sulphate. The petroleum-ether extract of the total carotenoids was then divided into two parts for further analysis by either Method 1 or Method 2.

Method 1. The petroleum-ether extract was chromatographed on bone meal (B.D.H. bone meal for carotene estimations). Continued elution with petroleum ether removed Fraction 1*a*, which was then passed through a column of alumina (B.D.H. aluminium oxide for chromatographic adsorption analysis) on which it formed two bands. The lower band was removed by elution with more petroleum ether and collected separately as Fraction 1*b*, and the upper band, which was the richest in colour, was eluted by petroleum ether containing 5 % (v/v) of acetone to give Fraction 1*c*. The pigment remaining on the bone meal column was eluted by acetone and collected as a pale straw-yellow solution (Fraction 1*d*).

Fraction 1*b* was divided into two parts and each was separately evaporated

almost to dryness over a water-bath, the final traces of liquid being removed in a stream of carbon dioxide. The residues were dissolved in carbon disulphide and petroleum ether respectively. Absorption spectra (Table I) of each of these solutions were recorded with a 'Unicam S.P. 500 Quartz Spectrophotometer'. The absorption maximum obtained for the solution in carbon disulphide is identical with that recorded by Karrer & Jucker (1948) for β-carotene. The absorption maximum for the solution in petroleum ether is very close to that obtained for β-carotene by Morton & Rosen (1949).

In order to confirm that Fraction 1*b* was β-carotene a mixed chromatogram was used. The petroleum-ether solution of the pigment was mixed with a solution of known β-carotene in the same solvent and the mixture chromatographed on a long column (15 × 1 cm.) of alumina. A single band was formed which did not split on slow elution with petroleum ether.

TABLE I. ABSORPTION MAXIMA OF CAROTENOID FRACTIONS IN Mμ

Fraction	Carbon disulphide	Pyridine	Petroleum ether
1*b*	485	—	449
1*c*	503	489	—
2*b*	485	—	449
2*c*	509	497–502	—

Fraction 1*c*, which was also epiphasic, was divided into two parts, each of which was evaporated to dryness and the residues dissolved in carbon disulphide and pyridine respectively. This fraction gave strong, well-coloured solutions, and spectrophotometer readings gave the absorption maxima recorded in Table I.

These maxima agree very closely with those given by Goodwin & Srisukh (1949) for esterified astaxanthin. This agreement, together with the fact that Fraction 1*c* was always epiphasic when shaken with a mixture of petroleum ether and 90 % methanol, leaves no doubt that the pigment in this fraction was esterified astaxanthin. It should be noted that the esterified astaxanthin (Fraction 1*c*) originally formed part of Fraction 1*a*, which was eluted from the bone-meal column with petroleum ether. This elution is similar to the experience of Morton & Rosen (1949), who found that esterified 'xanthophyll' was sometimes carried through a bone-meal column with light petroleum.

Fraction 1*d* was collected from the bone-meal column by elution with acetone. It was taken into petroleum ether and partitioned between this solvent and 90 % methanol. The pigment was found to be entirely hypophasic, suggesting the free forms of xanthophylls. From this solution it was taken back into petroleum ether, evaporated to dryness and dissolved in benzene. The benzene solution was chromatographed on zinc carbonate, and a single band formed which was eluted with ether containing 3 % methanol (v/v). The yield from this fraction was never sufficient to give a good sample for spectrophotometric measurement, but its behaviour on phase partition and

chromatography suggested that it contained one pigment only of the free xanthophyll type, possibly lutein or zeaxanthin.

Method 2. The remainder of the total carotenoid extract was partitioned between petroleum ether and 90 % methanol to give an epiphasic fraction (2*a*) and a hypophasic fraction (2*d*) respectively. Fraction 2*a* contained nearly all the pigment. It was evaporated to dryness slowly on a water-bath, the final traces of solvent being removed in a stream of CO_2. To the residue were added 2 ml. ethanol and 1 ml. of KOH (concentration of 160 g. KOH in 106 ml. H_2O), and this saponification mixture was heated and kept just bubbling for 3 min. The residue was cooled by adding distilled water and then extracted with ethyl ether. Some of the pigment passed into the ether but most remained in the lower layer of aqueous ethanolic KOH. On addition of a few drops of glacial acetic acid, followed by gentle shaking, all the pigment passed into the ether. (It is characteristic of astacene that it remains hypophasic in alkaline solution, even in the presence of excess water.) The ether extract was then evaporated to dryness and dissolved in petroleum ether. On addition of an equal volume of 90 % methanol partition took place to give an epiphase (Fraction 2*b*) and a hypophase (Fraction 2*c*).

Fraction 2*b* was dried over anhydrous sodium sulphate, and chromatographed on a column of alumina. Slow elution with the solvent failed to split the single band of pigment which was finally collected in a flask. This fraction was then examined in the spectrophotometer in CS_2 and in petroleum ether, and the maxima recorded were the same as those for β-carotene in Fraction 1*b* above.

Fraction 2*c* was taken from 90 % methanol into petroleum ether, and divided into two parts each of which was evaporated to dryness over a water-bath. The residues were dissolved in CS_2 and pyridine respectively and recordings made of the absorption spectra (Table I).

The positions of these maxima (cf. Karrer & Jucker, 1948, p. 242) and the behaviour of this fraction after saponification suggest that the pigment was astacene. Kuhn & Sörensen (1938) have shown that astacene does not occur naturally, but is produced in the course of saponification by the oxidation of astaxanthin. As the fraction from which the present yield of astacene was derived was originally epiphasic, it is probable that it was present in the integument in the form of esterified astaxanthin. This would agree with the finding of esterified astaxanthin in Fraction 1*c*.

Fraction 2*d* was very faint in colour. It was treated in the same way as Fraction 1*d*, and behaved the same way on chromatography. It probably represents the small amount of free xanthophyll found in Fraction 1*d*.

As a further check on the identity of the carotenoid pigments, and in order to test for the existence of a carotenoid-protein complex, a third system of extraction was used (Method 3).

Method 3. The integument was ground up with silver sand and extracted

in the first place with *n*-hexane to remove all the carotenoids which were not bound to a protein. This gave Fraction 3*a*. The residue of tissue was then extracted with acetone to give Fraction 3*b*.

Fraction 3*a* was relatively pale in colour. By means of phase partition and chromatography it gave weak solutions of β-carotene, esterified astaxanthin, and a free xanthophyll.

Fraction 3*b* was strong in colour and contained the greater part of the integumentary carotenoid pigment. It was entirely epiphasic and was found to contain esterified astaxanthin only. There was no evidence that β-carotene occurred in this fraction.

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Discussion

It is probable that the carotenoid pigments extracted from *A. rubens* by Lönnberg were not always fully separated into their constituents prior to spectroscopic determination. The presence of astaxanthin in this species was first noted by Karrer and Rübel. This has been confirmed in the present work, and it has also been found that in the integument it is present in the esterified form. The astaxanthin found in *A. rubens* is very closely comparable with that extracted from the hypodermis of *Homarus vulgaris* and *Nephrops norvegicus* by Goodwin & Srisukh (1949), and there is no doubt that, from the point of view of colour production, it is the most important of the integumentary carotenoids in *A. rubens*. In the dark-brown specimens of *A. rubens* used in the present investigation the greater part of the esterified astaxanthin is linked with a protein. This is similar to the condition found in the carapace and eggs of *Astacus gammarus* by Kuhn & Sörensen (1938). Carotenoids have also been extracted from a number of Pacific Coast echinoderms, including four species of asteroids, by Fox & Scheer (1941), but the yields were usually from the whole body, and so are not strictly comparable with the present results. They did, however, find that one of the predominant carotenoids in the asteroids was astaxanthin, but they did not record any protein linkage.

Summary

A preliminary analysis of the integument of dark-brown specimens of *Asterias rubens* has shown that the carotenoid pigments present are astaxanthin, β-carotene and a free xanthophyll. The last two occur only in small amounts. The astaxanthin is present in the esterified form, and represents the greater part of the total carotenoids.

Most of the astaxanthin is present in the form of an astaxanthin-protein complex, which is coloured brown or dark brown in the living animal.

REFERENCES

ABELOOS, M., 1926. Sur les pigments tégumentaires des Astéries. *C.R. Soc. Biol., Paris*, T. 94, pp. 19–21.

CUÉNOT, L., 1887. Contribution à l'étude anatomique des Astérides. *Arch. Zool. exp. gén.*, T. 5, *bis* suppl., 2e Mém., 144 pp.

EULER, H. VON & HELLSTRÖM, H., 1934. Ueber Asterinsäure, eine Carotinoidsäure aus Seesternen. *Z. physiol. Chemie*, Bd. 223, pp. 89–97.

FOX, D. L. & SCHEER, B. T., 1941. Comparative studies of the pigments of some Pacific coast echinoderms. *Biol. Bull. Woods Hole*, Vol. 80, pp. 441–53.

GOODWIN, T. W. & SRISUKH, S., 1949. Some observations on astaxanthin distribution in marine Crustacea. *Biochem. Journ.*, Vol. 45, pp. 268–70.

KARRER, P. & JUCKER, E., 1948. *Carotinoide*. Basel.

KUHN, R. & SÖRENSEN, N. A., 1938. Ueber Astaxanthin und Ovoverdin. *Ber. dtsch. chem. Ges.*, Bd. 71, p. 1879.

LÖNNBERG, E., 1931. Untersuchungen über das Vorkommen carotinoider Stoffe bei marinen Evertebraten. *Ark. Zool.*, Bd. 22, A 14, 49 pp.

—— 1933. Zur Kenntnis der Carotinoide bei marinen Evertebraten. *Ark. Zool.*, Bd. 25, A 1, 17 pp.

—— 1934. Weitere Beiträge zur Kenntnis der Carotinoide der marinen Evertebraten. *Ark. Zool.*, Bd. 26, A 7, 36 pp.

LUDWIG, H. & HAMANN, O., 1899. Echinodermen (Stachelhäuter). Die Seesterne. *Bronn's Klassen u. Ordnungen des Thierreiches*, Bd. 2, Abt. 3, Buch II.

MACMUNN, C. A., 1886. On the presence of haematoporphyrin in the integument of certain invertebrates. *Journ. Physiol.*, Vol. 7, pp. 240–52.

MORTON, R. A. & ROSEN, D. G., 1949. Carotenoids, vitamin A, and 7-dehydrosteroid in the frog (*Rana temporaria*). *Biochem. Journ.*, Vol. 45, pp. 612–27.

VEVERS, H. G., 1949. The biology of *Asterias rubens* L.: growth and reproduction. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 165–87.

TRACE ELEMENTS IN THE COMMON BROWN ALGAE AND IN SEA WATER

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Introduction

Sea water probably contains all the chemical elements, although a number of them have not yet been detected. Considerable information is available on the occurrence of various elements in marine plants and animals, but it is far from complete for any one biological group. Except for recent work by Spooner (1949), on the absorption of radioactive strontium and yttrium by marine algae, no detailed study of the trace elements in the brown algae, nor any attempt to correlate the trace elements in sea water with those in the algae, appears to have been carried out. The following is a brief résumé of the work that has been done in this field.

The distribution and concentration of iodine in the sea have received a great deal of attention because of their important roles in the physiology of man and terrestrial animals. The form in which iodine occurs in sea water is not clearly understood, but part of it is present as iodide and iodate. It is concentrated to a marked degree by the marine algae, and for many years the Phaeophyceae were used as a commercial source of iodine. The concentration of iodine and its seasonal variation in the brown marine algae have already been reported (Black, 1948*a*, *b*, 1949).

Considerable interest has recently been shown in the content of radioactive elements in sea water. Studies by Evans, Kip & Moberg (1938), and by Föyn, Karlik, Pettersson & Rona (1939), have shown that the radium content measured by the radon emanation technique varies between about 0·2 and $3{\cdot}0 \times 10^{-7}$ μg./l. in sea water of salinity approximately 35‰. These workers found that organisms concentrate the radium about one-hundredfold in their soft tissues, and calcareous structures show an increase in the radium : calcium ratio over that in the water. In a search for the radioactive precursors of radium, Karlik analysed a number of samples from various parts of the oceans and obtained a mean value of 1·5 μg./l. for uranium (Föyn *et al.* 1939).

Tables giving the trace elements which have so far been determined in sea water have been compiled by Sverdrup, Johnson & Fleming (1942, pp. 176–7), Harvey (1945, pp. 31–2), and Legendre (1947).

In 1919, Cornec carried out the first spectrographic analysis of marine plants and found the following elements: Ag, As, Co, Cu, Mn, Ni, Zn, Bi, Sn, Ca, Mo, Au, Sb, Ti, W and U. The analysis, however, was qualitative and the species investigated were not given.

The distribution of arsenic in marine algae has been studied by Jones (1922), and by Williams & Whetstone (1940). Jones determined the arsenic content of eleven varieties of British seaweeds and obtained a value of 125 mg./kg. for *Laminaria digitata*.

The titanium in a number of cryptogamic plants has been estimated by Bertrand & Voronca-Spirt (1930), while Meulen (1932) determined molybdenum in several species of algae and reported a figure of 0·16 mg. Mo/kg. dry weight.

Webb (1937), in his studies on the ultimate composition of biological material, carried out a spectrographic analysis of marine invertebrates and included the three algae, *Ulva lactuca* (frond), *Fucus serratus* (receptacles) and *Saccorhiza bulbosa* (stipes). Figures are given for Na, K, Ca, Mg, Sr, Ba, B, Al, Mn, Fe, Cu and Pb.

In 1938, Igelsrud, Thompson & Zwicker found the boron content of five marine algae to be 4·2–14·9 mg. B/kg. dry material, and Lagrange & Tchakirian (1939) examined *Lithothamnium* and detected spectrographically in the ash, apart from ordinary constituents, Ag, As, Be, Cu, Ge, Mn, Mo, Ni, Pb, Sb, Sn, Ti, U, W and Zn. The rare earths in similar algae have been examined by Servigne & Tchakirian (1939), who analysed the ashes of *L. calcareum* and found about 5 mg./kg. of Pr, Nd and Sm.

The radium content of a number of algae has been determined by Wiesner (1938). Seven fresh-water and sixteen salt-water algae from different localities were examined, and the results indicated considerable accumulation of radium by the plants.

In 1940, Öy discussed the physiological importance of iron, copper, manganese and boron, and determined these elements in several species of algae. Iron varied between 120 and 1330 mg./kg. dry matter, while *Ascophyllum nodosum* contained 1·1–1·4 mg./kg. copper, *Laminaria* 4 mg./kg., *Fucus serratus* 5·8–17·4 and *F. vesiculosus* 3·4–8·4 mg./kg. Manganese was present in the Fucaceae to the extent of 100–130 mg./kg., and boron 100 mg./kg.

A spectrographic analysis of a dried seaweed meal carried out by the Macaulay Institute for Soil Research was reported by Beharrell in 1942; and in 1941 Wilson & Fieldes estimated spectrographically eighteen of the minor elements of *Macrocystis pyrifera*. No further work appears to have been carried out since that time.

Experimental

With the exception of *Laminaria cloustoni*, which was collected at Cullipool, Luing Island, Argyllshire, and one sample of *L. digitata* from Ardencaple

Bay, Seil Island, Argyllshire, all the samples of algae were collected at Atlantic Bridge, which joins the Island of Seil with the mainland of Scotland.

Immediately after collection the samples were air-dried at 25–30° C. for 48 hr., with every precaution taken to prevent metallic contamination and, with the exception of the last two sets of samples, were milled in a small porcelain-edge runner mill. With the later samples, however, the milling was carried out in a Christy and Norris no. 8 laboratory mill.

The sea-water samples were collected 20 miles off Plymouth[1] at 20 m., and from $\frac{1}{2}$ m. at Atlantic Bridge and Ardencaple Bay. In the first series of experiments the samples of sea water were stored both in Pyrex and Polythene bottles, but the analyses were identical, thereby indicating that no difference in composition has resulted from diatoms adhering to the glass surface or from the straight surface adsorption of trace elements on the glass. Pyrex bottles were therefore used for the remainder of the samples.

In Table I, the washed frond of *L. digitata* was obtained by soaking the whole frond in 5 gallons of ordinary tap water for 24 hr., prior to air-drying and milling.

Analytical Methods Used

The trace-element analyses reported in this paper were carried out at the Macaulay Institute for Soil Research by a cathode layer arc spectrochemical technique, differing only in detail from that employed for plant materials (Mitchell, 1948). For a few elements semi-quantitative assessments only were made, but unless specifically indicated the results were obtained by a quantitative technique: directly on the ashed material (Farmer, 1950) for Cu, Ba, Sr, Mn, and by a method involving chemical concentration prior to spectrographic analysis (Mitchell & Scott, 1948) for Co, Ni, Mo, Fe, Pb, Sn, Zn, V, Ti, Cr and Ag. Even after concentration of the 100-fold order one or two of the elements reported, notably Sn, Ag, and in a few instances Pb, are close to the lower limit of determination, and these results may be somewhat less reliable than those for the other elements.

Discussion of Results

As with the major constituents of seaweed the results indicate that the content of trace elements depends on the species and on the stage of development, and that there is probably appreciable seasonal variation.

[1] The following determinations have been made on the 20 m. sample collected off Plymouth:

	Determination	Observer or analyst
Temperature	9·28° C.	Mr F. A. J. Armstrong
Salinity	35·12 ‰	Government chemist
Inorganic phosphate	16·0 μg./l. P	Mr F. A. J. Armstrong
Total phosphorus	19·2 μg./l. P	Mr F. A. J. Armstrong

No doubt some variation will occur in different habitats, where natural deposits and land drainage may influence the trace elements in the inshore waters where the algae are growing, but this has not been investigated.

It has already been shown (Black, 1948*a*, *b*, 1949) that iodine varies considerably in the different species and even in the same species, showing a progressive increase with the depth of immersion of the plant, increasing, for example, from 0·03% (dry basis) in *Pelvetia canaliculata* and *Fucus spiralis* to over 1% in *Laminaria cloustoni*. Although the seasonal variation is somewhat erratic, the iodine, which exists both in the organic and inorganic form,

TABLE I. TRACE-ELEMENT CONTENTS OF *LAMINARIA* FRONDS IN MG./KG. OVEN-DRIED MATERIAL

	Laminaria digitata frond. Collected July 1948, unwashed	*Laminaria digitata* frond. Collected July 1948, washed	*Laminaria cloustoni* frond. Collected Oct. 1947, unwashed
Total ash (% of dry matter) ...	24·2	11·8	13·8
Estimations quantitative			
Co	0·21	0·31	0·21
Ni	1·7	1·40	0·9
Mo	0·16	0·21	0·16
Pb	—	20	13
Sn	3·8	1·0	1·0
Zn	148	93	59
V	0·4	1·9	1·1
Ti	3	52	21
Cr	1·5	1·8	0·9
Ag	0·2	0·2	0·2
Fe	292	402	314
Estimations semi-quantitative			
Cu	120	70	30
Rb	25	80	30
Li	1	4	2
Ba	80	100	30
Sr	400	800	400
Mn	12	30	15

is generally at a maximum when the total ash and crude proteins are at a maximum. With the trace elements the reverse is true. In general, the trace elements are higher in May than in January and there appears to be no correlation between the trace-element content and the total mineral matter. If the phenomenon of trace-element concentration is one of ion exchange (Wassermann, 1949), it is reasonable to find that the concentration varies with the stage of development of the plant. The stipe which is perennial is consequently higher in these elements than the frond. It may also be, however, that the trace elements in the frond are utilized in sporogenesis, etc. It is interesting to find, therefore, that many of the trace elements such as Co, Ni, Mo, Fe, etc. (Table II), which may be essential for reproduction, are lower in a sporing than in a sterile frond.

Soaking a fresh *Laminaria* frond in water, although it removes a considerable amount of the water soluble mineral matter presumably in solution in the cell sap, does not remove the trace elements, which appear, therefore, to be in an insoluble form, possibly adsorbed on the colloids present, or combined with the polysaccharides such as alginic acid or fucoidin (Table I).

Samples of the various species collected in January 1949 (Table II) show considerable variation in trace-element contents, and *Fucus serratus* appears to be exceptional in concentrating iron to 717 mg./kg. and manganese to 800 mg./kg.

A comparison of the trace elements in a sporing and non-sporing frond of *Laminaria cloustoni* shows slight differences, and it may be, therefore, that the trace elements are utilized to some extent in reproduction.

A further set of samples taken in May 1949 shows that on the anhydrous basis the trace elements undergo quite appreciable seasonal variation. Despite the fact that the total ash has decreased the trace-element content shows considerable increases (Table III), e.g. in *Pelvetia canaliculata* nickel increases from 1·9, iron from 195, and titanium from 11·4 mg./kg. in January 1949, to 3·7, 565 and 37·8 mg./kg. respectively in May.

The samples taken in June 1950 (Table IV) differ quite appreciably from those taken in May 1949 (Table III). With the exception of *Fucus serratus*, the iron content, for example, is considerably higher in the 1950 samples, but this might be due to metal contamination, as the 1950 samples were milled in a C. and N. Mill, while the others were ground in a porcelain-edge runner mill.

The results in Table IV again show the differences which occur in the trace-element content of different species from the same habitat, with *F. spiralis* unaccountably high in most of the trace elements, for example, 308 mg./kg. of titanium as compared with 4 mg./kg. in *Laminaria digitata* frond. At this time of the year the dry-weight content of *Fucus spiralis* is very low, the plant having taken in large volumes of water preparatory to shedding its gametes. This is further evidence of a correlation which may exist between the trace-element content and the reproductive cycle of the plant. Even when the results are calculated on the wet basis (Table V) *F. spiralis* still contains higher concentrations of the trace elements, particularly titanium and iron, than the Laminariaceae.

Despite the fact that one of the samples of sea water was taken in February, 20 miles off Plymouth at a depth of 20 m., and the other from inshore waters at Ardencaple Bay and Atlantic Bridge in June, the differences in the trace elements estimated are quite insignificant, but the contents are higher than those recorded in the literature (Table VI).

In Table VII the 'concentration factor' shows the extent to which marine algae can concentrate the trace elements, *F. spiralis* containing 10,000 times more titanium than the surrounding sea water, although the majority of the factors are smaller.

TABLE II. TRACE-ELEMENT CONTENTS OF OVEN-DRIED SEAWEEDS (COLLECTED 12 JANUARY 1949) IN MG./KG.

Sample	Total ash (% of dry matter)	Co	Ni	Mo	Fe	Pb	Sn	Zn	V	Ti	Cr	Ag	Rb	Li	Sr	Ba	Mn	Cu
Pelvetia canaliculata	24·6	0·37	1·9	0·34	195	4	0·8	40	1·2	11	0·6	0·2	100	6	>2400	70	70	5
Ascophyllum nodosum	27·2	0·41	1·5	0·69	168	6	1·0	103	1·9	9	0·7	0·3	80	4	2600	50	50	4
Fucus serratus	27·4	0·47	1·6	0·40	717	21	1·2	79	3·3	9	2·6	0·6	170	6	>2800	80	800	11
Laminaria digitata frond	41·5	1·46	8·2	0·32	350	13	0·7	99	2·0	20	1·1	0·4	240	8	4000	120	80	20
L. digitata stipe	39·7	0·43	3·2	0·15	N.d.	N.d.	N.d.	N.d.	2·2	16	1·4	0·2	240	4	4000	60	100	16
L. cloustoni frond, sterile	32·4	0·56	2·0	0·50	283	10	0·7	117	1·3	19	1·2	0·7	250	6	3000	60	30	—
L. cloustoni frond, sporing	22·4	0·35	1·5	0·24	226	26	1·0	136	1·0	20	1·2	0·5	130	4	2200	65	30	15

TABLE III. TRACE-ELEMENT CONTENTS OF OVEN-DRIED SEAWEEDS (COLLECTED 26 MAY 1949) IN MG./KG.

Sample	Total ash (% of dry matter)	Co	Ni	Mo	Fe	Pb	Sn	Zn	V	Ti	Cr	Ag	Sr	Ba	Mn	Cu
Pelvetia canaliculata	21·64	0·72	3·7	0·35	565	5	1·3	47	2·6	38	1·2	0·2	>700	20	22	5
Fucus spiralis	24·34	1·39	6·0	0·29	638	5	1·8	62	1·9	27	0·9	0·2	>700	19	104	6
Ascophyllum nodosum	19·49	0·73	4·4	0·29	283	4	0·7	60	1·5	26	1·0	0·2	>700	13	27	4
F. serratus	21·77	0·84	3·2	0·65	375	10	1·3	70	2·0	20	0·7	0·3	>700	22	155	5
F. vesiculosus	23·97	0·65	3·8	0·34	221	2	0·5	60	1·9	28	1·8	0·2	>700	44	116	7
Laminaria digitata frond	31·84	0·29	2·4	0·19	138	2	1·0	64	0·6	5	0·4	0·3	>700	13	9	<3
L. digitata stipe	—	0·92	3·9	0·10	293	6	1·7	62	0·3	2	0·4	0·4	>700	15	10	5
L. cloustoni frond	32·16	0·25	1·6	0·14	159	12	1·4	76	0·9	10	1·5	0·3	>700	31	10	14

TABLE IV. TRACE-ELEMENT CONTENTS OF OVEN-DRIED SEAWEEDS (COLLECTED 27 JUNE 1950) IN MG./KG.

Sample	Total ash (% of dry matter)	Co	Ni	Mo	Fe	Pb	Sn	Zn	V	Ti	Cr	Ag	Sr	Ba	Mn	Cu
Pelvetia canaliculata	23·3	1·30	4·8	0·55	2040	13	2·2	90	3·2	60	1·2	0·3	720	34	51	16
Fucus spiralis	22·8	2·00	9·3	1·32	3380	5	N.d.	N.d.	11·9	308	3·7	0·4	420	64	121	31
Ascophyllum nodosum	20·4	0·73	3·7	0·89	1150	4	1·1	116	2·8	28	1·9	0·1	570	18	36	12
F. vesiculosus	19·5	0·91	5·9	0·34	730	7	1·1	105	1·7	27	1·5	0·2	730	22	102	10
F. serratus	18·0	0·63	4·5	0·21	320	4	0·5	63	0·6	7	0·7	0·2	520	16	120	6
Laminaria digitata frond	26·2	0·31	1·8	0·16	400	7	0·6	59	0·5	4	1·1	0·1	690	17	<30	5
L. digitata stipe	38·9	0·46	3·7	0·28	1260	16	2·8	92	0·7	8	1·8	0·4	1150	28	<30	11
L. digitata frond, Ardencaple Bay	29·7	0·22	2·1	0·17	410	4	0·2	71	0·7	4	1·8	0·0	950	18	<30	6
L. digitata stipe, Ardencaple Bay	37·8	0·62	5·7	0·34	1570	7	0·2	85	1·2	5	2·9	0·0	1120	20	<30	21

TABLE V. TRACE-ELEMENT CONTENTS OF WET SEAWEEDS (COLLECTED 27 JUNE 1950) IN MG./KG.

Sample	Co	Ni	Mo	Fe	Pb	Sn	Zn	V	Ti	Cr	Ag	Sr	Ba	Mn	Cu
Pelvetia canaliculata	—	1·1	0·14	473	3·0	0·51	21	0·74	14	0·28	0·07	167	7·9	12	3·7
Fucus spiralis	0·37	1·7	0·24	622	0·92	N.d.	N.d.	2·2	57	0·68	0·07	77	12	22	5·7
Ascophyllum nodosum	0·17	0·92	0·22	285	1·00	0·27	29	0·69	6·9	0·47	0·03	141	4·5	8·9	2·9
F. vesiculosus	0·21	1·36	0·07	169	1·6	0·25	24	0·39	9·2	0·35	0·05	169	5·1	24	2·3
F. serratus	0·12	0·87	0·04	62	0·78	0·10	12	0·12	1·4	0·14	0·04	101	3·1	23	1·2
Laminaria digitata frond, Atlantic Bridge	0·04	0·25	0·03	56	0·97	0·08	8·2	0·07	0·56	0·15	0·01	96	2·4	<4	0·7
L. digitata stipe, Atlantic Bridge	0·06	0·47	0·04	160	2·0	0·36	11·7	0·09	1·0	0·23	0·05	146	3·6	<3·8	1·4
L. digitata frond, Ardencaple Bay	0·03	0·36	0·03	71	0·69	0·03	12·2	0·12	0·69	0·31	0·0	163	3·1	<5·2	0·9
L. digitata stipe, Ardencaple Bay	0·07	0·64	0·03	176	0·78	0·24	9·5	0·13	0·56	0·32	0·0	125	2·2	<3·3	2·4

TABLE VI. TRACE-ELEMENT CONTENTS OF SEA WATER IN μG. PER LITRE

Sample	Co	Ni	Mo	Pb	Sn	Zn	V	Ti	Cr	Ag	Sr	Ba	Mn	Cu
Taken 20 miles off Plymouth at 20 m. on 22. ii. 50. Stored in Pyrex bottle	< 0·3	6	12	< 8	< 5	9	2·4	8	1·2	2·9	N.d.	N.d.	N.d.	N.d.
As in (1), but stored in Polythene bottle	< 0·3	5	12	< 8	< 5	13	2·7	9	2·5	2·1	N.d.	N.d.	N.d.	N.d.
Taken at Ardencaple Bay at ½ m. on 27. vi. 50. Stored in Pyrex bottle	< 0·3	1·5	12	< 5	< 5	11	5	6	1·6	< 0·4	10,000	< 1,000	< 3,000	< 3,000
Taken at Atlantic Bridge at ½ m. on 27. vi. 50. Stored in Pyrex bottle	< 0·3	1·5	16	< 5	< 5	21	7	6	1	< 0·4	9,000	< 1,000	< 3,000	< 3,000
Noddack (1940)*	0·1	0·5	0·5	5	3	14	—	—	—	0·15	—	—	3	4
Ernst & Hoermann (1936)*	—	0·1	0·3–0·7	—	—	—	0·2–0·3	—	—	—	—	—	—	—
Atkins (1936)*	—	—	—	—	—	< 8	—	—	—	—	—	—	—	10
Haber (1928)*	—	—	—	—	—	—	—	—	—	0·3	—	—	—	—
Goldschmidt (1937)*	—	—	—	—	—	—	—	—	—	—	—	50	—	—

* Quoted from Harvey (1945).

TABLE VII. 'CONCENTRATION FACTOR', OR RATIO OF TRACE-ELEMENT CONTENT IN ALGAE (FRESH WEIGHT) TO TRACE-ELEMENT CONTENT IN SEA WATER

Sample	Ni	Mo	Zn	V	Ti	Cr	Sr
Pelvetia canaliculata	700	8	1,000	100	2,000	300	20
Fucus spiralis	1,000	15	—	300	10,000	300	8
Ascophyllum nodosum	600	14	1,400	100	1,000	500	16
F. vesiculosus	900	4	1,100	60	2,000	400	18
F. serratus	600	3	600	20	200	100	11
Laminaria digitata frond, Atlantic Bridge	200	2	400	10	90	200	90
L. digitata stipe, Atlantic Bridge	300	3	600	10	200	230	16
L. digitata frond, Ardencaple Bay	200	2	1,000	20	100	200	18
L. digitata stipe, Ardencaple Bay	400	2	900	30	90	200	14

ACKNOWLEDGEMENTS

This work forms part of a programme of research and development of the Scottish Seaweed Research Association, and the writers are indebted to the Director for permission to publish. The writers also wish to thank the staff of the Plymouth Marine Biological Laboratory, who collected the water samples off Plymouth, and the staff of the Macaulay Institute for Soil Research, Aberdeen, for the very valuable assistance in carrying out the spectrographic analyses.

SUMMARY

Some common Scottish Laminariaceae and Fucaceae have been analysed spectrographically, and seventeen of the minor elements determined.

The results show that there is a seasonal variation and considerable variation in the content of these elements in different species taken from the same habitat.

With the Laminariaceae the trace elements are more concentrated in the perennial stipe than in the attached frond, and are generally less than in the Fucaceae.

Samples of sea water taken off Plymouth and the West Coast of Scotland have also been analysed spectrographically and fourteen of the minor elements determined.

Concentration factors are given showing the extent to which marine algae can accumulate the trace elements. Values of over 1000-fold concentration are reported. *Fucus spiralis*, for example, contains 10,000 times more titanium than the surrounding sea water.

REFERENCES

BEHARRELL, J., 1942. Seaweed as a food for livestock. *Nature*, Vol. 149, pp. 306–7.

BERTRAND, G. & VORONCA-SPIRT, C., 1930. Titanium in the cryptogamic plants. *Bull. Soc. Chim.*, Ser. IV, T. 47, pp. 102–4.

BLACK, W. A. P., 1948*a*. The seasonal variation in chemical constitution of some of the sublittoral seaweeds common to Scotland. *Journ. Soc. Chem. Ind.*, Vol. 67, pp. 165–76.

—— 1948*b*. The seasonal variation in chemical composition of some of the littoral seaweeds common to Scotland. Part I. *Ascophyllum nodosum*. *Journ. Soc. Chem. Ind.*, Vol. 67, pp. 355–7.

—— 1949. Seasonal variation in chemical composition of some of the littoral seaweeds common to Scotland. Part II. *Fucus serratus*, *F. vesiculosus*, *F. spiralis* and *Pelvetia canaliculata*. *Journ. Soc. Chem. Ind.*, Vol. 68, pp. 183–9.

CORNEC, E., 1919. Spectrographic studies of the ash of marine plants. *Comp. Rend. Acad. Sci. Paris*, T. 168, pp. 513–14.

EVANS, R. D., KIP, A. F. & MOBERG, E. G., 1938. The radium and radon content of Pacific Ocean water, life, and sediments. *Amer. Journ. Sci.*, Vol. 36, pp. 241–59.

FARMER, V. C., 1950. The spectrographic analysis of plant ash in the carbon arc. *Spectrochim. Acta*, Bd. 4, pp. 224–8.

FÖYN, E., KARLIK, B., PETTERSSON, H. & RONA, E., 1939. The radioactivity of sea water. *Göteborgs Vetensk. Samh. Handl.*, F. 5, Ser. B, Bd. 6, No. 12, 44 pp. (*Medd. Oceanograf. Inst.* Göteborg, 2.)

HARVEY, H. W., 1945. *Recent Advances in the Chemistry and Biology of Sea Water*. 164 pp. Cambridge.

IGELSRUD, I., THOMPSON, T. G. & ZWICKER, B. M. G., 1938. Boron content of sea water and of marine organisms. *Amer. Journ. Sci.*, Vol. 35, pp. 47–63.

JONES, A. J., 1922. The arsenic content of some of the marine algae. *Pharm. Journ.*, Vol. 109, pp. 86–7.

LAGRANGE, R. & TCHAKIRIAN, A., 1939. Sur la détermination spectrographique de quelques éléments existant en traces dans certaines algues calcaires (*Lithothamnium calcareum*). *Comp. Rend. Acad. Sci. Paris*, T. 209, pp. 58–9.

LEGENDRE, R., 1947. Les industries chimiques de la mer. *Bull. Inst. Oceanograph. Monaco*, Vol. 44, No. 922, 15 pp.

MEULEN, H. TER, 1932. Distribution of molybdenum. *Nature*, Vol. 130, p. 966.

MITCHELL, R. L., 1948. The spectrographic analysis of soils, plants and related materials. *Commw. Bur. Soil Sci. Tech. Comm.*, No. 44, 183 pp.

MITCHELL, R. L. & SCOTT, R. O., 1948. Applications of chemical concentration by organic reagents to spectrographic analysis. *Spectrochim. Acta*, Bd. 3, pp. 367–78.

ÖY, E., 1940. Content of iron, copper, manganese, and boron in seaweeds. *Tidsskr. Kemi Bergv.*, Vol. 20, pp. 114–17.

SERVIGNE, M. & TCHAKIRIAN, A., 1939. Sur la présence d'éléments des terres rares dans les Algues calcaires (*Lithothamnium calcareum*). *Comp. Rend. Acad. Sci. Paris*, T. 209, pp. 570–2.

SPOONER, G. M., 1949. Observations on the absorption of radioactive strontium and yttrium by marine algae. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 587–625.

SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H., 1942. *The Oceans, Their Physics, Chemistry and General Biology*. New York.

WASSERMANN, A., 1949. Cation adsorption by brown algae. The mode of occurrence of alginic acid. *Ann. Bot.*, Vol. 13, No. 49, pp. 79–88.

WEBB, D. A., 1937. Studies on the ultimate composition of biological material. Part II. Spectrographic analyses of marine invertebrates, with special reference to the chemical composition of their environment. *Sci. Proc. Roy. Dublin Soc.*, Vol. 21, pp. 505–39.

WIESNER, R., 1938. Determination of radium content of marine algae. *Sitzber. Akad. Wiss. Wien, Math.-Naturw. Klasse*, Abt. II*a*, Bd. 147, pp. 521–8. [*Chem. Abs.* 1939, Vol. 33, pp. 9360.]

WILLIAMS, K. T. & WHETSTONE, R. R., 1940. Arsenic distribution in soils and its presence in certain plants. *Tech. Bull. U.S. Dept. Agric.*, Vol. 732, pp. 1–20.

WILSON, S. H. & FIELDES, M., 1941. Studies in spectrographic analysis. II. Minor elements in a sea-weed (*Macrocystis pyrifera*). *New Zealand Journ. Sci. Tech.*, Vol. 23, No. 2B, pp. 47B–48B.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Blood Cell Formation in Certain Teleost Fishes

By W. T. Catton

Journ. Hematology, Vol. 6, 1951, pp. 39–60

The blood cells of brown trout (*Salmo trutta*) and common roach (*Rutilus rutilus*) are described, and some comparisons are made with the blood cells of the marine teleosts, *Ctenolabrus rupestris* and *Trigla cuculus*. Confirming previous authors, the sites of blood-cell formation in these teleost fishes are chiefly in the intertubular tissue of the kidneys. The structure of the intertubular tissue is described as that of a 'spongework' of reticular cells, with scattered endothelial elements, and enclosing in the meshes large numbers of blood-cell precursor elements in various stages of development. Vascular connexion with the peritubular capillaries is described. On the basis of histological study of the primitive blood-forming cells, a monophyletic scheme of development is proposed, in which the stem cell, derived from a reticular cell, is regarded as a large cell of lymphoid character ('large lymphoid haemoblast'). From cells of this type, the blood granulocytes develop by a process of differentiation. Blood erythrocytes and thrombocytes develop from small lymphoid cells of the same general character ('small lymphoid haemoblasts'). These small lymphoid cells may be derived from the larger cells by mitotic divisions, which are frequently seen. Alternatively, the small lymphoid cells may be derived from endothelial elements of the haematopoietic tissues. On this latter supposition, a close analogy may be drawn with the scheme of blood-cell formation in mammals, according to the work of Doan, Cunningham and Sabin. No evidence of such derivation of the small lymphoid cells could be observed. W.T.C.

Notes on some Larval Decapods (Crustacea) from Bermuda. II

By Marie V. Lebour

Proc. Zool. Soc. Lond., Vol. 120, 1951, pp. 743–7

These notes add to our knowledge of the larval decapods of Bermuda. New facts are given as regards *Amphion* and it is shown that a very late stage brings it nearer to the adult form, which is probably *Amphionides* as Gurney has suggested. A late larva of *Anchistioides antiguensis* (Schmitt) was found in deep-water plankton, and is of great interest as only the first and second

larvae are so far known. It is here shown that there is a first larval stage in the hippolytid *Trachycaris*, which corresponds exactly with a similar stage in most other carids, having the eyes covered and the supra-orbital spines still under the skin. M.V.L.

Giant Axons and Synergic Contractions in *Branchiomma vesiculosum*

By J. A. Colin Nicol

Journ. Exp. Biol., Vol. 28, 1951, pp. 22–31

The giant axons of the sabellid worm *Branchiomma vesiculosum* mediate quick synergic contractions of the longitudinal musculature. The neuromuscular functioning of this system was investigated by means of electrical stimulation (condenser discharges) and graphical recording. Single muscle-twitches occur at stimulation frequencies up to 2 per second, above which clonus, and finally tetanus result. At high rates of stimulation fatigue rapidly sets in; this fatigue is reversible. Maximal tension is developed about 255 msec. after the beginning of contraction, and relaxation occupies about 1·8 sec. With an isometric lever it has been shown that under repetitive stimulation maximal tension is developed initially, and there is no evidence for the existence of peripheral facilitation. The paper concludes with a discussion of the results in terms of the natural habits of the animal. J.A.C.N.

On a Giant Squid, *Ommastrephes caroli* Furtado, stranded at Looe, Cornwall

By W. J. Rees

Bull. Brit. Mus. (*Nat. Hist.*), *Zool.*, Vol. 1, 1950, pp. 31–41

A large specimen of the giant squid, *Ommastrephes caroli* Furtado, was stranded in live condition in November 1940. Standard measurements are given, together with a detailed account of the dentition of the sucker rings. Female specimens only are known. Most strandings occur along the east coast of Britain, with main strandings at Scarborough, the Dunbar-North Berwick area and at Buckie.

All authenticated records of this and other giant squids (*O. pteropus* and *Architeuthis* spp.) have been collected and plotted on maps. It appears that these species are oceanic forms which occasionally migrate into the North Sea and become enfeebled by unfavourable conditions during the winter months. The scanty evidence we now possess suggests that the adult squids inhabit the continental slope beyond the 100-fathom line. Two excellent photographs by Dr D. P. Wilson are included in the report. W.J.R.

On the Behaviour of *Sabella*

By G. P. Wells
Department of Zoology, University College, London
Proc. Roy. Soc., B, Vol. 138, 1951, pp. 278–99

The water currents which *Sabella spallanzanii* and *S. pavonina* drive through their tubes vary with time according to definite and characteristic patterns. These are described in detail, and the bearing of the results on the general physiology of the worms is considered.

In either species, the tube consists of a stiff stem and a more flexible root, and is open at both ends. The opening of the stem (anterior opening) is always well above the substratum. That of the root (posterior opening) was found to be above the surface of the substratum in *S. spallanzanii* but embedded in the mud in *S. pavonina*. This means that the tube can easily be irrigated in either direction in *S. spallanzanii* but tailwards only in *S. pavonina*.

Both species irrigate their tubes vigorously, whether the crown is expanded or withdrawn. In *S. spallanzanii*, pauses are brief and rare; the direction and velocity of irrigation often change and certain characteristic patterns are constantly reproduced. In *S. pavonina* there may be pauses of over an hour's duration and irrigation is tailwards only. The fact that the former species irrigates in either direction and the latter in one direction only is clearly correlated with the difference in form of their tubes. As the worms were studied under identical mechanical conditions, the behaviour difference is inherent.

Decapitation (removal of crown, collar and part or all of the thorax) has very little effect on the irrigation behaviour of either species. This suggests that the crown is unimportant as a respiratory organ.

A worm may still be very active, even though its crown is withdrawn into its tube. The suggestion is made that feeding may occur from the irrigation current when the crown is withdrawn. G.P.W.

The Integration of Activity Cycles in the Behaviour of *Arenicola marina* L.

By G. P. Wells and Elinor B. Albrecht
Journ. Exp. Biol., Vol. 28, 1951, pp. 41–50

Two distinct cyclic behaviour patterns are known to be important in the normal life of the lugworm: the feeding cycle of period about 6–7 min., originating in the oesophageal wall (*f* cycle), and the irrigation-defaecation cycle of period usually about 40 min., and probably originating in the nerve cord (*i-d* cycle). The integration of these two patterns was studied in a series

of dissected preparations. Neither pacemaker directly affects the rhythm of the other. The integration of the activities which they determine depends on variation in the extent to which their influences spread through the neuromuscular system. They appear to compete for territory. If they happen to discharge outbursts simultaneously, the *i-d* pacemaker dominates over most of the body wall, and the *f* pacemaker over the proboscis and mouth region.

G.P.W.

The Role of Oesophageal Rhythms in the Behaviour of *Arenicola ecaudata* Johnston

By G. P. Wells and Elinor B. Albrecht

Journ. Exp. Biol., Vol. 28, 1951, pp. 51–6

The brainless isolated extrovert of *A. ecaudata* traces a continuous, or nearly continuous, background of activity, upon which prominent spells of vigorous rhythmic contraction appear at intervals of the order of 30–40 min. Similar spells are sometimes shown by the corresponding preparation from *A. marina*, whose characteristic *f* cycle can be regarded as produced by the organization of the background activity of *ecaudata* into vigorous and regularly spaced outbursts. There is little evidence of a pacemaker role of the oesophagus in *ecaudata*.

G.P.W.

CLASSIFIED LIST OF PUBLICATIONS

VOLUMES XVI TO XXIX OF *THE JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION* AND OTHER PUBLICATIONS RECORDING THE RESULTS OF RESEARCHES CARRIED OUT AT THE PLYMOUTH LABORATORY FROM 1928 TO 1950

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Preface

It is now 25 years since I produced the 'List of Publications' in Volume XV of this Journal,[1] which brought the earlier 1913 list up to date.

Much has been published since then and there is an evident need for a supplementary list. Accordingly, Mr N. A. Holme has prepared the following classified list of the contents of Volumes XVI to XXIX of the *Journal of the Marine Biological Association* and of other publications recording the results of researches carried out at the Plymouth laboratory from 1928–1950.

The last list only recorded those publications containing research carried out under the auspices of the Marine Biological Association. Since 1927, however, an increasing number of papers have been published in the Journal dealing with research at other marine biological laboratories in the British Isles. It is felt that the inclusion of such papers is valuable, not only in supplying a complete index of contents to the Journal volumes concerned, but as a useful bibliography to much marine biological literature.

There has been some rearrangement in this new list. Papers dealing with general biological problems have been placed first, followed by papers on the biology of different groups. As previously an authors' index has been provided, from which can be obtained the section and reference number of any paper.

Within each section or subsection the papers have been arranged in date order. Cross-references between sections are given, but, in Sections XII to XXX, there are none between the various subsections of each main section.

[1] List of Publications recording the results of researches carried out under the auspices of the Marine Biological Association of the United Kingdom in their laboratory at Plymouth or on the North Sea Coast from 1886–1927. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 753–828, 1928.

F. S. R.

March 1951

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1. MOORE, H. B. & NEILL, R. G., 1930. An instrument for sampling marine muds. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 589–94.
2. MOORE, H. B., 1930. The muds of the Clyde sea area. I. Phosphate and nitrogen contents. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 595–607.
3. STEVEN, G. A., 1930. Bottom fauna and the food of fishes. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 677–705.
4. MOORE, H. B., 1931. The muds of the Clyde sea area. III. Chemical and physical conditions; rate and nature of sedimentation; and fauna. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 325–58.
5. LLOYD, B., 1931. Muds of the Clyde sea area. II. Bacterial content. *Journ. Mar. Biol Assoc.*, Vol. XVII, pp. 751–65.
6. SMITH, J. E., 1932. The shell gravel deposits and the infauna of the Eddystone grounds. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 243–78.
7. KITCHING, J. A., MACAN, T. T. & GILSON, H. C., 1934. Studies in sublittoral ecology. I. A submarine gully in Wembury Bay, South Devon. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 677–705.
8. KITCHING, J. A., 1937. Studies in sublittoral ecology. II. Recolonisation at the upper margin of the sublittoral region; with a note on the denudation of *Laminaria* forest by storms. *Journ. Ecol.*, Vol. XXV, pp. 482–95.
9. MARE, M. F., 1942. A study of a marine benthic community with special reference to the micro-organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 517–54.
10. HILL, M. N. & WILLMORE, P. L., 1947. Marine seismic prospecting. *Nature, Lond.*, Vol. 159, pp. 707–8.
11. COOPER, L. H. N., 1948. A submerged ancient cliff near Plymouth. *Nature, Lond.*, Vol. 161, p. 280.
12. RAYMONT, J. E. G., 1949. Further observations on changes in the bottom fauna of a fertilized sea loch. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 9–19.
13. CHAPMAN, G., 1949. The thixotropy and dilatancy of a marine soil. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 123–40.
14. HOLME, N. A., 1949. A new bottom-sampler. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 323–32.
15. STEPHENSON, W., 1949. Certain effects of agitation upon the release of phosphate from mud. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 371–80.
16. HOLME, N. A., 1950. The bottom fauna of Great West Bay. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 163–83.
17. KING, W. B. R., 1950. Floor of the English Channel. *Geol. Mag., Lond.*, Vol. LXXXVII, No. 5, pp. 383–4.
18. HOLME, N. A., 1951. Sampling the sea-bed. *Discovery*, Feb. 1951, pp. 59–63.

See also: Numerous papers on separate groups and species in sections XIII–XXX; Shore ecology (IV).

III. ESTUARINE ECOLOGY

1. PERCIVAL, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 81–108.
2. FRASER, J. H., 1932. Observations on the fauna and constituents of an estuarine mud in a polluted area. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 69–85.

3. ALEXANDER, W. B., SOUTHGATE, B. A. & BASSINDALE, R., 1932. The salinity of the water retained in the muddy foreshore of an estuary. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 297–8.
4. ALEXANDER, W. B., SOUTHGATE, B. A. & BASSINDALE, R., 1935. Survey of the River Tees. Part II. The estuary—chemical and biological. *D.S.I.R. Water Pollution Research*, Tech. Paper No. 5, H.M. Stationery Office. Summary: *Journ. Mar. Biol. Assoc.*, Vol. XX, 1936, pp. 717–24.
5. BASSINDALE, R., 1938. The intertidal fauna of the Mersey estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 83–98.
6. HARTLEY, P. H. T. & SPOONER, G. M., 1938. The ecology of the Tamar estuary. I. Introduction. *Journ. Mar. Biol. Assoc.*, Vol. XXII, 501–8.
7. COOPER, L. H. N. & MILNE, A., 1938. The ecology of the Tamar estuary. II. Under-water illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 509–27.
8. MILNE, A., 1938. The ecology of the Tamar estuary. III. Salinity and temperature conditions in the lower estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 529–42.
9. MILNE, A., 1940. The ecology of the Tamar estuary. IV. The distribution of the fauna and flora on buoys. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 69–87.
10. COOPER, L. H. N. & MILNE, A., 1939. The ecology of the Tamar estuary. V. Under-water illumination. Revision of data for red light. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 391–6.
11. SPOONER, G. M. & MOORE, H. B., 1940. The ecology of the Tamar estuary. VI. An account of the macrofauna of the intertidal muds. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 283–330.
12. BEANLAND, F. LOUISE, 1940. Sand and mud communities in the Dovey estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 589–611.
13. HOLME, N. A., 1949. The fauna of sand and mud banks near the mouth of the Exe estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 189–237.

See also: IV, 2, 8; Ecology of estuarine fish, XXIX D, 22.

IV. SHORE ECOLOGY

1. BRUCE, J. R., 1928. Physical factors on the sandy beach. I. Tidal, climatic and edaphic. II. Chemical changes—carbon dioxide concentration and sulphides. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 535–52, 553–65.
2. REID, D. M., 1930–2. Salinity interchange between sea-water in sand and over-flowing fresh-water at low tide. Parts I and II. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 609–14; Vol. XVIII, pp. 299–306.
3. PIRRIE, M. E., BRUCE, J. R. & MOORE, H. B., 1932. A quantitative study of the fauna of the sandy beach at Port Erin. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 279–96.
4. COLMAN, J., 1933. The nature of the intertidal zonation of plants and animals. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 435–76.
5. NICOL, E. A. T., 1935. The ecology of a salt-marsh. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 203–61.
6. MOORE, H. B., 1939. The colonization of a new rocky shore at Plymouth. *Journ. Animal Ecol.*, Vol. 8, pp. 29–38.
7. COLMAN, J., 1940. On the faunas inhabiting intertidal seaweeds. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 129–83.
8. REES, C. B., 1940. A preliminary study of the ecology of a mud-flat. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 185–99.

9. MOORE, H. B. & SPROSTON, N. G., 1940. Further observations on the colonization of a new rocky shore at Plymouth. *Journ. Anim. Ecol.*, Vol. 9, pp. 319–27.
10. WILSON, D. P., 1946. The seashore life of the British Isles. *Geographical Magazine*, Vol. XIX, pp. 264–71.
11. EVANS, R. G., 1947. The intertidal ecology of selected localities in the Plymouth neighbourhood. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 173–218.

See also: Numerous papers on separate groups and species in sections XIII–XXX; Estuarine ecology (III).

V. PLANKTON

1. RUSSELL, F. S., 1928. The vertical distribution of marine macroplankton. VI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 81–103.
2. RUSSELL, F. S., 1928. *Ibid.* VII. Observations on the behaviour of *Calanus finmarchicus*. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 429–54.
3. RUSSELL, F. S., 1928. *Ibid.* VIII. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 829–50.
4. RUSSELL, F. S., 1930. *Ibid.* IX. The distribution of the pelagic young of teleostean fishes in the daytime in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 639–76.
5. RUSSELL, F. S., 1931. *Ibid.* X. Notes on the behaviour of *Sagitta* in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 391–414.
6. RUSSELL, F. S., 1931. *Ibid.* XI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 767–84.
7. RUSSELL, F. S., 1934. *Ibid.* XII. Some observations on the vertical distribution of *Calanus finmarchicus* in relation to light intensity. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 569–84.
8. RUSSELL, F. S., 1928. A net for catching plankton near the bottom. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 105–8.
9. WILSON, D. P., 1929. Minute life in the sea. *Torquay Nat. Hist. Soc., Trans. and Proc.*, Vol. V, pp. 175–80.
10. RUSSELL, F. S., 1930. Do oceanic plankton animals lose themselves? *Nature, Lond.*, Vol. 125, p. 17.
11. RUSSELL, F. S., 1930. Vitamin content of marine plankton. *Nature, Lond.*, Vol. 126, p. 472.
12. GARDINER, A. C., 1931. The validity of single vertical hauls of the International Net in the study of the distribution of the plankton. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 449–72.
13. RUSSELL, F. S. & COLMAN, J. S., 1931–5. The zooplankton. Parts I–IV. *Sci. Rep. Great Barrier Reef Expedition*, 1928–9. British Museum (Nat. Hist.), Vol. II, No. 2, pp. 5–35 (1931); Vol. II, No. 6, pp. 159–76 (1934); Vol. II, No. 6, pp. 176–201 (1934); Vol. II, No. 7, pp. 203–76 (1935).
14. LEBOUR, M. V., 1932. Through the bath tap. *Science Progress*, No. 104, pp. 662–9.
15. RUSSELL, F. S., 1933. The seasonal distribution of macroplankton as shown by catches in the 2-metre stramin ring-trawl in off-shore waters off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 73–81.
16. SPOONER, G. M., 1933. Observations on the reactions of marine plankton to light. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 385–438.
17. LEBOUR, M. V., 1933. Plankton, or the floating life in the sea. *School Sci. Rev.*, No. 58, pp. 201–9.

18. GARDINER, A. C., 1934. Variations in the amount of macroplankton by day and night. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 559–67.
19. HARVEY, H. W., 1934. Measurement of phytoplankton population. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 761–73.
20. HARVEY, H. W., 1934. Annual variation of planktonic vegetation, 1933. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 775–92.
21. RUSSELL, F. S., 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 309–32.
22. HARVEY, H. W., COOPER, L. H. N., LEBOUR, M. V. & RUSSELL, F. S., 1935. Plankton production and its control. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 407–41.
23. HARVEY, H. W., 1935. Note concerning a measuring plankton-net. *Journ. Cons. Int. Explor. Mer*, Vol. X, pp. 179–84.
24. RUSSELL, F. S., 1935. A review of some aspects of zooplankton research. *Rapp. Cons. Explor. Mer*, Vol. XCV, pp. 3–30.
25. RUSSELL, F. S., 1936. Observations on the distribution of plankton animal indicators made on Col. E. T. Peel's yacht 'St George' in the mouth of the English Channel, July, 1935. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 507–22.
26. HARDY, A. C., 1936. The ecological relations between the herring and the plankton investigated with the Plankton Indicator. Part I. The object, plan and methods of the investigation. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 147–77.
27. LUCAS, C. E., 1936. *Ibid.* Part II. Zooplankton-herring correlations in the English fisheries. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 178–242.
28. HENDERSON, G. T. D., 1936. *Ibid.* Part III. The zooplankton-herring correlations in the Scottish fisheries. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 243–76.
29. HENDERSON, G. T. D., LUCAS, C. E. & FRASER, J. H., 1936. *Ibid.* Part IV. The relation between catches of herring and phytoplankton collected by the plankton indicator. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 277–91.
30. RUSSELL, F. S., 1936. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Rapp. Cons. Int. Explor. Mer*, Vol. C, pp. 7–10.
31. GROSS, F., 1937. Notes on the culture of some marine plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 753–68.
32. RUSSELL, F. S., 1937. Drift through the English Channel as shown by plankton distribution. *Assoc. Oceangr. Phys., Proc. Verb.*, No. 2, pp. 137–8.
33. GRAHAM, M. & HARDING, J. P., 1938. Some observations on the hydrology and plankton of the North Sea and English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 201–6.
34. REES, C. B., 1939. The plankton in the upper reaches of the Bristol Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 397–425.
35. RUSSELL, F. S., 1939. Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. *Journ. Cons. Int. Explor. Mer*, Vol. XIV, pp. 171–92.
36. MARE, M. F., 1940. Plankton production off Plymouth and the mouth of the English Channel in 1939. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 461–82.
37. MOORE, H. B., 1941. A wire-angle indicator for use when towing plankton nets. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 419–22.
38. HART, T. J., 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports*, Vol. XXI, pp. 261–356.
39. GARDINER, A. C., 1943. Measurement of phytoplankton population by the pigment extraction method. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 739–44.

40. HART, T. J., 1943. Darwin and water bloom. *Nature, Lond.*, Vol. 156, p. 661.
41. WIMPENNY, R. S., 1944. Plankton production between the Yorkshire coast and the Dogger Bank, 1933–1939. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 1–6.
42. ATKINS, W. R. G., 1945. Autotrophic flagellates as the major constituent of the oceanic phytoplankton. *Nature, Lond.*, Vol. 156, pp. 446–7.
43. ATKINS, W. R. G., 1945. Conditions for the vernal increase in the phytoplankton and a supposed lag in the process. *Nature, Lond.*, Vol. 156, p. 599.
44. HARDY, A. C. & PATON, W. N., 1947. Experiments on the vertical migration of plankton animals. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 467–526.
45. LEBOUR, M. V., 1947. Notes on the inshore plankton of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 527–47.
46. BARNES, H., 1949. A statistical study of the variation in vertical plankton hauls with special reference to the loss of the catch with divided hauls. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 429–46.
47. BARNES, H., 1949. On the volume measurement of water filtered by a plankton pump, with an observation on the distribution of planktonic animals. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 651–62.
48. HART, T. J., 1950. Zooplankton. *Chambers's Encyclopedia.*
49. ATKINS, W. R. G. & PARKE, M., 1951. Seasonal changes in the phytoplankton as indicated by chlorophyll estimations. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 609–18.

See also: Numerous papers on separate groups and species in sections XIII–XXX; Phytoplankton and nutrients, IX E, 2, 5, 23, 26, 30, F, 26; Breakdown of plankton organisms, IX E, 15; Plankton and nutrients, IX F, 15, 16; Chemical constituents of plankton, X, 7, 8, 12, 16; Phytoplankton, various papers in section XIII; Comparison of pump and net hauls, XXIII D, 39.

VI. CORROSION, MARINE GROWTHS AND LARVAL SETTLEMENT

1. ATKINS, W. R. G., 1928–36. The preservation of fishing nets by treatment with copper soaps and other substances. Parts I–III. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 219–35, 1928; XVI, pp. 583–8, 1930; XX, pp. 627–41, 1936.
2. ORTON, J. H., 1930. Experiments in the sea on the growth-inhibitive and preservative value of poisonous paints and other substances. With some chemical analyses by the Government Chemist. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 373–452.
3. ATKINS, W. R. G., 1931. The deterioration of fabrics exposed on a roof after treatment with fishing-net preservatives. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 473–7.
4. RUSSELL, F. S., 1934. *Marine Growths. Examination of ships.* Iron and Steel Institute Spec. Rept. 5. Second Report of the Corrosion Committee, pp. 153–6.
5. ATKINS, W. R. G. & PURSER, J., 1936. The preservation of fibre ropes for use in sea-water. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 643–54.
6. WILSON, D. P., 1936. Larval settlement and the substratum. *The Presidency College Zoology Magazine*, Madras, Vol. III, pp. 3–7.
7. ATKINS, W. R. G. & WARREN, F. J., 1941. The preservation of fishing nets, trawl twines and fibre ropes for use in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 97–107.
8. INSTITUTION OF CIVIL ENGINEERS: Discussion on Maintenance of Maritime Works. Introductory Notes: (1) Timber Structures (by F. V. M. BELL); (2) Reinforced Concrete (by G. L. HARGREAVES); (3) Steel (by E. L. BROWNING). Maritime and Waterways Engineering Division, 1948–9, 1949.

9. BARNES, H. & POWELL, H. T., 1950. Some observations on the effect of fibrous glass surfaces upon the settlement of certain sedentary marine organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 299–302.
10. DULY, S. J., 1950. The corrosion of steel by sea salt of given moisture content. *Journ. Soc. Chem. Ind.*, Vol. 69, pp. 304–6.

See also: Corrosion of metals, IX F, 2, 21; Settlement of polychaete larvae, XXI C, 5, 6, 11; Settlement of *Elminius*, XXIII D, 44.

VII. EXPERIMENTAL EMBRYOLOGY, REGENERATION AND HEREDITY

1. HOBSON, A. D., 1928. The action of isotonic salt solutions on the unfertilised eggs of *Thalassema neptuni*. *Brit. Journ. Exp. Biol.*, Vol. VI, pp. 65–78.
2. ORTON, J. H., 1928. The trail of the germ plasm. *Nature, Lond.*, Vol. 121, pp. 352–3.
3. CHOUCROUN, N., 1929. Sur l'hypothèse du rayonnement mitogénétique. *C.R. Acad. Sci., Paris*, T. CLXXXIX, pp. 782–4.
4. CHOUCROUN, N., 1930. On the hypothesis of mitogenetic radiation. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 65–74.
5. DARBY, H. H., 1930. Studies on growth acceleration in Protozoa and yeast. *Journ. Exp. Biol.*, Vol. VII, pp. 308–16.
6. BERRILL, N. J., 1931. Regeneration in *Sabella pavonina* (Sav.) and other Sabellid worms. *Journ. Exp. Zool.*, Vol. 58, pp. 495–523.
7. HÖRSTADIUS, S., 1935. Über die determination im Verlaufe der Eiachse bei Seeigeln. *Pubbl. Staz. Zool. Napoli*, Vol. XIV, pp. 251–479.
8. BERRILL, N. J. & MEES, D. M., 1936. Reorganization and regeneration in *Sabella*. I. Nature of gradient, summation and posterior regeneration. *Journ. Exp. Zool.*, Vol. 73, pp. 67–83.
9. BERRILL, N. J. & MEES, D. M., 1936. Reorganization and regeneration in *Sabella*. II. The influence of temperature. III. The influence of light. *Journ. Exp. Zool.*, Vol. 74, pp. 61–89.
10. COHEN, A. & BERRILL, N. J., 1936. The development of isolated blastomeres of the ascidian egg. *Journ. Exp. Zool.*, Vol. 74, pp. 91–117.
11. HÖRSTADIUS, S., 1936. Studien über heterosperme Seeigelmerogone nebst Bemerkungen übereinige Keimblattchimären. *Mém. Acad. Roy. d'Hist. Nat. Belg.*, Sér. 2, fasc. 3, pp. 801–80. Mélanges Paul Pelseneer.
12. BEAMS, H. W., 1937. The air turbine ultracentrifuge, together with some results upon ultracentrifuging the eggs of *Fucus serratus*. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 571–88.
13. HÖRSTADIUS, S., 1940. Change in inheritance in echinoid hybrids. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 99–113.
14. HÖRSTADIUS, S., LORCH, I. J. & DANIELLI, J. F., 1950. Differentiation of the sea urchin egg following reduction of the interior cytoplasm in relation to the cortex. *Exper. Cell Res.*, Vol. I, pp. 188–93.

See also: XXV B, 36; Regeneration in syllidian polychaetes, XXI B, 6, 23.

VIII. APPARATUS AND METHODS

1. ORTON, J. H., 1928. Imperishable labels for preserved organisms. *Nature, Lond.*, Vol. 122, p. 57.
2. ATKINS, W. R. G., 1928. Histological applications of measurements of acidity or alkalinity and of oxidation or reduction. *Microtomists' Vade Mecum*, Chapter 28, pp. 359–75. London.

3. GROVE, A. J., 1930. An apparatus for keeping marine organisms under circulation in narrow observational tanks. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 757–60.
4. MOORE, H. B., 1931. The specific identification of faecal pellets. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 359–65.
5. WILSON, D. P., 1933. A simple block trimmer for the Cambridge Rocking Microtome. *Journ. Roy. Micr. Soc.*, Ser. 3, Vol. LIII, pp. 25–7.
6. WILSON, D. P., 1933. An improved method of orientating minute specimens for section cutting. *Journ. Roy. Micr. Soc.*, Ser. 3, Vol. LIII, pp. 220–6.
7. WILSON, D. P., 1935. Under-water photography. *Practical Photography*, Vol. III, pp. 1113–23.
8. WILSON, D. P., 1936. The plunger jar. *The Aquarist and Pond-keeper*, Vol. VII, pp. 138–9.
9. GOHAR, H. A. F., 1937. The preservation of contractile marine animals in an expanded condition. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 295–9.
10. LEBOUR, M. V., 1944. The rearing of marine animals in captivity. *Rep. & Trans. Plymouth Institution & Devon & Cornwall Nat. Hist. Soc.*, Vol. XVIII, for the years 1936–43.
11. HICKLING, C. F., 1945. Marking fish with the electric tattooing needle. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 166–9.
12. HARDING, J. P., 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 141–53.
13. ALEEM, A. A., 1949. An apparatus for producing artificial tides. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 663–5.
14. BARNES, H. & BAGENAL, T. B., 1951. A statistical study of variability in catch obtained by short repeated trawls taken over an inshore ground. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 649–60.
15. STEVEN, G. A., 1950. *Nets. How to make, mend and preserve them.* 128 pp. London.
16. STEVEN, G. A., 1950. Art of net-making. *Ship and Boat Builder*, Nov. 1950, pp. 185–90.

See also: Physical and chemical methods—in the appropriate subsections of section IX; Bottom-samplers, II, 1, 14, 18; Bottom plankton net, V, 8; Validity of vertical hauls of the International net, V, 12; Measuring plankton net, V, 23; Hardy plankton indicator, V, 26; Culture of plankton organisms, V, 31; Wire-angle indicator for plankton net, V, 37; Measurement of phytoplankton by pigment extraction, V, 39; Variation in plankton hauls, V, 46; Plankton pump samples, V, 47; XXIII D, 39; Surveying *Laminaria* beds, XIV, 12; Rearing hydroids of medusae, XVIII B, 5.

IX. PHYSICS AND CHEMISTRY

A. *General*

1. HARVEY, H. W., 1928. *Biological Chemistry and Physics of Sea-water.* Cambridge University Press.
2. HARVEY, H. W., 1931. The fertility of the sea. *Fenska Kemist. Medd.*, No. 2, pp. 1–4.
3. ATKINS, W. R. G., 1932. The chemistry of sea-water in relation to the productivity of the sea. *Science Progress*, No. 106, Oct., pp. 298–312.
4. KEYS, A., CHRISTENSEN, E. H. & KROGH, A., 1935. The organic metabolism of sea-water with special reference to the ultimate food cycle in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 181–96.

5. ATKINS, W. R. G., 1944. Plant nutrients in the sea. *Nature, Lond.*, Vol. 154, pp. 489–90.
6. HARVEY, H. W., 1945. *Recent Advances in the Chemistry and Biology of Sea Water*. 164 pp. Cambridge University Press.
7. HARVEY, H. W., 1946. *Fertility of the Ocean*. Discussion on Oceanography, Linnean Society of London, pp. 5–8.
8. COOPER, L. H. N., 1948. Significant figures in analytical chemistry. *The Analyst*, Vol. 73, No. 870, pp. 508–9.
9. COOPER, L. H. N., 1948. The nutrient balance in the sea. *Research*, Vol. 1, 6 pp.
10. HARVEY, H. W., 1950. On the production of living matter in the sea off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 97–137.
11. ARMSTRONG, F. A. J. & ATKINS, W. R. G., 1950. The suspended matter of sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 139–43.

B. *Physics and physical chemistry*

1. NEILL, R. G., 1930. Apparatus for rapid electrometric titration. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 519–27.
2. COOPER, L. H. N., 1937. Oxidation-reduction potential in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 167–76.
3. COOPER, L. H. N., 1937. A relation between the lyotropic series and free energies. *Nature, Lond.*, Vol. 139, pp. 284–5.
4. LOWNDES, A. G., 1942. The displacement method of weighing living aquatic organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 555–74.
5. LOWNDES, A. G., 1943. Some applications of the displacement method of weighing living aquatic organisms. *Proc. Zool. Soc. Lond.*, A, Vol. 113, pp. 28–43.
6. ATKINS, W. R. G., 1944. Measurement of potential difference as a method for studying the action of water on lead pipes. *Nature, Lond.*, Vol. 154, pp. 211–12.
7. LOWNDES, A. G., 1945. The displacement method of weighing living aquatic organisms. *Nature, Lond.*, Vol. 155, pp. 520–1.
8. ATKINS, W. R. G., 1947. Electrical conductivity of river, rain and snow water. *Nature, Lond.*, Vol. 159, p. 674.

See also: Marine seismic prospecting, II, 10; Thixotropy and dilatancy of a marine soil, II, 13; Temperatures in the Tamar estuary, III, 8; Physical factors on sandy beach, IV, 1.

C. *Water movements*

1. HARVEY, H. W., 1929. Hydrodynamics of the waters south-east of Ireland. *Journ. Cons. Int. Explor. Mer*, Vol. IV, pp. 80–92.
2. HARVEY, H. W., 1930. Hydrography of the mouth of the English Channel, 1925–1928. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 791–820.
3. HARVEY, H. W., 1934. Hydrography of the mouth of the English Channel, 1929–1932. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 737–46.
4. CARRUTHERS, J. N., 1930. Further investigations upon the water movements in the English Channel. Drift-bottle experiments in the summers of 1927, 1928 and 1929, with critical notes on drift-bottle experiments in general. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 241–75.
5. CARRUTHERS, J. N., 1934. The flow of water past the Seven Stones Lightvessel. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 921–30.

6. CARRUTHERS, J. N., LAWFORD, A. L. & VELEY, V. F. C., 1950. Studies of water movements and winds at lightvessels. II. At the Seven Stones Lightvessel near the Scilly Isles. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 587–608.
7. COOPER, L. H. N., 1947. Internal waves and upwelling of oceanic water from mid-depths on to a continental shelf. *Nature, Lond.*, Vol. 159, pp. 579–80.
8. COOPER, L. H. N. & VAUX, D., 1949. Cascading over the continental slope of water from the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 719–50.

See also: Plankton and water movements, V, 21, 25, 30, 32, 33, 35.

D. *Light*

1. POOLE, H. H. & ATKINS, W. R. G., 1928. Further photo-electric measurements of the penetration of light into sea-water. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 455–83.
2. POOLE, H. H. & ATKINS, W. R. G., 1929. Photo-electric measurements of submarine illumination throughout the year. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 297–324.
3. ATKINS, W. R. G. & POOLE, H. H., 1929. Methods for the photo-electric and photo-chemical measurement of daylight. *Rept. Conference Empire Meteorologists Agric. Sect.*, London, pp. 67–89. (Reprinted *Biol. Rev.*, 1930, Vol. 5, pp. 91–113.)
4. ATKINS, W. R. G. & POOLE, H. H., 1929. The integration of light by photo-electrolysis. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 159–64.
5. ATKINS, W. R. G. & POOLE, H. H., 1929. The photo-electric measurement of the illumination in buildings. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 173–87.
6. ATKINS, W. R. G. & POOLE, H. H., 1929. Photo-electric measurements of illumination in relation to plant distribution. Part II. Measurements with portable galvanometers. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 295–309.
7. ATKINS, W. R. G. & STANBURY, F. A., 1930. *Ibid.* Part III. Certain spruce, larch, oak and holm oak woods. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 517–31.
8. ATKINS, W. R. G. & POOLE, H. H., 1931. *Ibid.* Part IV. Changes in the colour composition of daylight in the open and in shaded situations. *Sci. Proc. R. Dub. Soc.*, Vol. XX, pp. 13–48.
9. ATKINS, W. R. G. & POOLE, H. H., 1929. The uranyl oxalate method of daylight photometry and its photo-electric standardization. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 321–39.
10. ATKINS, W. R. G. & POOLE, H. H., 1929. The photo-chemical and photo-electric measurement of the radiation from a mercury vapour lamp. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 355–61.
11. ATKINS, W. R. G. & POOLE, H. H., 1930. The photo-chemical and photo-electric measurement of submarine illumination. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 509–14.
12. ATKINS, W. R. G. & POOLE, H. H., 1930. Methods for the photo-electric and photo-chemical measurement of daylight. *Biol. Rev.*, Vol. 5, pp. 91–113.
13. ATKINS, W. R. G. & POOLE, H. H., 1930. The photo-electric recording of daylight. *Nature, Lond.*, Vol. 125, pp. 305–6.
14. ATKINS, W. R. G. & POOLE, H. H., 1930. On the photo-electric measurement of daylight. *Photo-electric cells and their applications*, pp. 128–37. London.
15. ATKINS, W. R. G. & POOLE, H. H., 1931. A preliminary comparison of the neon lamp and potentiometer methods of submarine photo-electric photometry. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 617–31.

16. GALL, D. C. & ATKINS, W. R. G., 1931. Apparatus for the photo-electric measurement of submarine illumination assembled for the U.S.A. Research Ship, *Atlantis*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 1017–28.
17. ATKINS, W. R. G., 1931. The penetration of light through successive layers of tissue paper. *Nature, Lond.*, Vol. 128, p. 545.
18. ATKINS, W. R. G., 1931. Observations on the photo-electric measurement of the radiation from mercury vapour lamps and from the sun, and on the effects of such radiation upon the skin. *Sci. Proc. R. Dub. Soc.*, Vol. XX, pp. 49–65.
19. ATKINS, W. R. G., 1931. Some experiments on the accuracy obtainable with gas-filled photo-electric cells. *Sci. Proc. R. Dub. Soc.*, Vol. XX, pp. 67–73.
20. ATKINS, W. R. G., 1932. The measurement of daylight in relation to plant growth. *Emp. For. Journ.*, Vol. XI, pp. 42–52.
21. ATKINS, W. R. G., 1932. Solar radiation and its transmission through air and water. *Journ. Cons. Int. Explor. Mer*, Vol. VII, pp. 171–211.
22. ATKINS, W. R. G. & POOLE, H. H., 1933. The use of cuprous oxide and other rectifier photo cells in submarine photometry. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 67–72.
23. POOLE, H. H. & ATKINS, W. R. G., 1933. Reversal of the current from a cuprous oxide photo cell in red light. *Nature, Lond.*, Vol. 131, p. 133.
24. POOLE, H. H. & ATKINS, W. R. G., 1933. Reversal of current in rectifier photo-cells. *Nature, Lond.*, Vol. 131, pp. 547–8.
25. ATKINS, W. R. G. & POOLE, H. H., 1933. The photo-electric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc.*, B, Vol. 222, pp. 129–64.
26. ATKINS, W. R. G. & POOLE, H. H., 1933. Photo-electric measurement of submarine illumination: an outline of the methods and the results. *Rep. Fifth Pacific Sci. Congress*, III: A. 5. 27 (1934), pp. 2129–39.
27. POOLE, H. H. & ATKINS, W. R. G., 1933. Experiments on the suitability of some rectifier photo-cells for the measurement of daylight. *Sci. Proc. R. Dub. Soc.*, Vol. XX, pp. 537–46.
28. POOLE, H. H. & ATKINS, W. R. G., 1934. The use of a selenium rectifier photo-electric cell for submarine photometry. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 727–36.
29. POOLE, H. H. & ATKINS, W. R. G., 1934. Measurement of the current generated by a rectifier photo-electric cell. *Nature, Lond.*, Vol. 134, p. 810.
30. POOLE, H. H. & ATKINS, W. R. G., 1933. Some measurements of the brightness of various parts of the sky by means of a rectifier photo-electric cell. *Sci. Proc. R. Dub. Soc.*, Vol. XXI, pp. 1–8.
31. POOLE, H. H. & ATKINS, W. R. G., 1934. The measurement of the current generated by rectifier photo-cells. *Sci. Proc. R. Dub. Soc.*, Vol. XXI, pp. 133–9.
32. POOLE, H. H. & ATKINS, W. R. G., 1935. The standardization of photo-electric cells for the measurement of visible light. *Phil. Trans. Roy. Soc.*, A, Vol. 235, pp. 1–27.
33. ATKINS, W. R. G. & POOLE, H. H., 1936. The photo-electric measurement of the diurnal and seasonal variations in daylight and a globe integrating photometer. *Phil. Trans. Roy. Soc.*, A, Vol. 235, pp. 245–72.
34. ATKINS, W. R. G. & POOLE, H. H., 1936. Photo-electric measurements of the luminous efficiency of daylight. *Proc. Roy. Soc.*, B, Vol. 121, pp. 1–17.
35. RUSSELL, F. S., 1936. Submarine illumination in relation to animal life. *Rapp. Cons. Int. Explor. Mer*, Vol. CI, Pt. 2, 8 pp.

36. POOLE, H. H., 1936. The photo-electric measurement of submarine illumination in off-shore waters. *Rapp. Cons. Int. Explor. Mer*, Vol. CI, Pt. 2, 12 pp.
37. POOLE, H. H. & ATKINS, W. R. G., 1936. The standardization of photo-electric cells for the measurement of energy. *Sci. Proc. R. Dub. Soc.*, Vol. XXI, pp. 363–79.
38. ATKINS, W. R. G., BALL, N. G. & POOLE, H. H., 1937. The photo-electric measurement of the diurnal variations in daylight in temperate and tropical regions. *Proc. Roy. Soc.*, A, Vol. 160, pp. 526–39.
39. ATKINS, W. R. G., POOLE, H. H. & STANBURY, F. A., 1937. The measurement of the intensity and the colour of the light in woods by means of emission and rectifier photo-electric cells. *Proc. Roy. Soc.*, B, Vol. 121, pp. 427–50.
40. ATKINS, W. R. G., 1937. The transmission of light and total radiation by leaves. *Proc. Roy. Soc.*, B, Vol. 122, pp. 26–9.
41. POOLE, H. H. & ATKINS, W. R. G., 1937. The penetration into the sea of light of various wave-lengths as measured by emission or rectifier photo-electric cells. *Proc. Roy. Soc.*, B, Vol. 123, pp. 150–65.
42. BAYLISS, L. E., 1938. The photographic method for recording average illuminations. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 99–118.
43. ATKINS, W. R. G., 1938. Daylight in relation to climate and health. *Brit. Med. Journ.*, No. 4053, p. 565.
44. ATKINS, W. R. G., CLARKE, G. L., PETTERSSON, H., POOLE, H. H., UTTERBACK, C. L. & ANGSTRÖM, A., 1938. Measurement of submarine daylight. *Journ. Cons. Int. Explor. Mer*, Vol. XIII, pp. 37–57.
45. ATKINS, W. R. G., 1938. Photo-electric measurements of the seasonal variations in daylight around 0·41μ from 1930 to 1937. *Proc. Roy. Soc.*, A, Vol. 165, pp. 453–65.
46. ATKINS, W. R. G., 1939. Illumination in algal habitats. *Botaniska Notiser*, pp. 145–57.
47. ATKINS, W. R. G. & POOLE, H. H., 1940. A cubical photometer for studying the angular distribution of submarine daylight. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 271–81.
48. ATKINS, W. R. G. & ROTHSCHILD, M., 1940. Photo-electric measurements of daylight under alpine conditions. *Journ. Roy. Met. Soc.*, Vol. 66, pp. 13–21.
49. POOLE, H. H. & ATKINS, W. R. G., 1941. The effect of wave-length on the relation between the intensity of illumination and the current in selenium rectifier photo-cells. *Sci. Proc. R. Dub. Soc.*, Vol. XXII, pp. 395–400.
50. ATKINS, W. R. G., 1945. Apparent clearing of the sky at dusk. *Nature, Lond.*, Vol. 155, p. 110.
51. ATKINS, W. R. G., 1945. Daylight and its penetration into the sea. *Trans. Illuminating Eng. Soc.* (London), Vol. X, No. 7, pp. 1–12.
52. ATKINS, W. R. G., 1947. Size versus colour in air-sea rescue. *Nature, Lond.*, Vol. 159, pp. 612–13.
53. MOORE, J. G., 1947. The determination of the depths and extinction coefficients of shallow water by air photography using colour filters. *Phil. Trans. Roy. Soc.*, A, Vol. 240, pp. 163–217.
54. ATKINS, W. R. G. & ELLISON, M. A., 1947. Photoelectric measurements of the seasonal variations in daylight at Plymouth, from 1938 to March 1941, compared with the years 1930 to 1937. *Proc. Roy. Soc.*, A, Vol. 191, pp. 467–84.
55. ATKINS, W. R. G., POOLE, H. H. & WARREN, F. J., 1949. A balance-by-depth method for the photoelectric measurement of the vertical extinction coefficient of water. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 751–5.

56. GALL, M. H. W., 1949. Measurements to determine extinction coefficients and temperature gradients in the North Sea and English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 757–80.

See also: Underwater illumination in estuaries, III, 7, 10; Reactions of plankton to light, V, 7, 16, 18; Illumination in relation to plant life, XIII, 5, 15; Solar radiation constant and fisheries, XXIX D, 20.

E. *Phosphorus, silicon and nitrogen*

1. HARVEY, H. W., 1928. Nitrate in the sea. II. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 183–90.
2. ATKINS, W. R. G., 1928. Seasonal variations in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 191–205.
3. HARVEY, H. W., 1929. Methods of estimating phosphates and nitrates in sea-water. *Rapp. Cons. Int. Explor. Mer*, Vol. LIII, pp. 68–74.
4. ATKINS, W. R. G., 1930. Seasonal changes in the nitrite content of sea-water. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 515–18.
5. ATKINS, W. R. G., 1930. Seasonal variations in the phosphate and silicate content of sea-water in relation to the phytoplankton crop. Part V. November 1927 to April 1929, compared with earlier years from 1923. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 821–52.
6. COOPER, L. H. N., 1932. The determination of nitrate in the sea by means of reduced strychnine. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 161–6.
7. ATKINS, W. R. G., 1932. Nitrate in sea-water and its estimation by means of diphenylbenzidine. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 167–92.
8. COOPER, L. H. N., 1933. Chemical constituents of biological importance in the English Channel, November, 1930, to January, 1932. Part I. Phosphate, silicate, nitrate, nitrite, ammonia. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 677–728.
9. COOPER, L. H. N., 1933. *Ibid.* Part II. Hydrogen ion concentration, excess base, carbon dioxide, and oxygen. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 729–53.
10. COOPER, L. H. N., 1933. *Ibid.* Part III. June–December, 1932. Phosphate, silicate, nitrite, hydrogen ion concentration, with a comparison with wind records. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 55–62.
11. IBAÑEZ, O. G., 1933. Note on the effect of salts in the determination of phosphate in sea-water by Deniges' method. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 326–8.
12. COOPER, L. H. N., 1933. A system of rational units for reporting nutrient salts in sea-water. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 331–4.
13. HONIG, C., 1934. Nitrates in aquarium water. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 723–5.
14. IBAÑEZ, O. G., 1934. Preservation of sea-water samples with fluoride for phosphate estimation by Deniges' method. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 329–30.
15. COOPER, L. H. N., 1935. The rate of liberation of phosphate in sea water by the breakdown of plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 197–200.
16. COOPER, L. H. N., 1937. 'Organic' phosphorus in sea water from the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 673–7.
17. COOPER, L. H. N., 1937. On the ratio of nitrogen to phosphorus in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 177–82.

18. COOPER, L. H. N., 1937. The nitrogen cycle in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 183–204.
19. COOPER, L. H. N., 1938. Salt error in determinations of phosphate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 171–8.
20. COOPER, L. H. N., 1938. Redefinition of the anomaly of the nitrate-phosphate ratio. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, p. 179.
21. COOPER, L. H. N., 1938. Phosphate in the English Channel, 1933–8, with a comparison with earlier years, 1916 and 1923–32. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 181–95.
22. HICKLING, C. F., 1938. The distribution of phosphates in the south-western area in April 1938. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 197–200.
23. HARVEY, H. W., 1940. Nitrogen and phosphorus required for the growth of phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 115–23.
24. BARNES, H., 1941. A note on the determination of very small quantities of hydroxylamine by Blom's method. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 109–10.
25. HARVEY, H. W., 1941. On changes taking place in sea water during storage. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 225–33.
26. CHU, S. P., 1946. The utilization of organic phosphorus by phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 285–95.
27. COOPER, L. H. N., 1948. Particulate ammonia in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 322–5.
28. COOPER, L. H. N., 1948. Phosphate and fisheries. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 326–36.
29. HARVEY, H. W., 1948. The estimation of phosphate and of total phosphorus in sea waters. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 337–59.
30. MARSHALL, S. M. & ORR, A. P., 1948. Further experiments on the fertilization of a sea loch (Loch Craiglin). The effect of different plant nutrients on the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 360–79.
31. ARMSTRONG, F. A. J., 1949. A source of error in the absorptiometric determination of inorganic and total phosphorus in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 701–5.
32. ARMSTRONG, F. A. J. & HARVEY, H. W., 1950. The cycle of phosphorus in the waters of the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 145–62.
33. COOPER, L. H. N., 1950. The nitrogen cycle. *Chambers's Encyclopedia.*

See also: Phosphate and nitrogen in muds of Clyde sea area, II, 2; Release of phosphate from muds, II, 15; Composition of plankton, X, 7, 12, 13; Phosphate and fisheries, XXIX D, 20.

F. *Chemistry (other than phosphorus, silicon and nitrogen)*

1. KAPP, E. M., 1928. The precipitation of calcium and magnesium from sea water by sodium hydroxide. *Biol. Bull. Woods Hole*, Vol. LV, pp. 453–8.
2. ATKINS, W. R. G., 1928. Lecture experiments on the hydrogen ion concentration changes in the rusting of iron. *Nature, Lond.*, Vol. 121, p. 615.
3. ATKINS, W. R. G., 1928. The alkalinity of sea water. *Science of the Sea.* Ed. G. H. Fowler and E. J. Allen (2nd ed.), Ch. II, pp. 76–92.
4. BROWN, E. M., 1929. Notes on the hydrogen ion concentration, excess base, and carbon dioxide pressure of marine aquarium waters. *Proc. Zool. Soc., Lond.*, pp. 601–13.
5. ATKINS, W. R. G., 1930. Some geochemical applications of measurements of hydrogen ion concentration. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, pp. 455–60.

6. ATKINS, W. R. G., 1931. Note on the condition of the water in a marine aquarium. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 479–81.
7. IBAÑEZ, O. G., 1931. On the colorimetric determination of pH in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 483–8.
8. BUCH, K., WATTENBERG, H. & HARVEY, H. W., 1931. Apparent dissociation constants of carbon dioxide in sea water of different salt contents. *Nature, Lond.*, Vol. 128, pp. 411–12.
9. ATKINS, W. R. G., 1932. The copper content of sea water. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 193–7.
10. BREDER, C. M. & SMITH, H. W., 1932. On the use of sodium bicarbonate and calcium in the rectification of sea water in aquaria. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 199–200.
11. COOPER, L. H. N., 1932. On the effect of long continued additions of lime to aquarium sea water. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 201–2.
12. ATKINS, W. R. G., 1932. Preparation of sulphuric acid free from nitric acid. *Nature, Lond.*, Vol. 129, p. 98.
13. BUCH, K., HARVEY, H. W., WATTENBERG, H. & GRIPENBERG, S., 1932. Über das Kohlensäuresystem im Meerwasser. *Rapp. Cons. Int. Explor. Mer*, Vol. LXXIX, 70 pp.
14. ATKINS, W. R. G., 1933. The rapid estimation of the copper content of sea water. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 63–6.
15. COOPER, L. H. N., 1934. The variation of excess base with depth in the English Channel with reference to the seasonal consumption of calcium by plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 747–54.
16. COOPER, L. H. N., 1935. Iron in the sea and in marine plankton. *Proc. Roy. Soc.*, B, Vol. 118, pp. 419–38.
17. ATKINS, W. R. G., 1935. The determination of zinc in water by means of sodium diethyldithiocarbamate. *The Analyst*, Vol. 60, pp. 400–1.
18. ATKINS, W. R. G., 1936. The estimation of zinc in sea water using sodium diethyldithiocarbamate. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 625.
19. HARVEY, H. W., 1937. Note on colloidal ferric hydroxide in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 221–5.
20. COOPER, L. H. N., 1937. Some conditions governing the solubility of iron. *Proc. Roy. Soc.*, B, Vol. 124, pp. 299–307.
21. ATKINS, W. R. G., 1937. Note on the use of sodium diethyldithiocarbamate for detecting the solubility corrosion of metals. *Trans. Faraday Soc.*, Vol. XXXIII, pp. 431–2.
22. COOPER, L. H. N. & WILSON, D. P., 1939. Formation of native lead under laboratory conditions. *Nature, Lond.*, Vol. 143, p. 207.
23. SMITH, C. L., 1941. The solubility of calcium carbonate in tropical sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 235–42.
24. ATKINS, W. R. G., 1944. Measurement of potential difference as a method for studying the action of water on lead pipes. *Nature, Lond.*, Vol. 154, pp. 211–12.
25. BARNES, H., 1946. The estimation in sea-water solutions of micro-quantities of mercury in the presence of copper by means of dithizone. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 303–11.
26. HARVEY, H. W., 1947. Manganese and the growth of phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 562–79.
27. COOPER, L. H. N., 1948. The distribution of iron in the waters of the western English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 279–313.
28. COOPER, L. H. N., 1948. Some chemical considerations on the distribution of iron in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 314–21.

29. ATKINS, W. R. G., 1948. Note on the spectroscopic and biological detection of potassium in sea water and 'potassium-free' artificial sea water. *Journ. Cons. Int. Explor. Mer*, Vol. XV, pp. 169–72.
30. HARVEY, H. W., 1949. On manganese in sea and fresh waters. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 155–64.
31. SPOONER, G. M., 1949. Observations on the absorption of radioactive strontium and yttrium by marine algae. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 587–625.

See also: IX E, 9; Muds of Clyde sea area, II, 4; Salinity, etc., in estuaries, III, 3, 4, 8; Chemical conditions on a sandy beach, IV, 1, 2; Preservation of nets with copper soaps, VI, 1; Supply of iron to diatoms, XIII, 14; Replacement of potassium by rubidium in *Nitzschia*, XIII, 10; Chemical constitution of algae, XIV, 16, 17, 20.

X. CHEMICAL CONSTITUENTS OF LIVING MATTER. BIOCHEMISTRY

1. CHANNON, H. J., 1928. The biological significance of the unsaponifiable matter of oils. III. Fish-liver oils. *Biochem. Journ.*, Vol. 22, pp. 51–9.
2. BOYLAND, E., 1928. Chemical changes in muscle, Parts II–III. *Biochem. Journ.*, Vol. 22, pp. 362–80.
3. SZENT-GYÖRGYI, A., 1928. Observations on the function of peroxidase systems and the chemistry of the adrenal cortex. Description of a new carbohydrate derivative. *Biochem. Journ.*, Vol. 22, pp. 1387–409.
4. EGGLETON, P. & EGGLETON, G. P., 1928. Further observations on phosphagen. *Journ. Physiol.*, Vol. 65, pp. 15–24.
5. FOX, H. M. & RAMAGE, H., 1931. A spectrographic analysis of animal tissues. *Proc. Roy. Soc.*, B, Vol. 108, pp. 157–73.
6. MCCANCE, R. A. & SHIPP, H. L., 1933. The magnesium and other inorganic constituents of some marine invertebrates. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 293–6.
7. COOPER, L. H. N., 1934. The determination of phosphorus and nitrogen in plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 755–9.
8. COOPER, L. H. N., 1935. A note on manganese in marine plankton. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 201–2.
9. MCCANCE, R. A. & SHACKLETON, L. R. B., 1937. The metallic constituents of marine gastropods. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 269–71.
10. MCCANCE, R. A. & MASTERS, M., 1937. The chemical composition and the acid base balance of *Archidoris britannica*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 273–9.
11. OCHOA, S., 1938. Enzymic phosphorylations in invertebrate muscle. *Biochem. Journ.*, Vol. 32, pp. 237–42.
12. COOPER, L. H. N., 1939. Phosphorus, nitrogen, iron and manganese in marine zooplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 387–90.
13. HARRISON, R. J., 1940. Phosphorus and iron in *Sagitta setosa* and *Sagitta elegans*. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 125–8.
14. LOWNDES, A. G., 1941. Rapid determination of water in animals and plants. *Nature, Lond.*, Vol. 148, p. 79.
15. LOWNDES, A. G., 1942. Rapid determination of fat in animals and plants. *Nature, Lond.*, Vol. 150, p. 291.
16. ATKINS, W. R. G., 1943. Determination of the water content of wood and other substances by means of ternary azeotropic mixtures. *Nature, Lond.*, Vol. 151, p. 449.

17. HAYES, F. R. & PELLUET, D., 1947. The inorganic constitution of molluscan blood and muscle. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 580–9.
18. BROWN, C. H., 1950. Quinone tanning in the animal kingdom. *Nature, Lond.*, Vol. 165, p. 275.
19. BALDWIN, E. & YUDKIN, W. H., 1950. The annelid phosphagen: with a note on phosphagen in Echinodermata and Protochordata. *Proc. Roy. Soc.*, B, Vol. 136, pp. 614–31.

See also: Vitamin content of plankton, V, 11; Chlorophyll estimations of phytoplankton, V, 49; Interrenal cell tissue, XI B, 1; Carbohydrates of crab nerve, XI C, 3; Phosphagen in plain muscle, XI E, 16; Cozymase in invertebrate muscle, XI E, 23; Biochemistry of electric organs of *Raia clavata*, XI E, 24; Chemical constitution of algae, XIV, 16, 17, 20; Fat content of the flounder, XXIX C, 12.

XI. PHYSIOLOGY

A. *General*

1. HILL, A. V., 1929. The maintenance of life and irritability in isolated animal tissues. *Nature, Lond.*, Vol. 123, pp. 723–30.

B. *Cytology*

1. FRASER, A., 1928. Brown coloration in interrenal cell tissue. *Nature, Lond.*, Vol. 122, p. 206.
2. HARRIS, J. E., 1935. Studies on living protoplasm. I. Streaming movements in the protoplasm of the egg of *Sabellaria alveolata* (L.). *Journ. Exp. Biol.*, Vol. XII, pp. 65–79.
3. BERRILL, N. J., 1935. Cell division and differentiation in asexual and sexual developments. *Journ. Morph.*, Vol. LVII, pp. 353–427.

See also: Under separate groups and species.

C. *Nerve*

1. LEVIN, A., 1927. Fatigue, retention of action current and recovery in crustacean nerve. *Journ. Physiol.*, Vol. 63, pp. 113–29.
2. HOLMES, E. G. & HOLMES, B. E., 1928. Observations on the metabolism of nervous tissue. *Minerva Medica*, Vol. VIII, No. 23 *bis*, 8 pp.
3. HOLMES, E. G., 1929. Carbohydrates of crab nerve. *Biochem. Journ.*, Vol. 23, pp. 1182–6.
4. FURUSAWA, K., 1929. The depolarisation of crustacean nerve by stimulation or oxygen want. *Journ. Physiol*, Vol. 67, pp. 325–42.
5. HILL, A. V., 1929. The heat production and recovery of crustacean nerve. *Proc. Roy. Soc.*, B, Vol. 105, pp. 153–76.
6. IZQUIERDO, J. J., 1930. On the influence of the extra-cardiac nerves upon sino-auricular conduction in the heart of *Scyllium*. *Journ. Physiol.*, Vol. 69, pp. 29–47.
7. BLASCHKO, H., CATTELL, McK. & KAHN, J. L., 1931. On the nature of the two types of response in the neuro-muscular system of the crustacean claw. *Journ. Physiol.*, Vol. 73, pp. 25–35.
8. HILL, A. V., 1932. *Chemical wave transmission in nerve.* Camb. Univ. Press.
9. SERENI, E. & YOUNG, J. Z., 1932. Nervous degeneration and regeneration in cephalopods. *Pubbl. Staz. Zool. Napoli*, Vol. XII, pp. 173–208.
10. COWAN, S. L., 1933. The effect of veratrine on the electrical response of crab's nerve. *Journ. Physiol.*, Vol. 77, p. 27 *P*.

11. BERESINA, M. & FENG, T. P., 1933. The heat production of crustacean nerve. *Journ. Physiol.*, Vol. 77, pp. 111–38.
12. COWAN, S. L. & ING, H. R., 1933. The effect of quaternary ammonium salts on nerve. *Journ. Physiol.*, Vol. 79, pp. 75–82.
13. COWAN, S. L., 1933. Action of quaternary ammonium salts on nerve. *Nature, Lond.*, Vol. 131, p. 658.
14. YOUNG, J. Z., 1933. The autonomic nervous system of selachians. *Quart. Journ. Micr. Sci.*, Vol. 75, pp. 571–624.
15. WIERSMA, C. A. G., 1933. Vergleichende Untersuchungen über das periphere Nerven-Muskelsystem von Crustaceen. *Z. vergl. Physiol.*, Bd. XIX, pp. 349–85.
16. BOGUE, J. Y. & ROSENBERG, H., 1934. Action potentials in nerve of *Sepia*. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 83, pp. 21*P*–22*P*.
17. ROSENBERG, H., 1934. The strength-duration curves of two non-medullated nerves. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 83, pp. 23*P*–24*P*.
18. GERARD, R. W., 1934. The irritability of a non-medullated nerve. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 83, pp. 24*P*–25*P*.
19. COWAN, S. L., 1934. The action of potassium and other ions on the injury potential and action current in *Maia* nerve. *Proc. Roy. Soc.*, B, Vol. 115, pp. 216–60.
20. BUGNARD, L. & HILL, A. V., 1935. Electric excitation of the fin nerve of *Sepia*. *Journ. Physiol.*, Vol. 83, pp. 425–38.
21. BAYLISS, L. E., COWAN, S. L. & SCOTT, D., Jr., 1935. The action potentials in *Maia* nerve before and after poisoning with veratrine and yohimbine hydrochlorides. *Journ. Physiol.*, Vol. 83, pp. 439–54.
22. ROSENBERG, H., 1935. The excitation of medullated and non-medullated nerves by currents of short duration. *Journ. Physiol.*, Vol. 84, pp. 50–69.
23. COWAN, S. L. & ING, H. R., 1935. Quaternary ammonium salts and the action currents in nerve. *Journ. Physiol.*, Vol. 84, pp. 90–110.
24. FISCHER, E., 1936. The action of a single vagal volley on the heart of the eel and the turtle. *Amer. Journ. Physiol.*, Vol. CXVII, pp. 596–608.
25. KATZ, B., 1936. Curarization in the neuro-muscular system of crabs. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 86, pp. 14*P*–15*P*.
26. BOGUE, J. Y. & ROSENBERG, H., 1936. Excitability of sensory fibres in *Maia* nerve. *Journ. Physiol.*, Vol. 87, pp. 67–72.
27. BOGUE, J. Y. & ROSENBERG, H., 1936. Electrical responses of *Maia* nerve to single repeated stimuli. *Journ. Physiol.*, Vol. 87, pp. 158–80.
28. KATZ, B., 1936. Neuro-muscular transmission in crabs. *Journ. Physiol.*, Vol 86, pp. 45*P*–46*P* and Vol. 87, pp. 199–221.
29. BOGUE, J. Y., ROSENBERG, H. & YOUNG, J. Z., 1936. Electrotonus in the fin nerve of *Sepia*. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 86, pp. 6*P*–7*P*.
30. BOGUE, J. Y., CHANG, I. & ROSENBERG, H., 1936. Osmotic pressure and velocity of impulse in *Maia* nerve. *Proc. Physiol. Soc., Journ. Physiol.*, Vol. 87, pp. 89*P*–91*P*.
31. SOLANDT, D. Y., 1936. The measurement of 'accommodation' in nerve. *Proc. Roy. Soc.*, B, Vol. 119, pp. 355–79.
32. YOUNG, J. Z., 1936. The giant nerve fibres and epistellar body of cephalopods. *Quart. Journ. Micr. Sci.*, Vol. 78, pp. 367–86.
33. HALL, D. M. & PANTIN, C. F. A., 1937. The nerve-net in the Actinozoa. V. Temperature and facilitation in *Metridium senile*. *Journ. Exp. Biol.*, Vol. XIV, pp. 71–8.

34. PUMPHREY, R. J. & YOUNG, J. Z., 1938. The rates of conduction of nerve fibres of various diameters in cephalopods. *Journ. Exp. Biol.*, Vol. xv, pp. 453–66.
35. DANIELLI, J. F., 1939. The resistance of nerve in relation to interpolar length. *Journ. Physiol.*, Vol. 96, pp. 65–73.
36. YOUNG, J. Z., 1939. Fused neurons and synaptic contacts in the giant nerve fibres of cephalopods. *Phil. Trans. Roy. Soc.*, B, Vol. 229, pp. 465–503.
37. SANDERS, F. K. & YOUNG, J. Z., 1940. Learning and other functions of the higher nervous centres of *Sepia*. *Journ. Neurophysiol.*, Vol. III, pp. 501–26.
38. WEBB, D. A. & YOUNG, J. Z., 1940. Electrolyte content and action potential of the giant nerve fibres of *Loligo*. *Journ. Physiol.*, Vol. 98, pp. 299–313.
39. WATERMAN, T. H., 1941. A comparative study of the effects of ions on whole nerve and isolated single nerve fibre preparations of crustacean neuromuscular systems. *Journ. Cell. Comp. Physiol.*, Vol. 18, pp. 109–26.
40. HOLMES, W., PUMPHREY, R. J. & YOUNG, J. Z., 1941. The structure and conduction velocity of the medullated nerve fibres of prawns. *Journ. Exp. Biol.*, Vol. XVIII, pp. 50–4.
41. YOUNG, J. Z., 1944. Giant nerve-fibres. *Endeavour*, Vol. III, pp. 108–13.
42. HODGKIN, A. L. & HUXLEY, A. F., 1945. Resting and action potentials in single nerve fibres. *Journ. Physiol.*, Vol. 104, pp. 176–95.
43. NICOL, J. A. C. & YOUNG, J. Z., 1946. Giant nerve fibre of *Myxicola infundibulum* (Grube). *Nature, Lond.*, Vol. 158, p. 167.
44. HODGKIN, A. L. & HUXLEY, A. F., 1946. Potassium leakage from an active nerve-fibre. *Nature, Lond.*, Vol. 158, pp. 376–7.
45. NICOL, J. A. C., SMYTH, C. N. & WHITTERIDGE, D., 1947. Conduction velocity in relation to axon diameter in *Myxicola infundibulum*. *XVII Int. Physiol. Congr.*, Oxford, 1947, pp. 243–4 (Abstract).
46. NICOL, J. A. C., 1948. The function of the giant axon of *Myxicola infundibulum* Montagu. *Canad. Journ. Res.*, Vol. 26, D, pp. 212–22.
47. NICOL, J. A. C., 1948. The giant nerve-fibres in the central nervous system of *Myxicola* (Polychaeta Sabellidae). *Quart. Journ. Micr. Sci.*, Vol. 89, pp. 1–45.
48. NICOL, J. A. C., 1948. The giant axons of annelids. *Quart. Rev. Biol.*, Vol. 23, pp. 291–323.
49. KATZ, B., 1949. Neuro-muscular transmission in invertebrates. *Biol. Rev.*, Vol. 24, pp. 1–20.
50. HODGKIN, A. L. & KATZ, B., 1949. The effect of calcium on the axoplasm of giant nerve fibres. *Journ. Exp. Biol.*, Vol. XXVI, pp. 292–4.
51. HODGKIN, A. L. & KATZ, B., 1949. The effect of sodium ions on the electrical activity of the giant axon of the squid. *Journ. Physiol.*, Vol. 108, pp. 37–77.
52. HODGKIN, A. L. & KATZ, B., 1949. The effect of temperature on the electrical activity of the giant axon of the squid. *Journ. Physiol.*, Vol. 109, pp. 240–9.
53. HILL, D. K., 1950. Advances in the physiology of peripheral nerve. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 241–6.
54. HILL, D. K., 1950. The effect of stimulation on the opacity of a crustacean nerve trunk and its relation to fibre diameter. *Journ. Physiol.*, Vol. 111, pp. 283–303.
55. HILL, D. K., 1950. The volume change resulting from stimulation of a giant nerve fibre. *Journ. Physiol.*, Vol. 111, pp. 304–27.
56. KEYNES, R. D. & LEWIS, P. R., 1950. Determination of the ionic exchange during nervous activity by activation analysis. *Nature, Lond.*, Vol. 165, pp. 809–10.

See also: Under separate groups and species.

D. *Sense organs*

1. HILLIER, W. T., 1931. The lateral line sense-organs. *Proc. Roy. Soc. Med.*, 8 pp.
2. LÖWENSTEIN, O. & SAND, A., 1936. The activity of the horizontal semicircular canal of the dogfish, *Scyllium canicula*. *Journ. Exp. Biol.*, Vol. XIII, pp. 416–28.
3. LÖWENSTEIN, O. & SAND, A., 1936. The significance of the spontaneous discharge from the horizontal ampulla of the dogfish. *Proc. Physiol. Soc.*, *Journ. Physiol.*, Vol. 86, pp. 43 *P*–44 *P*.
4. BAYLISS, L. E., LYTHGOE, R. J. & TANSLEY, K., 1936. Some new forms of visual purple found in sea fishes with a note on the visual cells of origin. *Proc. Roy. Soc.*, B, Vol. 120, pp. 95–113.
5. FESSARD, A. & SAND, A., 1937. Stretch receptors in the muscles of fishes. *Journ. Exp. Biol.*, Vol. XIV, pp. 383–496.
6. SAND, A., 1937. Peripheral excitation and inhibition of a sense organ. *Journ. Physiol.*, Vol. 89, pp. 47*P*–49*P*.
7. SAND, A., 1937. The mechanism of the lateral sense organs of fishes. *Proc. Roy. Soc.*, B, Vol. 123, pp. 472–95.
8. SAND, A., 1938. Autonomous rhythmical activity of sense organs. *Nature, Lond.*, Vol. 141, pp. 285–6.
9. SAND, A., 1938. The function of the ampullae of Lorenzini, with some observations on the effect of temperature on sensory rhythms. *Proc. Roy. Soc.*, B, Vol. 125, pp. 524–53.
10. LÖWENSTEIN, O. & SAND, A., 1940. The individual and integrated activity of the semicircular canals of the elasmobranch labyrinth. *Journ. Physiol.*, Vol. 99, pp. 89–101.
11. LÖWENSTEIN, O. & SAND, A., 1940. The mechanism of the semicircular canal. A study of the responses of single-fibre preparations to angular accelerations and to rotation at constant speed. *Proc. Roy. Soc.*, B, Vol. 129, pp. 256–75.
12. SAND, A., 1940. The mechanism of acustico-lateral sense organs in fishes, with special reference to problems in the physiology of semicircular canals. *Proc. Roy. Soc. Med.*, Vol. XXXIII, pp. 741–50.
13. LÖWENSTEIN, O., 1948. Oscillographic analysis of the non-acoustic functions of the vertebrate ear. *Nature, Lond.*, Vol. 161, pp. 652–4.
14. LÖWENSTEIN, O. & ROBERTS, T. D. M., 1948. Oscillographic analysis of the gravity and vibration responses from the labyrinth of the thornback ray (*Raja clavata*). *Nature, Lond.*, Vol. 162, pp. 852–3.
15. LÖWENSTEIN, O. & ROBERTS, T. D. M., 1949. The equilibrium function of the otolith organs of the thornback ray. *Journ. Physiol.*, Vol. 110, pp. 392–415.

See also: Under separate groups and species.

E. *Effectors*

1. WELLS, G. P., 1928. The action of potassium on muscle preparations from invertebrates. *Brit. Journ. Exp. Biol.*, Vol. V, pp. 258–82.
2. HOBSON, A. D., 1928. The effect of electrolytes on the muscle of the fore-gut of *Dytiscus marginalis* with special reference to the action of potassium. *Brit. Journ. Exp. Biol.*, Vol. V, pp. 385–93.
3. GRAY, J., 1929. The mechanism of ciliary movement. *Amer. Nat.*, Vol. LXIII, pp. 68–81.
4. PANTIN, C. F. A., 1930. On the physiology of amoeboid movement. V. Anaerobic movement. *Proc. Roy. Soc.*, B, Vol. 105, pp. 538–55.

5. PANTIN, C. F. A., 1930. *Ibid.* VI. The action of oxygen. *Proc. Roy. Soc.*, B, Vol. 105, pp. 555–64.
6. PANTIN, C. F. A., 1930. *Ibid.* VII. The action of anaesthetics. *Proc. Roy. Soc.*, B, Vol. 105, pp. 565–79.
7. PANTIN, C. F. A., 1931. *Ibid.* VIII. A. The action of certain non-electrolytes. B. A note on the iso-electric point of the proteins of a marine amoeba. *Journ. Exp. Biol.*, Vol. VIII, pp. 365–78.
8. BOZLER, E., 1930. Untersuchungen zur Physiologie der Tonusmuskeln. *Z. vergl. Physiol.*, Bd. XII, pp. 579–602.
9. HICKLING, C. F., 1931. A new type of luminescence in fishes. III. The gland in *Coelorhynchus coelorhynchus* Risso. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 853–75.
10. HEWER, H. R., 1931. Studies in colour-changes in fish. Part V. The colour patterns in certain flat-fish and their relation to the environment. *Journ. Linn. Soc.* (*Zool.*), Vol. XXXVII, pp. 493–513.
11. IZQUIERDO, J. J., 1931. A study of the crustacean heart muscle. *Proc. Roy. Soc.*, B, Vol. 109, pp. 229–51.
12. BRONK, D. W., 1932. The heat production and economy of maintained contractions in crustacean muscle. *Journ. Cell. and Comp. Physiol.*, Vol. 2, pp. 285–94.
13. SIMPSON, W. W. & OGDEN, E., 1932. The physiological significance of urea. I. The elasmobranch heart. *Journ. Exp. Biol.*, Vol. IX, pp. 1–5.
14. YOUNG, J. Z., 1933. Comparative studies on the physiology of the iris. II. *Uranoscopus* and *Lophius*. *Proc. Roy. Soc.*, B, Vol. 112, pp. 242–9.
15. PANTIN, C. F. A., 1934. On the excitation of crustacean muscle. I. *Journ. Exp. Biol.*, Vol. XI, pp. 11–27.
16. EGGLETON, M. G., 1934. A physiological study of phosphagen in plain muscle. *Journ. Physiol.*, Vol. 82, pp. 79–87.
17. NICHOLLS, J. V. V., 1934. Reaction of the smooth muscle of the gastro-intestinal tract of the skate to stimulation of autonomic nerves in isolated nerve-muscle preparations. *Journ. Physiol.*, Vol. 83, pp. 56–67.
18. WYKES, U. M., 1936. Observations on pigmentary co-ordination in elasmobranchs. *Journ. Exp. Biol.*, Vol. XIII, pp. 460–6.
19. YOUNG, J. Z., 1936. The innervation and reaction to drugs of the viscera of teleostean fish. *Proc. Roy. Soc.*, B, Vol. 120, pp. 303–18.
20. HOGBEN, L., 1936. The pigmentary effector system. VII. The chromatic function in elasmobranch fishes. *Proc. Roy. Soc.*, B, Vol. 120, pp. 142–58.
21. WYKES, U. M., 1937. The photic control of pigmentary responses in teleost fishes. *Journ. Exp. Biol.*, Vol. XIV, pp. 79–86.
22. WINTON, F. R., 1937. The changes in viscosity of an unstriated muscle (*Mytilus edulis*) during and after stimulation with alternating, interrupted and uninterrupted direct currents. *Journ. Physiol.*, Vol. 88, pp. 492–511.
23. OCHOA, S. & OCHOA, C. G., 1937. Cozymase in invertebrate muscle. *Nature, Lond.*, Vol. 140, p. 1097.
24. BALDWIN, E., 1938. Biochemistry of the electric organs of *Raia clavata*. *Biochem. Journ.*, Vol. 32, pp. 888–94.
25. HOLMES, W., 1940. The colour changes and colour patterns of *Sepia officinalis* L. *Proc. Zool. Soc. Lond.*, A, Vol. 110, pp. 17–35.
26. WELLS, G. P., 1942. The action of potassium on echinoderm, molluscan and crustacean muscle. *Journ. Exp. Biol.*, Vol. XVIII, pp. 213–22.
27. HOLMES, W., 1943. Innervation of crustacean muscles. *Nature, Lond.*, Vol. 151, pp. 531–2.

28. LOWNDES, A. G., 1947. Recent work on flagellar movement. *Science Progress*, Vol. XXXV, pp. 62–8.
29. CHAPMAN, G., 1949. The mechanism of opening and closing of *Calliactis parasitica*. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 641–50.

See also: Under separate groups and species. For physiology of neuro-muscular systems see section XI C; Chemical changes in muscle, X, 2, 11.

F. *Behaviour*

1. BULL, H. O., 1928. Studies on conditioned responses in fishes. Part I. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 485–533.
2. BULL, H. O., 1930. *Ibid.* Part II. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 615–37.
3. BULL, H. O., 1935. *Ibid.* Part III. Wave-length discrimination in *Blennius pholis* L. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 347–64.
4. BULL, H. O., 1935. *Ibid.* Part V. On the controlling influence of normal behaviour traits upon capacity to form experimental conditioned motor responses under certain conditions. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 365–70.
5. BULL, H. O., 1936. *Ibid.* Part VII. Temperature perception in teleosts. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 1–27.
6. RUSSELL, F. S., 1932. Behaviour in invertebrates. *Nature, Lond.*, Vol. 129, p. 473.
7. CATE, J. T., 1934. Unisegmental reflexes in the dogfish. *Journ. Physiol.*, Vol. 82, pp. 179–83.
8. GRAY, J. & SAND, A., 1936. The locomotory rhythm of the dogfish (*Scyllium canicula*). *Journ. Exp. Biol.*, Vol. XIII, pp. 200–9.
9. GRAY, J. & SAND, A., 1936. Spinal reflexes of the dogfish (*Scyllium canicula*). *Journ. Exp. Biol.*, Vol. XIII, pp. 210–18.
10. LISSMANN, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). I. Reflex behaviour. *Journ. Exp. Biol.*, Vol. XXIII, pp. 143–61.
11. LISSMANN, H. W., 1946. *Ibid.* II. The effect of deafferentation. *Journ. Exp. Biol.*, Vol. XXIII, pp. 162–76.
12. WELLS, G. P. & DALES, R. P., 1950. Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 661–80.

See also: Under separate groups and species. Reactions of plankton to light, V, 16; Larval settlement, VI, 6, 9; XXI C, 5, 6, 11; XXIII D, 44; Opening and closing of *Calliactis*, XI E, 29.

G. *Osmotic and ionic regulation*

1. MARGARIA, R., 1931. The osmotic changes in some marine animals. *Proc. Roy. Soc.*, B, Vol. 107, pp. 606–24.
2. HÖFLER, K., 1931. Plasmolyseverlauf und Wasserpermeabilität. *Protoplasma*, Bd. XII, pp. 564–79.
3. BATEMAN, J. B., 1932. The osmotic relations between white and yolk in the hen's egg. *Journ. Exp. Biol.*, Vol. IX, pp. 322–31.
4. HUKUDA, K., 1932. Change of weight of marine animals in diluted media. *Journ. Exp. Biol.*, Vol. IX, pp. 61–8.
5. DAVSON, H. & DANIELLI, J. F., 1938. Studies of the permeability of erythrocytes. V. Factors in cation permeability. *Biochem. Journ.*, Vol. 32, pp. 991–1001.

6. Panikkar, N. K. & Sproston, N. G., 1941. Osmotic relations of some metazoan parasites. *Parasitology*, Vol. xxxiii, pp. 214–23.

See also: Under separate groups and species. Osmotic pressure and impulse in *Maia* nerve, XI C, 30; Ionic exchange during nervous activity, XI C, 56; Physiology of contractile vacuoles, XI H, 1, 2.

H. *Excretion*

1. Kitching, J. A., 1934. The physiology of contractile vacuoles. I. Osmotic relations. *Journ. Exp. Biol.*, Vol. xi, pp. 364–81.
2. Kitching, J. A., 1936. *Ibid.* II. The control of body volume in marine Peritricha. *Journ. Exp. Biol.*, Vol. xiii, pp. 11–27.
3. Grafflin, A. L., 1935. Renal function in marine teleosts. I. Urine flow and urinary chloride. *Biol. Bull. Woods Hole*, Vol. 69, pp. 391–402.

See also: Under separate groups and species.

J. *Feeding, digestion and absorption*

1. Yonge, C. M., 1928. Feeding mechanisms in the invertebrates. *Biol. Rev.*, Vol. 3, pp. 21–76.
2. Portmann, A. D. & Bidder, A. M., 1928. Yolk-absorption in *Loligo* and the function of the embryonic liver and pancreas. *Quart. Journ. Micr. Sci.*, Vol. 72, pp. 301–24.
3. Dawes, B., 1930. The absorption of fats and lipoids in the plaice (*P. platessa* L.). *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 75–102.
4. Mansour-Bek, J. J., 1930. Analyse der proteolytischen Enzyme von *Maja squinado* durch die Adsorptionsmethode. *Proc. Kon. Akad. Wetensch. Amsterdam*, Vol. xxxiii, pp. 858–70.
5. Yonge, C. M., 1931. Digestive processes in marine invertebrates and fishes. *Journ. Cons. Int. Explor. Mer*, Vol. vi, pp. 175–212.
6. Graham, A., 1931. On the optimum hydrogen ion concentration and temperature of the style enzyme of *Pecten maximus*. *Proc. Roy. Soc.*, B, Vol. 108, pp. 84–95.
7. Yonge, C. M., 1935. On some aspects of digestion in ciliary feeding animals. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 341–6.
8. Thomas, H. W. & Harvey, H. W., 1943. Absorption of iron. *Brit. Med. Journ.*, p. 83.

See also: Under separate groups and species. Absorption of radioactive strontium and yttrium by Algae, IX F, 31.

K. *Respiration and circulation*

1. Cook, S. F., 1928. The action of potassium cyanide and potassium ferricyanide on certain respiratory pigments. *Journ. Gen. Physiol.*, Vol. xi, pp. 339–48.
2. Bělehrádek, J. & Bělehrádková, M., 1929. Influence of age on the temperature coefficient of the respiration rate in leaves of *Scolopendrium scolopendrium* Karst. *New Phytol.*, Vol. xxviii, pp. 313–18.
3. Borden, M. A., 1931. A study of the respiration and of the function of hæmoglobin in *Planorbis corneus* and *Arenicola marina*. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 709–38.
4. Bassindale, R., Southgate, B. A. & Pentelow, F. T. K., 1933. The effect of cyanides on the gill colour of fish. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 671–6.
5. Florkin, M., 1933. Recherches sur les Hémérythrines. *Arch. Int. Physiol.*, T. xxxvi, pp. 247–328.

6. Cowan, S. L., 1933. The CO_2 dissociation curves and the buffering of crab's muscle and nerve preparations. *Journ. Exp. Biol.*, Vol. x, pp. 401–11.
7. Fox, H. M., 1933. The blood circulation of animals possessing chlorocruorin. *Proc. Roy. Soc.*, B, Vol. 112, pp. 479–95.
8. Cowan, S. L., 1935. The pH and CO_2 combining capacity of *Maia* blood. *Proc. Physiol. Soc.*, *Journ. Physiol.*, Vol. 84, pp. 53 *P*–54 *P*.
9. Humphrey, G. F., 1948. The effect of narcotics on the endogenous respiration and succinate oxidation in oyster muscle. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 504–12.

See also: Under separate groups and species.

L. *Vitamins and drugs*

1. Bacq, Z. M., 1937. Nouvelles observations sur l'acétylcholine et la choline-estérase chez les invertébrés. *Arch. Int. Physiol.*, T. xliv, pp. 174–89.
2. Bacq, Z. M. & Nachmansohn, D., 1937. Cholinesterase in invertebrate muscles. *Journ. Physiol.*, Vol. 89, pp. 368–71.
3. Atkins, W. R. G., 1943. The vitamin C saturation test. *Brit. Med. Journ.*, 27 Feb. 1943.
4. Atkins, W. R. G., 1943. Vitamin C saturation test of Harris and Abbasy. *Nature, Lond.*, Vol. 151, p. 21.

See also: Under separate groups and species. Reaction to drugs of viscera of teleosts, XI E, 19.

XII. BACTERIA AND FUNGI

1. Atkins, D., 1929. On a fungus allied to the Saprolegniaceae found in the pea-crab *Pinnotheres*. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 203–19.
1*a*. Lloyd, B., 1930. Bacteria of the Clyde sea area: a quantitative investigation. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 879–907.
2. Naylor, G. L., 1930. Note on the distribution of *Lichina confinis* and *L. pygmaea* in the Plymouth district. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 909–18.
3. Stewart, M. M., 1932. The bacterial flora of the slime and intestinal contents of the haddock (*Gadus aeglefinus*). *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 35–50.
4. Sproston, N. G., 1944. *Ichthyosporidium hoferi* (Plehn & Mulsow, 1911), an internal fungoid parasite of the mackerel. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 72–98.
5. Aleem, A. A., 1950. The occurrence of *Eurychasma Dicksonii* (Wright) Magnus in England and Sweden. *Medd. fr. Göteborgs Bot. Trädgärd*, xviii, pp. 239–45. (*Contr. Mar. Bot. Inst. Göteborg*, No. 2.)
6. Aleem, A. A., 1950. A fungus in *Ectocarpus granulosus* C. Agardh near Plymouth. *Nature, Lond.*, Vol. 165, p. 119.

See also: Bacteria of Clyde sea area, II, 5; Benthic micro-organisms, II, 9; Growth of yeast, VII, 5; Relation of bacteria to diatoms in the sea, XIII, 16; Bacteria-free cultures, XIII, 22; Fungus on *Zostera*, XV, 3.

XIII. UNICELLULAR ALGAE

1. Marshall, S. M. & Orr, A. P., 1928. The photosynthesis of diatom cultures in the sea. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 321–60.
2. Lebour, M. V., 1928. Floating plants (Phytoplankton) and borderland forms. *Science of the Sea*, ed. by G. H. Fowler and E. J. Allen (2nd ed.). Oxford. Ch. iv, pp. 150–64.

3. MARSHALL, S. M. & ORR, A. P., 1930. A study of the spring diatom increase in Loch Striven. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 853–78.
4. LEBOUR, M. V., 1930. *The Planktonic Diatoms of Northern Seas.* Ray Society, London.
5. STANBURY, F. A., 1931. The effect of light of different intensities, reduced selectively and non-selectively, upon the rate of growth of *Nitzschia closterium*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 633–53.
6. YONGE, C. M., 1931. Symbiotic Algae of corals. *Nature, Lond.*, Vol. 128, p. 760.
7. HARVEY, H. W., 1931. On the rate of photosynthesis by diatoms. *Rapp. Cons. Int. Explor. Mer*, Vol. LXXV, p. 70.
8. GHAZZAWI, F. M., 1933. The littoral diatoms of the Liverpool and Port Erin shores. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 165–76.
9. HARVEY, H. W., 1933. On the rate of diatom growth. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 253–76.
10. STANBURY, F. A., 1934. Replacement of potassium by rubidium in *Nitzschia closterium*. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 931–9.
11. WIMPENNY, R. S., 1936. The size of diatoms. I. The diameter variation of *Rhizosolenia styliformis* Brightw. and *R. alata* Brightw. in particular and of pelagic marine diatoms in general. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 29–60.
12. WIMPENNY, R. S., 1946. *Ibid.* II. Further observations on *Rhizosolenia styliformis* (Brightwell). *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 271–84.
13. GARSTANG, W., 1937. On the size-changes of diatoms and their oceanographic significance. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 83–96.
14. HARVEY, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 205–19.
15. JENKIN, P. M., 1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 301–43.
16. WAKSMAN, S. A., STOKES, J. L. & BUTLER, M. R., 1937. Relation of bacteria to diatoms in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 359–73.
17. GROSS, F., 1937. The life-history of some marine plankton diatoms. *Phil. Trans. Roy. Soc.*, B, Vol. 228, pp. 1–48.
18. HARVEY, H. W., 1939. Substances controlling the growth of a diatom. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 499–520.
19. GROSS, F., 1940. The development of isolated resting spores into auxospores in *Ditylum brightwelli* (West.). *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 375–80.
20. GROSS, F., 1940. The osmotic relations of the plankton diatom *Ditylum brightwelli* (West.). *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 381–415.
21. WILSON, D. P. & LUCAS, C. E., 1942. *Nitzschia* cultures at Hull and at Plymouth. *Nature, Lond.*, Vol. 149, p. 331.
22. CHU, S. P., 1946. Note on the technique of making bacteria-free cultures of marine diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 296–302.
23. WILSON, D. P., 1946. The triradiate and other forms of *Nitzschia closterium* (Ehrenberg) Wm. Smith, forma *minutissima* of Allen and Nelson. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 235–70.
24. PARKE, M., 1949. Studies on marine flagellates. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 255–86.

25. ALEEM, A. A., 1949. A quantitative method for estimating the periodicity of diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 713–17.

See also: Papers on phytoplankton in section V; IX, E 2, 5, 23; Benthic micro-organisms, II, 9; Autotrophic flagellates in plankton, V, 42; 'Tractellum' of flagellates, XVI A, 17; Swimming of flagellates, XVI C, 1; Rearing oyster larvae, XXV B, 34.

XIV. MULTICELLULAR ALGAE

1. WESTBROOK, M. A., 1928. Contributions to the cytology of tetrasporic plants of *Rhodymenia palmata* (L.) Grev., and some other Florideae. *Ann. Bot., Lond.*, Vol. 42, pp. 149–72.
2. KYLIN, H., 1928. Entwicklungsgeschichtliche Florideenstudien. *Lunds Univ. Årsskr.*, N.F. Avd. 2, Bd. XXIV, 127 pp.
3. WESTBROOK, M. A., 1930. *Compsothamnion thuyoides* (Smith) Schmitz. *Journ. Bot.*, Vol. LXVIII, pp. 353–64.
4. HÖFLER, K., 1931. Hypotonietod und osmotische Resistenz einiger Rotalgen. *Oesterr, Botan. Zeitschr.* Jahrg. 80, H. 1, pp. 51–71.
5. HÖFLER, K., 1932. Plasmolyseformen bei *Chaetomorpha* und *Cladophora*. *Protoplasma*, Bd. XVI, pp. 189–214.
6. WESTBROOK, M. A., 1934. *Antithamnion spirographidis* Schiffner. *Journ. Bot.*, Vol. LXII, pp. 65–8.
7. WESTBROOK, M. A., 1935. Observations on nuclear structure in the Florideae. *Beihefte Bot. Centralb.*, Bd. LIII, Abt. A, pp. 564–85.
8. LEWIS, E. A., 1936. An investigation of the seaweeds within a marked zone of the shore at Aberystwyth, during the year 1933–34 (with special reference to the use of the spores as food for oyster larvæ). *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 615–20.
9. NAYLOR, G. L., 1936. The fucoids of St John's Lake, Plymouth, including a hitherto undescribed form of *Fucus spiralis*. *Revue Algolog.*, T. VII, pp. 425–39.
10. BIEBL, R., 1937. Ökologische und Zellphysiologische Studien an Rotalgen der Englischen Südküste. *Beihefte Bot. Centralb.*, Bd. LVII, Abt. A, pp. 381–424.
11. BIEBL, R., 1937. Zur Protoplasmatischen Anatomie der Rotalgen. *Protoplasma*, Bd. XXVIII, pp. 562–81.
12. CHAPMAN, V. J., 1944. Methods of surveying *Laminaria* beds. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 37–60.
13. JOHNSON, T., 1947. The antherozoids of *Dictyopteris*. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, p. 138.
14. PARKE, MARY, 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 651–709.
15. PARKE, MARY, 1948. *Laminaria ochroleuca* De La Pylaie growing on the coast of Britain. *Nature, Lond.*, Vol. 162, pp. 295–6.
16. BLACK, W. A. P. & DEWAR, E. T., 1949. Correlation of some of the physical and chemical properties of the sea with the chemical constitution of the Algae. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 673–99.
17. BLACK, W. A. P., 1950. The seasonal variation in weight and chemical composition of the common British Laminariaceae. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 45–72.
18. PARKE, MARY W., 1950. Notes on the Plymouth marine flora: Algal records for the Plymouth region. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 257–61.

19. SPOONER, G. M., 1950. Notes on the Plymouth marine flora: Additional records of *Laminaria ochroleuca* de la Pylaie. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 261–2.
20. BLACK, W. A. P., 1950. The seasonal variation in the cellulose content of the common Scottish Laminariaceae and Fucaceae. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 379–87.
21. KNIGHT, M. & PARKE, M., 1951. A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 439–514.
22. WOODWARD, F. N., 1950. The Scottish Seaweed Research Association. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 719–25.

See also: Denudation of *Laminaria* forest, II, 9; Zonation of shore algae, IV, 4; Faunas inhabiting intertidal sea weeds, IV, 7; Ultracentrifuging eggs of *Fucus*, VII, 12; Relation to light, IX D, 46; Absorption of strontium and yttrium, IX F, 31; Fungus in *Ectocarpus*, XII, 6; Algal infection of *Balanus*, XXIII A, 16; Algal production and food of the limpet, XXV C, 10.

XV. FLOWERING PLANTS

1. ATKINS, W. R. G. & FENTON, E. W., 1930. The distribution of pasture plants in relation to soil acidity and other factors. *Sci. Proc. R. Dub. Soc.*, Vol. XIX, N.S., pp. 533–47.
2. CHAMBERS, R. & HÖFLER, K., 1931. Micrurgical studies on the tonoplast of *Allium cepa*. *Protoplasma*, Bd. XII, pp. 338–55.
3. TUTIN, T. G., 1934. The fungus on *Zostera marina*. *Nature, Lond.*, Vol. 134, p. 573.
4. TUTIN, T. G., 1936. New species of *Zostera* from Britain. *Journ. Bot.*, Vol. LXXIV, pp. 227–30.
5. ATKINS, W. R. G., 1938. The disappearance of *Zostera marina*. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 207–10.
6. TUTIN, T. G., 1938. The autecology of *Zostera marina* in relation to its wasting disease. *New Phytol.*, Vol. 37, pp. 50–71.
7. ATKINS, W. R. G., 1947. Disappearance of *Zostera marina*. *Nature, Lond.*, Vol. 159, p. 477.
8. WILSON, D. P., 1949. The decline of *Zostera marina* L. at Salcombe and its effects on the shore. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 395–412.

See also: Relation to light, IX D, 6, 7, 8, 20, 39, 40; Respiration, XI K, 2; Water content of wood, X, 16.

XVI. PROTOZOA

A. *Systematics and morphology*

1. PIXELL-GOODRICH, H., 1929. The gregarines of *Cucumaria*; *Lithocystis minchinii* Woode and *Lithocystis cucumariae* n.sp. *Quart. Journ. Micr. Sci.*, Vol. 73, pp. 275–87.
2. MACKINNON, D. L. & ROY, H. N., 1929. Lankester's 'Gregarine' from the eggs of *Thalassema neptuni*. *Nature, Lond.*, Vol. 124, p. 877.
3. HERON-ALLEN, E. & EARLAND, A., 1930. The Foraminifera of the Plymouth district. I and II. *Journ. Roy. Micr. Soc.*, Ser. III, Vol. L, pp. 46–84, 161–99.
4. ROY, H. N., 1930. Studies on some Sporozoa in polychaete worms. I. Gregarines of the genus *Selenidium*. *Parasitology*, Vol. 22, pp. 370–98.

5. MACKINNON, D. L. & ROY, H. N., 1931. Notes on the ciliate *Boveria stevensi* Issel from *Galeomma turtoni* Sowerby at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 577–82.
6. MACKINNON, D. L. & ROY, H. N., 1931. An amoeba from the intestine of an ascidian at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 583–6.
7. JEPPS, M. W., 1931. Note on a marine Labyrinthula. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 833–8.
8. MACKINNON, D. L. & ROY, H. N., 1931. Observations on dicystid gregarines from marine worms. *Quart. Journ. Micr. Sci.*, Vol. 74, pp. 439–66.
9. MACKINNON, D. L. & ROY, H. N., 1931. A new protozoan, *Hyperidion thalassemae*, n.gen., n.sp., from the intestine of *Thalassema neptuni* Gärtner. *Quart. Journ. Micr. Sci.*, Vol. 74, pp. 467–75.
10. GARNJOBST, L., 1934. Studies on *Stylonethes sterkii* sp.nov. I. Morphology and systematic position. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 707–22.
11. FOWELL, R. R., 1936. Observations on the Sporozoa inhabiting the gut of the polychaete worm *Polydora flava* Claparède. *Parasitology*, Vol. 28, pp. 414–30.
12. MACKINNON, D. L. & RAY, H. N., 1937. A coccidian from the eggs of *Thalassema neptuni* Gaertner. *Parasitology*, Vol. 29, pp. 457–68.
13. JEPPS, M. W., 1937. On the protozoan parasites of *Calanus finmarchicus* in the Clyde sea area. *Quart. Journ. Micr. Sci.*, Vol. 79, pp. 589–658.
14. DIBB, M. J., 1938. *Selenocystis foliata* (Ray) from *Scolelepis fuliginosa* Clpde. and its identity with *Haplozoon* sp. *Parasitology*, Vol. 30, pp. 296–308.
15. JEPPS, M. W., 1942. Studies on *Polystomella* Lamarck (Foraminifera). *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 607–66.
16. EARLAND & JEPPS, M. W., 1943. A note on an abnormal specimen of *Elphidium crispum* (L.). *Journ. Roy. Micr. Soc.*, Ser. 3, Vol. 63, pp. 43–7.
17. LOWNDES, A. G., 1943. The term *Tractellum* in flagellate organisms. *Nature, Lond.*, Vol. 152, p. 51.
18. MYERS, E. H., 1943. Life activities of Foraminifera in relation to marine ecology. *Proc. Amer. Phil. Soc.*, Vol. 86, pp. 439–58.
19. TRIPATHI, Y. R., 1948. A new species of ciliate, *Trichodina branchicola*, from some fishes at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 440–50.
20. DAS, S. M., 1948. British Folliculinidae (Ciliata, Heterotricha). *Nature, Lond.*, Vol. 162, p. 534.
21. DAS, S. M., 1949. British Folliculinidae (Ciliata, Heterotricha). *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 381–93.
22. TRIPATHI, Y. R., 1949. Some new Myxosporidia from Plymouth with a proposed new classification of the order. *Parasitology*, Vol. 39, pp. 110–18.

B. *Reproduction and development*

1. HENTSCHEL, C. C., 1930. On the correlation of the life history of the acephaline gregarine, *Gonospora*, with the sexual cycle of its host. II. *Gonospora* (*Kalpidorhynchus*) *arenicolae*. *Parasitology*, Vol. 22, pp. 505–9.
2. HERON-ALLEN, E., 1930. The further and final researches of Joseph Jackson Lister upon the reproductive processes of *Polystomella crispa* (Linné). *Smithsonian Misc. Coll.*, Vol. 82, pp. 1–11.
3. MYERS, E. H., 1940. Observations on the origin and fate of flagellated gametes in multiple tests of *Discorbis* (Foraminifera). *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 201–26.

See also: Growth acceleration, VII, 5.

C. *Physiology*

1. LOWNDES, A. G., 1944. The swimming of unicellular flagellate organisms. *Proc. Zool. Soc., Lond.*, A, Vol. 113, pp. 99–107.
2. LOWNDES, A. G., 1944. The swimming of *Monas stigmatica* Pringsheim and *Peranema tricophorum* (Ehrbg.) Stein and *Volvox* sp. Additional experiments on the working of a flagellum. *Proc. Zool. Soc., Lond.*, Vol. 114, pp. 325–38.
3. LOWNDES, A. G., 1945. Swimming of *Monas stigmatica*. *Nature, Lond.*, Vol. 155, p. 579.
4. LOWNDES, A. G., 1945. The swimming of *Euglena* and flagellar movement in general. *School Science Review*, June 1945, pp. 319–30.

See also: Ciliary motion, XI E, 3; Amoeboid motion, XI E, 4–7; Flagellar movement, XI E, 28; Contractile vacuoles, XI H, 1, 2.

D. *Ecology*

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

See also: Benthic micro-organisms, II, 9; *Orchitophrya* on *Asterias*, XXVII, 21.

XVII. PORIFERA

1. BURTON, M., 1930. Additions to the sponge fauna at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 489–507.
2. BORLEY, H. J. H., 1931. Some additions to the sponge fauna of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 839–45.
3. CRAWSHAY, L. R., 1939. Studies in the market sponges. I. Growth from the planted cutting. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 553–74.
4. JEPPS, M. W., 1947. Contribution to the study of the sponges. *Proc. Roy. Soc.*, B, Vol. 134, pp. 408–17.
5. BURTON, M., 1948. The synonymies of *Haliclona angulata* (Bowerbank) and *H. arcoferus* Vosmaer. *Ann. Mag. Nat. Hist.*, Ser. 12, Vol. 1, pp. 273–84.
6. BURTON, M., 1948. The ecology and natural history of *Tethya aurantium* Pallas. *Ann. Mag. Nat. Hist.*, Ser. 12, Vol. 1, pp. 122–30.
7. JØRGENSEN, C. B., 1949. Feeding-rates of sponges, lamellibranchs and ascidians. *Nature, Lond.*, Vol. 163, p. 912.

XVIII. COELENTERATA

A. *Systematics and morphology*

1. CARLGREN, O. & STEPHENSON, T. A., 1928. The British Edwardsidae. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 1–31.
2. STEPHENSON, T. A., 1928. *The British Sea Anemones*, Vol. I, 148 pp. Ray Society, publ. No. 113.

2*a*. STEPHENSON, T. A., 1929. On methods of reproduction as specific characters in sea anemones. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 131–72.

3. STEPHENSON, T. A., 1929. On the nematocysts of sea anemones. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 173–201.
4. STEPHENSON, T. A., 1929. A contribution to actinian morphology: the genera *Phellia* and *Sagartia*. *Trans. Roy. Soc. Edinb.*, Vol. LVI, pp. 121–39.
5. LEBOUR, M. V., 1930. *Protohydra*, a very simple animal. *Science Progress*, pp. 64–9.

6. Payne, N. M., 1931. Hydroid pigments. I. General discussion and pigments of the Sertulariidae. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 739–49.
7. Yonge, C. M., 1932. A note on *Balanophyllia regia*, the only eupsammiid coral in the British fauna. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 219–24.
8. Rawlinson, R., 1934. A comparative study of *Metridium senile* (L.) var. *dianthus* (Ellis) and a dwarf variety of this species occurring in the River Mersey, with a discussion on the systematic position of the genus *Metridium*. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 901–19.
9. Rawlinson, R., 1935. *Edwardsia callianthus* spec. nov. A new British species from Menai Straits. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 129–46.
10. Russell, F. S., 1936. On the hydroid of *Laodicea undulata* (Forbes & Goodsir). *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 581–7.
11. Russell, F. S., 1936. On a new species of medusa, *Eucheilota hartlaubi* n.sp. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 589–94.
12. Russell, F. S. & Rees, W. J., 1936. On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrady, with a review of the genus *Zanclea*. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 107–30.
13. Rees, W. J., 1936. On a new species of hydroid, *Staurocoryne filiformis*, with a revision of the genus *Staurocoryne* Rotch, 1872. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 135–42.
14. Rees, W. J., 1938. Observations on British and Norwegian hydroids and their medusae. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 1–42.
15. Russell, F. S., 1938–40. On the nematocysts of Hydromedusae. I, II and III. *Journ. Mar. Biol. Assoc.*, Vols. xxiii, pp. 145–65, 347–59; xxiv, pp. 515–23.
16. Eales, N. B., 1938. *Lucernaria discoidea*, a new species from the Channel Islands. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 167–70.
17. Russell, F. S., 1938–9. Jelly-Fish. I. Scyphomedusae. II. Hydromedusae. III. Conclusion. *School Science Review*, No. 78, pp. 268–79; No. 79, pp. 436–49; No. 80, pp. 588–93.
18. Rees, W. J., 1939. The hydroid of the medusa *Dipurena halterata* (Forbes). *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 343–6.
19. Russell, F. S., 1939. On the medusa *Gossea brachymera* Bigelow. *Proc. Zool. Soc., Lond.*, B, Vol. 108, pp. 707–10.
20. Rees, W. J., 1939. A revision of the genus *Campanulina* van Beneden 1847. *Ann. Mag. Nat. Hist.*, Ser. 11, Vol. 3, pp. 433–47.
21. Russell, F. S., 1940. On some medusae of the genera *Podocoryne* and *Phialopsis*. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 525–31.
22. Rees, W. J., 1941. Notes on British and Norwegian hydroids and medusae. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 129–41.
23. Manton, S. M., 1941. On the hydrorhiza and claspers of the hydroid *Myriothela cocksi* (Vigurs). *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 143–50.
24. Fox, D. L. & Pantin, C. F. A., 1941. The colours of the plumose anemone *Metridium senile* (L.). *Phil. Trans. Roy. Soc.*, B, Vol. 230, pp. 415–50.
25. Rees, W. J., 1941. The hydroid of the medusa *Cosmetira pilosella* Forbes. *Proc. Roy. Soc. Edinb.*, B, Vol. lxi, pp. 55–8.
26. Lowndes, A. G., 1942. Percentage of water in jelly-fish. *Nature, Lond.*, Vol. 150, pp. 234–5.
27. Lowndes, A. G., 1943. Water content of medusae. *Nature, Lond.*, Vol. 151, p. 226.
28. Fox, D. L. & Pantin, C. F. A., 1944. Pigments in the Coelenterata. *Biol. Rev.*, Vol. 19, pp. 121–34.

29. Lebour, M. V., 1947. An interesting young *Velella* in the Plymouth plankton. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 548–50.
30. Rees, W. J., 1947. On the systematic position of the hydroid genera *Hipolytus* Murbach, 1899, and *Dahlgrenella* Miles, 1937. *Ann. Mag. Nat. Hist.*, Ser. 11, Vol. xiii, pp. 102–6.
31. Pyefinch, K. A. & Downing, F. S., 1949. Notes on the general biology of *Tubularia larynx* Ellis & Solander. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 21–43.
32. Russell, F. S., 1949. On the hydroid of *Eutima gracilis* (Forbes & Goodsir). *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 479–80.
33. Russell, F. S., 1949–50. Fiches d'identification du Zooplankton. Hydromedusae. Family: Tubulariidae. Sheet 2. (1939.) Hydromedusae. Family: Tubulariidae (cont.). Family: Margelopsidae. Sheet 28. (1950.) Hydromedusae. Family: Corynidae. Sheet 29. (1950.) *Cons. Int. Explor. Mer*, Copenhagen.

B. *Reproduction and development*

1. Faulkner, G. H., 1929. The early prophases of the first oocyte division as seen in life in *Obelia geniculata*. *Quart. Journ. Micr. Sci.*, Vol. 73, pp. 225–42.
2. Russell, F. S., 1936. On the first stage of the medusa *Eucheilota clausa* (Hincks) [= *E. hartlaubi* Russell]. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 131–3.
3. Rees, W. J., 1937. The development of the hydroid *Corymorpha nutans* M. Sars from the egg. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 743–6.
4. Rees, W. J., 1937. On a remarkable process of bud formation in a gymnoblastic hydroid (*Heterostephanus* sp.). *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 747–51.
5. Rees, W. J. & Russell, F. S., 1937. On rearing the hydroids of certain medusae, with an account of the methods used. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 61–82.
6. Russell, F. S., 1938. On the development of *Muggiaea atlantica* Cunningham. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 441–6.
7. Rees, W. J., 1941. On the life history and developmental stages of the medusa *Podocoryne borealis*. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 307–16.

C. *Physiology*

1. Bateman, J. B., 1932. The osmotic properties of medusae. *Journ. Exp. Biol.*, Vol. ix, pp. 124–7.
2. Yonge, C. M., Yonge, M. J. & Nicholls, A. G., 1932. Studies on the physiology of corals. VI. The relationship between respiration in corals and the production of oxygen by their zooxanthellae. *Sci. Rept. Gt. Barrier Reef Exped.*, Vol. 1, No. 8.
3. Woollard, H. H. & Harpman, J. A., 1939. Discontinuity in the nervous system of coelenterates. *Journ. Anat.*, Vol. lxxiii, pp. 559–62.
4. Ross, D. M. & Pantin, C. F. A., 1940. Factors influencing facilitation in Actinozoa. The action of certain ions. *Journ. Exp. Biol.*, Vol. xvii, pp. 61–73.
5. Lowndes, A. G., 1942. Ciliary movement and the density of *Pleurobrachia*. *Nature, Lond.*, Vol. 150, pp. 579–80.
6. Pantin, C. F. A., 1942. The excitation of nematocysts. *Journ. Exp. Biol.*, Vol. xix, pp. 294–310.
7. Pantin, C. F. A. & Pantin, A. M., 1943. The stimulus to feeding in *Anemonia sulcata*. *Journ. Exp. Biol.*, Vol. xx, pp. 6–13.
8. Ross, D. M., 1945. Facilitation in sea anemones. I. The action of drugs. II. Tests on extracts. *Journ. Exp. Biol.*, Vol. xxii, pp. 21–31, 32–5.

9. BATHAM, E. J. & PANTIN, C. F. A., 1950. Muscular and hydrostatic action in the sea-anemone, *Metridium senile* (L.). *Journ. Exp. Biol.*, Vol. XXVII, pp. 264–89.
10. BATHAM, E. J. & PANTIN, C. F. A., 1950. Inherent activity in the sea-anemone, *Metridium senile* (L.). *Journ. Exp. Biol.*, Vol. XXVII, pp. 290–301.
11. BATHAM, E. J. & PANTIN, C. F. A., 1950. Phases of activity in the sea-anemone, *Metridium senile* (L.), and their relation to external stimuli. *Journ. Exp. Biol.*, Vol. XXVII, pp. 377–99.

See also Nerve-net, XI C, 33; Opening and closing of *Calliactis*, XI E, 29.

D. *Ecology*

1. BERRILL, N. J., 1930. On the occurrence and habits of the siphonophore, *Stephanomia bijuga* (Delle Chiaje). *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 753–5.
2. SANDERSON, A. R., 1930. The coelenterate plankton of the Northumbrian coast during the year 1924. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 219–32.
3. WATSON, H. G., 1930. The coelenterate plankton of the Northumbrian coast during the year 1925. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 233–9.
4. RUSSELL, F. S., 1931. Notes on *Cyanea* caught in the ring-trawl in the Plymouth area during the years 1925 to 1930. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 573–6.
5. RUSSELL, F. S. & KEMP, S., 1932. Pelagic animals off the south-west coasts of the British Isles. *Nature, Lond.*, Vol. 130, p. 664.
6. RUSSELL, F. S., 1934. On the occurrence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 555–8.
7. RAWLINSON, R., 1936. The occurrence of *Diadumene cincta* T. A. Stephenson in the River Roach, Essex. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 91–3.
8. LUCAS, C. E. & HENDERSON, G. T. D., 1936. On the association of jelly-fish and other organisms with catches of herring. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 293–304.
9. RUSSELL, F. S., 1938. The Plymouth offshore medusa fauna. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 411–39.
10. CORBIN, P. G. & PANIKKAR, N. K., 1942. The distribution of *Arachnactis albida* M. Sars in the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 509–16.
11. WILSON, D. P., 1947. The Portuguese Man-of-War *Physalia physalis* L., in British and adjacent seas. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 139–72.

See also: Symbiotic algae of corals, XIII, 6.

XIX. PLATYHELMINTHES

A. *Systematics and morphology*

1. JONES, E. I. & ROTHSCHILD, M., 1932. On the sporocyst and cercaria of a marine distomid trematode from *Nucula*. *Parasitology*, Vol. 24, pp. 260–4.
2. JONES, E. I., 1933. Studies on the Monogenea of Plymouth. *Gastrocotyle trachuri* v. Ben. and Hesse, 1863. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 227–32.
3. ATKINS, D., 1933. *Rhopalura granosa* sp.nov., an orthonectid parasite of a lamellibranch *Heteranomia squamula* L. with a note on its swimming behaviour. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 233–52.

4. JONES, E. I., 1933. On *Ceratotrema furcolabiata* n.g. et n.sp. and *Hemiphera sharpei* n.sp., two new digenetic trematodes of British marine fishes. *Parasitology*, Vol. 25, pp. 248–54.
5. JONES, E. I., 1933. Studies on the Monogenea (Trematoda) of Plymouth. I. *Microbothrium caniculae* (Johnstone 1911). *Parasitology*, Vol. 25, pp. 329–31.
6. ATKINS, D., 1934. Two parasites of the common cockle *Cardium edule*; a rhabdocoele, *Paravortex cardii* Hallez and a copepod, *Paranthessius rostratus* (Canu). *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 669–76.
7. LEBOUR, M. V., 1935. *Hemiuris communis* in *Acartia*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 371–2.
8. ROTHSCHILD, M., 1935. The trematode parasites of *Turritella communis* Lmk. from Plymouth and Naples. *Parasitology*, Vol. 27, pp. 152–70.
9. BAYLIS, H. A., 1938. On two species of the trematode genus *Didymozoon* from the mackerel. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 485–92.
10. ROTHSCHILD, M., 1938. *Cercaria sinitzini* n.sp., a cystophorous cercaria from *Peringia ulvae* (Pennant, 1777). *Novitates Zoolog.*, Vol. XLI, pp. 42–57.
11. ROTHSCHILD, M., 1938. Notes on the classification of cercariae of the superfamily Notocotyloidea (Trematoda) with special reference to the excretory system. *Novitates Zoolog.*, Vol. XLI, pp. 75–83.
12. ROTHSCHILD, M., 1938. Further observations on the effect of trematode parasites on *Peringia ulvae* (Pennant) 1777. *Novitates Zoolog.*, Vol. XLI, pp. 84–102.
13. ROTHSCHILD, M., 1938. The excretory system of *Cercaria coronanda* n.sp. together with notes on its life-history and the classification of cercariae in the superfamily Opisthorchioidea Vogel 1934 (Trematoda). *Novitates Zoolog.*, Vol. XLI, pp. 148–63.
14. ROTHSCHILD, M., 1938. A note on the fin-folds of cercariae of the superfamily Opisthorchioidea Vogel 1934 (Trematoda). *Novitates Zoolog.*, Vol. XLI, pp. 170–3.
15. ROTHSCHILD, M., 1939. Large and small flame-cells in a cercaria (Trematoda). *Novitates Zoolog.*, Vol. XLI, p. 376.
16. ROTHSCHILD, M. & SPROSTON, N. G., 1941. The metacercaria of *Cercaria doricha* Roths. 1934, or a closely related species. *Parasitology*, Vol. 33, pp. 359–62.
17. ROTHSCHILD, M., 1941. The metacercaria of a Pleurolophocerca cercaria parasitizing *Peringia ulvae* (Pennant), 1777. *Parasitology*, Vol. 33, pp. 439–44.
18. ROTHSCHILD, M., 1942. A seven-year-old infection of *Cryptocotyle lingua* Creplin in the winkle *Littorina littorea* L. *Journ. Parasit.*, Vol. XXVIII, p. 350.
19. SPROSTON, N. G., 1945. The genus *Kuhnia* n.g. (Trematoda: Monogenea). An examination of the value of some specific characters, including factors of relative growth. *Parasitology*, Vol. 36, pp. 176–90.
20. SPROSTON, N. G., 1945. A note on the comparative anatomy of the clamps in the superfamily Diclidophoroidea (Trematoda: Monogenea). *Parasitology*, Vol. 36, pp. 191–4.
21. SPROSTON, N. G., 1946. A synopsis of the monogenetic trematodes. *Trans. Zool. Soc. Lond.*, Vol. XXV, pp. 185–600.
22. REES, W. J., 1947. A cercaria of the genus *Haplocladus* from *Nucula nucleus* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 602–4.
23. SPROSTON, N. G., 1948. On the genus *Dinobothrium* van Beneden (Cestoda), with a description of two new species from sharks, and a note on *Monorygma* sp. from the electric ray. *Parasitology*, Vol. 39, pp. 73–90.

B. *Reproduction and development*

1. Jones, E. I., 1933. Fertilisation and egg formation in a digenetic trematode, *Podocotyle atomen*. *Parasitology*, Vol. 24, pp. 545–7.
2. Rothschild, M., 1936–40. Rearing animals in captivity for the study of trematode life histories. I. *Larus ridibundus* L., the black-headed gull. II. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 143–5; Vol. xxiv, pp. 613–17.
3. Rothschild, M., 1939. A note on the life cycle of *Cryptocotyle lingua* (Creplin) 1825 (Trematoda). *Novitates Zoolog.*, Vol. xli, pp. 178–80.
4. Rothschild, M., 1941. Note on life-histories of the genus *Paramonostomum* Lühe 1909 (Trematoda Notocotylidae) with special reference to the excretory vesicle. *Journ. Parasit.*, Vol. xxvii, pp. 363–5.
5. Rothschild, M., 1942. A further note on life-history experiments with *Cryptocotyle lingua* (Creplin, 1825). *Journ. Parasit.*, Vol. xxviii, pp. 91–2.

C. *Physiology*

1. Pantin, C. F. A., 1931. The adaptation of *Gunda ulvae* to salinity. I. The environment. *Journ. Exp. Biol.*, Vol. viii, pp. 63–72.
2. Weil, E. & Pantin, C. F. A., 1931. The adaptation of *Gunda ulvae* to salinity. II. The water exchange. *Journ. Exp. Biol.*, Vol. viii, pp. 73–81.
3. Pantin, C. F. A., 1931. The adaptation of *Gunda ulvae* to salinity. III. The electrolyte exchange. *Journ. Exp. Biol.*, Vol. viii, pp. 82–94.

D. *Ecology*

1. Leigh-Sharpe, W. H., 1933. Note on the occurrence of *Graffilla gemmelipara* Linton (Turbellaria) at Plymouth. *Parasitology*, Vol. 25, No. 1, 1 p.
2. Ritchie, A. D., 1934. The habitat of *Procerodes ulvae*. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 663–8.
3. Chrenko, F., 1934. A list of parasitic Rhabdocoela (Turbellaria) of Plymouth. *Parasitology*, Vol. 26, pp. 114–16.
4. Lysaght, A. M., 1943. The incidence of larval trematodes in males and females of the gastropod *Littorina neritoides* (L.) on the Plymouth Breakwater. *Parasitology*, Vol. 35, pp. 17–22.
5. Atkins, W. R. G., 1947. A suggested repellent for schistosome cercariae. *Journ. Hygiene*, Vol. 45, 1 p.

See also: Parasites of Mollusca, XXV A, 22–4, B, 37, 39; Parasitic worms from fish, XXIX D, 7.

XX. NEMERTINEA, NEMATODA AND CHAETOGNATHA

1. Thynne, M. A., 1930. Thread worms. Report on maternity and child welfare work in the City of Plymouth. *M.O.H. Report on Health of Plymouth in* 1930, App. II, pp. 51–4.
2. John, C. C., 1931. On the anatomy of the head of *Sagitta*. *Proc. Zool. Soc.*, pp. 1307–19.
3. Russell, F. S., 1932. On the biology of *Sagitta*. The breeding and growth of *Sagitta elegans* Verrill in the Plymouth area, 1930–1. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 131–45.
4. Russell, F. S., 1932. *Ibid.* II. The breeding and growth of *Sagitta setosa* J. Müller in the Plymouth area, 1930–31, with a comparison with that of *S. elegans* Verrill. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 147–60.

5. RUSSELL, F. S., 1933. *Ibid.* III. A further observation on the growth and breeding of *Sagitta setosa* in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 555–8.
6. RUSSELL, F. S., 1933. *Ibid.* IV. Observations on the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 559–74.
7. BAYLIS, H. A., 1933. The nematode genus *Ascarophis* van Beneden. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. XI, pp. 111–17.
8. JOHN, C. C., 1933. Habits, structure and development of *Spadella cephaloptera*. *Quart. Journ. Micr. Sci.*, Vol. 75, pp. 625–96.
9. STIASNY-WIJNHOFF, G., 1934. Some remarks on North Atlantic non-pelagic Polystilifera. *Quart. Journ. Micr. Sci.*, Vol. 77, pp. 167–90.
10. SMITH, J. E., 1935. The early development of the nemertean *Cephalothrix rufifrons*. *Quart. Journ. Micr. Sci.*, Vol. 77, pp. 335–81.
11. BACQ, Z. M., 1937. L''Amphiporine' et la 'némertine' poisons des vers némertiens. *Arch. Int. Physiol.*, T. XLIV, pp. 190–204.
12. RUSSELL, F. S., 1949. Chaetognatha. Fiches d'identification du Zooplancton. No. 1. *Cons. Int. Explor. Mer*, Copenhagen (1939).
13. PIERCE, E. L., 1941. The occurrence and breeding of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in parts of the Irish Sea. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 113–24.
14. PARRY, D. A., 1944. Structure and function of the gut in *Spadella cephaloptera* and *Sagitta setosa*. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 16–36.
15. FRASER, J. H., 1949. The occurrence of unusual species of Chaetognatha in Scottish plankton collections. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 489–91.

See also: Vertical migrations of *Sagitta* in the sea, V, 5; *Sagitta* as indicator of water movements, V, 21, 25, 30, 35; Phosphorus and iron in *Sagitta*, X, 13; Parasitic worms from fish, XXIX, D, 7.

XXI. ANNELIDA, GEPHYREA

A. *Systematics and morphology*

1. LEIGH-SHARPE, W. H., 1928. *Thalassema neptuni* Gaertner—a British echiuroid. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. 2, pp. 499–504.
2. MEYER, A., 1929. Über Cölombewimperung und cölomatische Kreislaufsysteme bei Wirbellosen. II. Teil. (Sipunculoidea, Polychaeta Errantia.) Ein Beitrag zur Histophysiologie und Phylogenese des Cölomsystems. *Zeit. f. wiss. Zool.*, Bd. CXXXV, pp. 495–538.
3. FAULKNER, G. H., 1930. The anatomy and the histology of bud-formation in the serpulid *Filograna implexa*, together with some cytological observations on the nuclei of the neoblasts. *Journ. Linn. Soc., Zool.*, Vol. XXXVII, pp. 109–90.
4. GOODRICH, E. S., 1931. Notes on *Protodrilus*. *Quart. Journ. Micr. Sci.*, Vol. 74, pp. 303–19.
5. OKADA, YÔ K., 1933. Syllidian miscellany. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 641–53.
6. OKADA, YÔ K., 1933. Remarks on the reversible asymmetry in the opercula of the polychaete *Hydroides*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 655–70.
7. LEIGH-SHARPE, W. H., 1933. The Hirudinea of Plymouth, I. *Parasitology*, Vol. 25, pp. 255–62.

8. HUTH, W., 1933. *Ophryotrocha* Studien I. Zur cytologie der Ophryotrochen. *Zeitschr. f. Zellforsch. u. Mikr. Anat.*, Bd. xx, pp. 309–81.
9. WILSON, D. P., 1937. A double-tailed *Eulalia*. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 663–71.
10. KNIGHT-JONES, E. W., 1940. The occurrence of a marine leech, *Abranchus blennii* n.sp., resembling *A. sexoculatus* (Malm.), in North Wales. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 533–41.
11. LEBOUR, M. V., 1942. Stellate chromatophores in the Polychaeta. *Nature, Lond.*, Vol. 150, pp. 209–10.
12. EWER, D. W., 1946. *Sabella pavonina* Savigny var. *bicoronata* Hornell and the genus *Spirographis* Viviani (Polychaeta, Sabellidae). *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 426–31.
13. HANSON, J., 1948. The genera *Apomatus* and *Protula* (Polychaeta, Serpulidae). *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 581–4.
14. BACKLUND, H. O., 1948. *Lumbricillus reynoldsoni* n.sp., an enchytraeid from the beaches of North Wales. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 710–17.
15. WELLS, G. P., 1950. The anatomy of the body wall and appendages in *Arenicola marina* L., *Arenicola claparedii* Levinsen and *Arenicola ecaudata* Johnston. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 1–44.
16. HANSON, J., 1950. The blood-system in the Serpulimorpha (Annelida, Polychaeta). II. The anatomy of the blood-system in the Sabellidae, and a comparison of Sabellidae and Serpulidae. *Quart. Journ. Micr. Sci.*, Vol. 91, pp. 369–78.

B. *Reproduction and development*

1. WILSON, D. P., 1928. The post-larval development of *Loimia medusa* Sav. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 129–49.
2. BERRILL, N. J., 1928. Regeneration in the polychaet *Chaetopterus variopedatus*. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 151–8.
3. WILSON, D. P., 1928. The larvae of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 567–603.
4. WILSON, D. P., 1929. The larvae of the British sabellarians. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 221–69.
5. OKADA, Yô K., 1929. Sacconereis of *Procerastea*. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 325–8.
6. OKADA, Yô K., 1929. Regeneration and fragmentation in the syllidian polychaetes. (Studies on the Syllidæ. II.) *Arch. EntwMeck. Org.*, Bd. 115, pp. 542–600.
7. OKADA, Yô K., 1930. Incubation-habit in a phyllodocid polychaete, *Notophyllum foliosum* Sars. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 475–7.
8. OKADA, Yô K., 1930. A remark on the constitution of larval syllids. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 479–87.
9. WILSON, D. P., 1932. The development of *Nereis pelagica* Linnæus. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 203–17.
10. OKADA, Yô K., 1932. Les possibilités de la régénération de la tête chez le Polychète *Myxicola aesthetica* (Clap.). *Annot. Zool. Jap.*, Vol. xiii, pp. 535–50.
11. WILSON, D. P., 1932. On the Mitraria larva of *Owenia fusiformis* Delle Chiaje. *Phil. Trans. Roy. Soc.*, B, Vol. 221, pp. 231–334.
12. WILSON, D. P., 1933. The larval stages of *Notomastus latericeus* Sars. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 511–18.

13. Day, J. H., 1934. Development of *Scolecolepis fuliginosa* (Claparède). *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 633–54.
14. Okada, Yô K., 1934. Régénération de la tête chez le polychète *Myxicola aesthetica* (Clap.). *Bull. Biol.*, T. lxviii, pp. 340–81.
15. Okada, Yô K., 1934. Formation de têtes dans la stolonisation des polychètes syllidiens. *Bull. Soc. Zool. France*, T. lix, pp. 388–405.
16. Okada, Yô K., 1935. Stolonization in *Myrianida*. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 93–8.
17. Wilson, D. P., 1936. Notes on the early stages of two polychaetes, *Nephthys hombergi* Lamarck and *Pectinaria koreni* Malmgren. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 305–10.
18. Wilson, D. P., 1936. The development of *Audouinia tentaculata* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 567–79.
19. Nolte, W., 1936. Annelidenlarven. *Nordisches Plankton*, Lief. xxiii, pp. x, 59–169.
20. Wilson, D. P., 1936. The development of the sabellid *Branchiomma vesiculosum*. *Quart. Journ. Micr. Sci.*, Vol. 78, pp. 543–603.
21. Okada, Yô K., 1937. La stolonisation et les caractères sexuels du stolon chez les syllidiens polychètes. (Études sur les syllidiens III.) *Jap. Journ. Zoology*, Vol. vii, pp. 441–90.
22. Nolte, W., 1937. Die Zucht und Konservierung der Polychaetenlarven. *Journ. Cons. Int. Explor. Mer*, Vol. xii, pp. 51–76.
23. Okada, Yô K., 1938. An internal factor controlling posterior regeneration in syllid polychaetes. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 75–8.
24. Meyer, A., 1938. Der Rogen (spawn) und die Entwicklung der Trochophora von *Eulalia viridis* (Phyllodocidae). *Biolog. Generalis*, Bd. xiv, pp. 333–89.
25. Wilson, D. P., 1948. The larval development of *Ophelia bicornis* Savigny. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 540–53.
26. Newell, G. E., 1948. A contribution to our knowledge of the life history of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 554–80.
27. Newell, G. E., 1949. The later larval life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 635–9.
28. Dales, R. Phillips, 1950. The reproduction and larval development of *Nereis diversicolor* O. F. Müller. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 321–60.

See also: Action of salt solutions on eggs of *Thalassema*, VII, 1; Regeneration, VII, 6, 8, 9; Streaming in Sabellarian egg, XI B, 2; Larval settlement, XXI C, 5, 6, 11.

C. *Physiology*

1. Okada, Yô K., 1928. Feeding organs and feeding habits of *Autolytus edwarsi* St Joseph. *Quart. Journ. Micr. Sci.*, Vol. 72, pp. 219–45.
2. Meyer, A., 1929. On the coelomic cilia and circulation of the body-fluid in *Tomopteris helgolandica*. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 271–6.
3. Nicol, E. A. T., 1930. The feeding mechanism, formation of the tube, and physiology of digestion in *Sabella pavonina*. *Trans. Roy. Soc. Edin.*, Vol. lvi, pp. 537–98.
4. Faouzi, H., 1931. Tube formation in *Pomatoceros triqueter* L. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 379–84.

5. Day, J. H. & Wilson, D. P., 1934. On the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* (Claparède). *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 655–62.
6. Wilson, D. P., 1937. The influence of the substratum on the metamorphosis of *Notomastus* larvae. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 227–43.
7. Wells, G. P., 1937. Studies on the physiology of *Arenicola marina* L. I. The pacemaker role of the oesophagus, and the action of adrenaline and acetylcholine. *Journ. Exp. Biol.*, Vol. xiv, pp. 117–57.
8. Cragg, J. B., 1939. The physiology of maturation and fertilization in *Pomatoceros triqueter* (L.). I. The nature of the material. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 483–97.
9. Wu, K. S., 1939. The action of drugs, especially acetylcholine, on the annelid body wall (*Lumbricus*, *Arenicola*). *Journ. Exp. Biol.*, Vol. xvi, pp. 251–7.
10. Ewer, D. W. & Ewer, R. F., 1943. Osmotic regulation in *Sabella pavonina*. *Nature, Lond.*, Vol. 152, pp. 598–9.
11. Wilson, D. P., 1948. The relation of the substratum to the metamorphosis of *Ophelia* larvae. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 723–60.
12. Wells, G. P., 1949. Respiratory movements of *Arenicola marina* L.: intermittent irrigation of the tube, and intermittent aerial respiration. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 447–64.
13. Wells, G. P., 1949. The behaviour of *Arenicola marina* L. in sand, and the role of spontaneous activity cycles. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 465–78.
14. Nicol, J. A. C., 1950. Responses of *Branchiomma vesiculosum* (Montagu) to photic stimulation. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 303–20.

See also: Annelid phosphagen, X, 19; Nerve physiology, XI C, 43, 45, 46, 47, 48; Spontaneous activity patterns, XI F, 12; Respiration, XI K, 3, 5, 7.

D. *Ecology*

1. Reid, D. M., 1929. On some factors limiting the habitat of *Arenicola marina*. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 109–16.
2. Wells, G. P., 1945. The mode of life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 170–207.
3. Chapman, G. & Newell, G. E., 1949. The distribution of lugworms (*Arenicola marina* L.) over the flats at Whitstable. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 627–34.

See also: Parasites, XVI A, 2, 8, 11, 12, 14.

XXII. ROTIFERA

1. Hollowday, E. D., 1949. A preliminary report on the Plymouth marine and brackish-water Rotifera. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 239–53.

XXIII. CRUSTACEA

A. *Systematics and morphology*

1. Okada, Yô K., 1928. Note on the tail-organs of *Acetes*. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. 1, pp. 308–10.
2. Leigh-Sharpe, W. H., 1928. *Brachiella obesa*, a parasitic copepod of *Trigla cuculus*, with a description of the male. *Parasitology*, Vol. 20, pp. 25–31.

3. Boschma, H., 1929. *Galatheascus striatus*—a new rhizocephalan. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 73–9.
4. Sexton, E. W., Clark, A. R. & Spooner, G. M., 1930–2. Some new eye-colour changes in *Gammarus chevreuxi* Sexton. Parts I and II. *Journ. Mar. Biol. Assoc.*, Vols. xvii, pp. 189–218; xviii, pp. 307–36.
5. Spooner, G. M., 1932. An experiment on breeding wild pairs of *Gammarus chevreuxi* at a high temperature, with an account of two new recessive types of red eye. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 337–53.
6. Sexton, E. W., 1932. Degeneration and loss of the eye in the amphipod, *Gammarus chevreuxi* Sexton. Part I. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 355–93.
7. Alexandrowicz, J. S., 1932. The innervation of the heart of the Crustacea. I. Decapoda. *Quart. Journ. Micr. Sci.*, Vol. 75, pp. 181–249.
8. Gray, P., 1933. *Mycophilus rosovula* n.sp., a notodelphoid copepod parasitic within *B.* (*Botrylloides*) *leachii* Sav., with a description of the nauplius and notes on the habits. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 523–7.
9. Bassindale, R., 1933. Abnormal eyes in wild *Gammarus zaddachi* Sexton. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 297–8.
10. Gurney, R., 1933. Notes on some Copepoda from Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 299–304.
11. Atkins, D., 1933. *Pinnotherion vermiforme* Giard and Bonnier, an entoniscid infecting *Pinnotheres pisum*. *Proc. Zool. Soc. Lond.*, pp. 319–63.
12. Sexton, E. W. & Clark, A. R., 1933. Further mutations in the amphipod *Gammarus chevreuxi* Sexton. *Nature, Lond.*, Vol. 131, pp. 201–2.
13. Young, J. Z., 1933. Extra legs on the tails of crabs. *Nature, Lond.*, Vol. 132, p. 785.
14. Sexton, E. W. & Clark, A. R., 1934. New developments in *Gammarus chevreuxi* Sexton. *Nature, Lond.*, Vol. 133, p. 27.
15. Shen, C. J., 1934. A comparative study of the statocysts of Eumalacostraca, with special reference to the Macrura. *Proc. Zool. Soc. Lond.*, pp. 534–57.
16. Parke, M. & Moore, H. B., 1935. The biology of *Balanus balanoides*. II. Algal infection of the shell. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 49–56.
17. Moore, H. B., 1935. The biology of *Balanus balanoides*. III. The soft parts. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 263–77.
18. Sexton, E. W., Clark, A. R. & Spooner, G. M., 1935. First appearance of red-eye in the wild *Gammarus chevreuxi* Sexton. *Nature, Lond.*, Vol. 136, p. 836.
19. Leigh-Sharpe, W. H., 1935. *Epibrachiella impudica* (Nordmann) (Copepoda). *Parasitology*, Vol. 27, pp. 101–6.
20. Leigh-Sharpe, W. H., 1935. Some new and rare Lernaeidae (Copepoda) from Plymouth. *Parasitology*, Vol. 27, pp. 107–10.
21. Leigh-Sharpe, W. H., 1935. *Anchistrotus laquens* n.sp. a parasitic copepod of *Serranus cabrilla*. *Parasitology*, Vol. 27, pp. 266–9.
22. Leigh-Sharpe, W. H., 1935. Two copepods (*Lernaeenicus*) parasitic on *Clupea*. *Parasitology*, Vol. 27, pp. 270–5.
23. Sexton, E. W. & Clark, A. R., 1936. Variations in the white pigment of the eye in *Gammarus chevreuxi* Sexton, with a description of a new genetic type, the 'Clotted Eye'. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 691–9.
24. Sexton, E. W. & Clark, A. R., 1936. Heterozygotes in a wild population of *Gammarus chevreuxi* Sexton. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 319–56.

25. Sexton, E. W. & Clark, A. R., 1936. A summary of the work on the amphipod *Gammarus chevreuxi* Sexton carried out at the Plymouth Laboratory (1912–1936). *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 357–414.
26. Lebour, M. V., 1936. Notes on the Plymouth species of *Spirontocaris* (Crustacea). *Proc. Zool. Soc. Lond.*, pp. 89–104.
27. Lebour, M. V., 1936. Notes on the Plymouth *Processa* (Crustacea). *Proc. Zool. Soc. Lond.*, pp. 609–17.
28. Crawford, G. I., 1937. A review of the amphipod genus *Corophium* with notes on the British species. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 589–630.
29. Watkin, E. E., 1938. A revision of the amphipod genus *Bathyporeia* Lindström. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 211–36.
30. Nicholls, A. G., 1939. Some new sand-dwelling copepods. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 327–41.
31. Sexton, E. W., 1939. On a new species of *Gammarus* (*G. tigrinus*) from Droitwich district. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 543–51.
32. Kemp, S., 1939. On *Acanthephyra purpurea* and its allies (Crustacea Decapoda: Hoplophoridae). *Ann. Mag. Nat. Hist.*, Ser. 11., Vol. 4, pp. 568–79.
33. Sexton, E. W. & Spooner, G. M., 1940. An account of *Marinogammarus* (Schellenberg) gen.nov. (Amphipoda), with a description of a new species, *M. pirloti*. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 633–82.
34. Watkin, E. E., 1941. The male of the amphipod *Haustorius arenarius* Slabber. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 303–5.
35. Sexton, E. W., 1942. The relation of *Gammarus zaddachi* Sexton to some other species of *Gammarus* occurring in fresh, estuarine and marine waters. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 575–606.
36. Lebour, M. V., 1943. The crab. *School Sci. Rev.*, No. 94, pp. 319–27.
37. Thomas, H. J., 1944. Tegumental glands in the Cirripedia Thoracica. *Quart. Journ. Micr. Sci.*, Vol. 84, pp. 257–82.
38. Lebour, M. V., 1944. Shrimps and prawns. *School Sci. Rev.*, No. 96, pp. 209–16.
39. Lebour, M. V., 1945. The lobster and its relatives. *School Sci. Rev.*, No. 99, pp. 208–14.
40. Gurney, R., 1947. Some notes on parasitic Copepoda. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 133–7.
41. Segerstråle, S. G., 1947. New observations on the distribution and morphology of the amphipod, *Gammarus zaddachi* Sexton, with notes on related species. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 219–44.
42. Pike, R. B., 1947. *Galathea* (in part). L.M.B.C. Memoir, xxxiv. Liverpool University Press, 178 pp.
43. Pyefinch, K. A., 1948. Methods of identification of the larvae of *Balanus balanoides* (L.), *B. crenatus* Brug. and *Verruca stroemia* O. F. Müller. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 451–63.
44. Graham, M., 1949. A note on the theory of a dwarf race of lobsters on the Norfolk coast. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 481–7.
45. Tattersall, O. S., 1949. Notes on Plymouth Mysidacea. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 781–9.
46. Sexton, E. W., 1949. The multiform species *Jassa falcata* (Montagu 1808). Crustacea, Amphipoda. *Proc. Linn. Soc.*, Vol. 161, 1948–9, pp. 144–5. (Abstract of Exhibit by Dr Isabella Gordon, Linn. Soc., General Meeting, April 1949.)
47. Lebour, M. V., 1949. Some new Decapod Crustacea from Bermuda. *Proc. Zool. Soc.*, Vol. 118, pp. 1107–17.

48. LEBOUR, M. V., 1950. Some euphausids from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 119, pp. 823–37.
49. LOWNDES, A. G., 1950. The males of *Canthocamptus bidens* Schmeil. *Proc. Zool. Soc. Lond.*, Vol. 120, pp. 395–403.

See also: Nerve fibres of Crustacea, XXV A, 24*a*.

B. *Reproduction and development*

1. SEXTON, E. W., 1928. On the rearing and breeding of *Gammarus* in laboratory conditions. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 33–55.
2. MACDONALD, R., 1928. The life history of *Thysanoessa raschii*. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 57–79.
3. LEBOUR, M. V., 1928. Studies of the Plymouth Brachyura. II. The larval stages of *Ebalia* and *Pinnotheres*. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 109–23.
4. FROST, W. E., 1928. The nauplius larva of *Anelasma squalicola* (Lovén). *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 125–8.
5. KUNKEL, B. W. & ROBERTSON, J. A., 1928. Contributions to the study of relative growth in *Gammarus chevreuxi*. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 655–81.
6. LEBOUR, M. V., 1928. The larval stages of the Plymouth Brachyura. *Proc. Zool. Soc. Lond.*, pp. 473–560.
7. GURNEY, R., 1930. The larva of *Nicothoë astaci* and its systematic position. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 453–9.
8. GURNEY, R., 1930. The larval stages of the copepod *Longipedia*. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 461–74.
9. LEBOUR, M. V., 1930. The larvae of the Plymouth Galatheidae. I. *Munida banffica*, *Galathea strigosa* and *Galathea dispersa*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 175–87.
10. LEBOUR, M. V., 1931. *Ibid.* II. *Galathea squamifera* and *Galathea intermedia*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 385–90.
11. LEBOUR, M. V., 1930. The larval stages of *Caridion*, with a description of a new species *C. steveni*. *Proc. Zool. Soc. Lond.*, pp. 181–94.
12. LEBOUR, M. V., 1931. The larvae of the Plymouth Caridea. I. The larvae of the Crangonidae. II. The larvae of the Hippolytidae. *Proc. Zool. Soc. Lond.*, pp. 1–9.
13. LEBOUR, M. V., 1932. *Ibid.* III. The larval stages of *Spirontocaris cranchii* (Leach). *Proc. Zool. Soc. Lond.*, pp. 131–7.
14. LEBOUR, M. V., 1932. *Ibid.* IV. The Alpheidae. *Proc. Zool. Soc. Lond.*, pp. 463–9.
15. LEBOUR, M. V., 1931. Further notes on larval Brachyura. *Proc. Zool. Soc. Lond.*, pp. 93–6.
16. GRAY, P., 1933. The nauplii of *Notodelphys agilis* Thorell and *Doropygus porcicauda* Brady. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 519–22.

16*a*. OGILVIE, H. S. & GIBBONS, S. G., 1933. The developmental stages of *Oithona helgolandica* and *Oithona spinirostris* with a note on the occurrence of body spines in cyclopoid nauplii. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 529–50.

17. RUSSELL, F. S., 1933. On the occurrence of young stages of Caligidae on pelagic young fish in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 551–3.
18. ORTON, J. H. & FORD, E., 1933. The post-puerulus of *Palinurus vulgaris* Latr. *Proc. Zool. Soc. Lond.*, pp. 181–8.

19. Krainska, M. K., 1934. Recherches sur le développement d'*Eupagurus prideauxi* Leach. I. Segmentation et gastrulation. *Bull. Acad. Polon. Sci. et Lettres. Cl. Sci. Math. et Nat.*, B, pp. 149–65.
20. Lebour, M. V., 1934. Larval Crustacea (Decapoda and Stomatopoda). Expedition S. A. R. Prince Leopold of Belgium, Duke of Brabant, to the Extreme East (1932). *Bulletin du Musée royal d'Histoire Naturelle de Belgique*, T. x, No. 8., 24 pp.
21. Lebour, M. V., 1934. Stomatopod larvae; Résultats scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mémoires du Musée royal d'Histoire Naturelle de Belgique*, hors série, T. III, fasc. 16, 17 pp.
22. Gurney, R., 1934. The development of certain parasitic Copepoda of the families Caligidae and Clavellidae. *Proc. Zool. Soc. Lond.*, pp. 177–217.
23. Lebour, M. V., 1934. The life-history of *Dromia vulgaris*. *Proc. Zool. Soc. Lond.*, pp. 241–9.
24. Nicholls, A. G., 1935. The larval stages of *Longipedia coronata* Claus, *L. scotti* G. O. Sars, and *L. minor* T. and A. Scott, with a description of the male of *L. scotti*. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 29–45.
25. Moore, H. B., 1935. The growth rate of *Balanus hameri* (Ascanius). *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 57–63.
26. Ramult, M., 1935. Observations on the embryonic larval development in *Sacculina* (Rhizocephala) in changed osmotic conditions of medium. *Bull. Int. Acad. Polon. Sci. Lettres*, B, II, Nos. 3–5, pp. 87–109.
27. Shen, C. J., 1935. An investigation of the post-larval development of the shore-crab, *Carcinus maenas*, with special reference to the external secondary sexual characters. *Proc. Zool. Soc. Lond.*, pp. 1–33.
28. Sexton, E. W., 1935. Fertilisation of successive broods of *Gammarus chevreuxi*. *Nature, Lond.*, Vol. 136, p. 477.
29. Day, J. H., 1935. The life-history of *Sacculina*. *Quart. Journ. Micr. Sci.*, Vol. 77, pp. 549–83.
30. Day, J. H., 1935. Heterogonic growth in the abdomen of *Carcinus maenas*. *Rept. Dove Mar. Lab.*, Ser. III, No. 3, pp. 49–59.
31. Orton, J. H., 1936. Experiments in the sea on rate of growth of some Crustacea Decapoda. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 673–89.
32. Bassindale, R., 1936. The developmental stages of three English barnacles: *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli) and *Verruca stroemia* (O. F. Müller). *Proc. Zool. Soc. Lond.*, pp. 57–74.
33. Lebour, M. V., 1937. The newly hatched larva of *Spirontocaris spinus* (Sowerby) var. *lilljeborgi* Danielssen. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 101–4.
34. Yonge, C. M., 1938. The nature and significance of the membranes surrounding the developing eggs of *Homarus vulgaris* and other Decapoda. *Proc. Zool. Soc. Lond.*, A, Vol. 107, pp. 499–517.
35. Lebour, M. V., 1938. The newly hatched larva of *Callianassa affinis* Holmes. *Proc. Zool. Soc. Lond.*, B, Vol. 108, pp. 47–8.
36. Howes, N. H., 1939. Observations on the biology and post-embryonic development of *Idotea viridis* (Slabber) (Isopoda, Valvifera) from New England Creek, south-east Essex. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 279–310.
37. Gurney, R. & Lebour, M. V., 1939. The larvae of the decapod genus *Naushonia*. *Ann. Mag. Nat. Hist.*, Ser. II, Vol. 3, pp. 609–14.
38. Lebour, M. V., 1940. The larvae of the Pandalidae. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 239–52.

39. Foxon, G. E. H., 1940. Notes on the life history of *Sacculina carcini* Thompson. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 253–64.
40. Harrison, R. J., 1940. On the biology of the Caprellidae. Growth and moulting of *Pseudoprotella phasma* Montagu. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 483–93.
41. Lebour, M. V., 1940. The larvae of the British species of *Spirontocaris* and their relation to *Thor* (Crustacea Decapoda). *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 505–14.
42. Gurney, R. & Lebour, M. V., 1940. Larvae of decapod Crustacea. Part VI. The genus *Sergestes*. *Discovery Reports*, Vol. xx, pp. 1–68.
43. Lebour, M. V., 1941. Notes on thalassinid and processid larvae (Crustacea Decapoda) from Bermuda. *Ann. Mag. Nat. Hist.*, Ser. 11, Vol. 7, pp. 401–20.
44. Gurney, R. & Lebour, M. V., 1941. On the larvae of certain Crustacea Macrura, mainly from Bermuda. *Journ. Linn. Soc. (Zool.)*, Vol. xli, pp. 89–181.
45. Sproston, N. G., 1942. The developmental stages of *Lernaeocera branchialis* (Linn.). *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 441–66.
46. Cheng, C., 1942. On the fecundity of some gammarids. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 467–75.
47. MacKay, D. C. G., 1942. Relative growth of the European edible crab, *Cancer pagurus*. I. Growth of the carapace. *Growth*, Vol. vi, pp. 251–8.
48. MacKay, D. C. G., 1943. *Ibid.* II. Growth of the abdomen. *Growth*, Vol. vii, pp. 217–26.
49. MacKay, D. C. G., 1943. *Ibid.* III. Growth of the sternum and appendages. *Growth*, Vol. vii, pp. 401–12.
50. Lebour, M. V., 1943. The larvae of the genus *Porcellana* (Crustacea Decapoda) and related forms. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 721–37.
51. Lebour, M. V., 1944. The larval stages of *Portumnus* (Crustacea Brachyura) with notes on some other genera. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 7–15.
52. Lebour, M. V., 1944. Larval crabs from Bermuda. *Zoologica*, Vol. xxix, pp. 113–28.
53. Yonge, C. M., 1946. Permeability and properties of the membranes surrounding the developing egg of *Homarus vulgaris*. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 432–8.
54. Cheng, C., 1947. On the fertility of marine Cladocera with a note on the formation of the resting egg in *Evadne nordmanni* Lovén and *Podon intermedius* Lilljeborg. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 551–61.
55. Knight-Jones, E. W. & Waugh, G. D., 1949. On the larval development of *Elminius modestus* Darwin. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 413–28.
56. Lebour, M. V., 1949. The last larva and post-larva of *Typton spongicola* from Plymouth (Crustacea Decapoda). *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 667–72.
57. Lebour, M. V., 1950. Notes on some larval decapods (Crustacea) from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 120, pp. 369–79.

C. *Physiology*

1. Cannon, H. G., 1928. On the feeding mechanism of the copepods, *Calanus finmarchicus* and *Diaptomus gracilis*. *Brit. Journ. Exp. Biol.*, Vol. vi, pp. 131–44.
2. Bain, W. A., 1929. The action of adrenaline and of certain drugs upon the isolated crustacean heart. *Quart. Journ. Exp. Phys.*, Vol. xix, pp. 297–308.

3. Pinhey, K. G., 1930. Tyrosinase in crustacean blood. *Brit. Journ. Exp. Biol.*, Vol. vii, pp. 19–36.
4. Nicholls, A. G., 1931. Studies on *Ligia oceanica*. I. A. Habitat and effect of change of environment on respiration. B. Observations on moulting and breeding. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 655–73.
5. Nicholls, A. G., 1931. Studies on *Ligia oceanica*. Part II. The processes of feeding, digestion and absorption, with a description of the structure of the foregut. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 675–707.
6. Huxley, J. S. & Richards, O. W., 1931. Relative growth of the abdomen and carapace of the shore-crab *Carcinus maenas*. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 1001–15.
7. Alexandrowicz, J. S., 1931. Quelques expériences sur la fonctionnement du système nerveux du coeur des Crustaces Isopodes. *C.R. Soc. Biol., Paris*, T. cviii, pp. 1270–2.
8. Nicol, E. A. T., 1932. The feeding habits of the Galatheidea. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 87–106.
9. Yonge, C. M., 1932–6. On the nature and permeability of chitin. I. The chitin lining the foregut of decapod Crustacea and the function of the tegumental glands. II. The permeability of the uncalcified chitin lining the foregut of *Homarus*. *Proc. Roy. Soc.*, B, Vol. 111, pp. 298–329 (1932); Vol. 120, pp. 15–41 (1936).
10. Bateman, J. B., 1933. Osmotic and ionic regulation in the shore crab, *Carcinus maenas*, with notes on the blood concentration of *Gammarus locusta* and *Ligia oceanica*. *Journ. Exp. Biol.*, Vol. x, pp. 355–71.
11. Cannon, H. G., 1933. On the feeding mechanism of certain marine ostracods. *Trans. Roy. Soc. Edin.*, Vol. lvii, pp. 739–64.
12. Foxon, G. E. H., 1934. Notes on the swimming methods and habits of certain crustacean larvae. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 829–49.
13. Moore, H. B., 1934. The biology of *Balanus balanoides*. I. Growth rate and its relation to size, season and tidal level. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 851–68.
14. Dennell, R., 1934. The feeding mechanism of the cumacean crustacean *Diastylis bradyi*. *Trans. Roy. Soc. Edin.*, Vol. lviii, pp. 125–42.
15. Lang, D. & Yonge, C. M., 1935. The function of the tegumental glands in the statocyst of *Homarus vulgaris*. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 333–9.
16. Löwenstein, O., 1935. The respiratory rate of *Gammarus chevreuxi* in relation to differences in salinity. *Journ. Exp. Biol.*, Vol. xii, pp. 217–21.
17. Lowndes, A. G., 1935. The swimming and feeding of certain calanoid copepods. *Proc. Zool. Soc. Lond.*, pp. 687–715.
18. Harvey, H. W., 1937. Note on selective feeding by *Calanus*. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 97–100.
19. Broekhuysen, G. J., 1937. Some notes on sex recognition in *Carcinides maenas* (L.). *Arch. Néerland. de Zool.*, Vol. iii, pp. 156–64.
20. Kleinholz, L. H. & Welsh, J. H., 1937. Colour changes in *Hippolyte varians*. *Nature, Lond.*, Vol. 140, pp. 851–2.
21. Dennell, R., 1937. On the feeding mechanism of *Apseudes talpa*, and the evolution of the peracaridan feeding mechanisms. *Trans. Roy. Soc. Edin.*, Vol. lix, pp. 57–78.
22. Kleinholz, L. H., 1938. Studies in the pigmentary system of Crustacea. IV. The unitary versus the multiple hormone hypothesis of control. *Biol. Bull. Woods Hole*, Vol. 75, pp. 510–32.

23. Welsh, J. H., 1938. Occurrence of acetylcholine in nervous tissue of crustaceans and its effect on the crab heart. *Nature, Lond.*, Vol. 142, p. 151.
24. Waldes, V., 1938. Ueber die chemische Beeinflussung des Rhythmus und der Retraktionsdauer der Cirren von *Balanus perforatus*. *Zeitsch. vergl. Physiol.*, Bd. 26, pp. 347–61.
25. Watkin, E. E., 1939. The swimming and burrowing habits of some species of the amphipod genus *Bathyporeia*. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 457–65.
26. Welsh, J. H., 1939. Chemical mediation in crustaceans. I. The occurrence of acetylcholine in nervous tissues and its action on the decapod heart. *Journ. Exp. Biol.*, Vol. xvi, pp. 198–219.
27. Panikkar, N. K., 1939. Osmotic behaviour of *Palaemonetes varians* Leach. *Nature, Lond.*, Vol. 144, pp. 866–7.
28. Foxon, G. E. H., 1940. The reactions of certain mysids to stimulation by light and gravity. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 89–97.
29. Panikkar, N. K., 1940. Osmotic properties of the common prawn. *Nature, Lond.*, Vol. 145, p. 108.
30. Panikkar, N. K., 1940. Influence of temperature on osmotic behaviour of some Crustacea and its bearing on problems of animal behaviour. *Nature, Lond.*, Vol. 146, pp. 366–7.
31. Lowndes, A. G. & Panikkar, N. K., 1941. A note on the changes in water content of the lobster (*Homarus vulgaris* M. Edw.) during moult. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 111–12.
32. Panikkar, N. K., 1941. Osmoregulation in some palaemonid prawns. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 317–59.
33. Sproston, N. G. & Hartley, P. H. T., 1941. Observations on the bionomics and physiology of *Trebius caudatus* and *Lernaeocera branchialis* (Copepoda). *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 393–417.
34. Panikkar, N. K., 1941. Osmotic behaviour of the fairy shrimp, *Chirocephalus diaphanus* Prevost. *Journ. Exp. Biol.*, Vol. xviii, pp. 110–14.
35. Holmes, W., 1942. The giant myelinated nerve fibres of the prawn. *Phil. Trans. Roy. Soc.*, B, Vol. 231, pp. 293–311.
36. Lowndes, A. G., 1943. Density of crabs and lobsters. *Nature, Lond.*, Vol. 151, p. 336.
37. Rowett, H. G. Q., 1946. A comparison of the feeding mechanisms of *Calma glaucoides* and *Nebaliopsis typica*. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 352–7.
38. Knowles, F. G. W., 1950. The control of retinal pigment migration in *Leander serratus*. *Biol. Bull. Woods Hole*, Vol. 98, pp. 66–80.
39. Dresel, E. I. B. & Moyle, V., 1950. Nitrogenous excretion of amphipods and isopods. *Journ. Exp. Biol.*, Vol. xxvii, pp. 210–24.
40. Krishnan, G., 1950. Sinus gland and tyrosinase activity in *Carcinus maenas*. *Nature, Lond.*, Vol. 165, pp. 364–5.
41. Raymont, J. E. G. & Gauld, D. T., 1951. The respiration of some planktonic copepods. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 681–93.
42. Gauld, D. T., 1951. The grazing rate of planktonic copepods. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 695–706.

See also: Vertical distribution of *Calanus*, V, 2, 7; Nerve physiology, XI C, 1, 3, 4, 5, 7, 10, 11, 15, 19, 21, 26, 27, 30, 40, 54; Neuro-muscular transmission, XI C, 25, 28, 39; Muscle physiology, XI E, 11, 12, 15, 26, 27; Digestion, XI J, 4; Respiration, XI K, 6, 8.

D. *Ecology*

1. Hart, T. J., 1930. Preliminary notes on the bionomics of the amphipod, *Corophium volutator* Pallas. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 761–89.
2. Gardiner, A. C., 1933. Vertical distribution in *Calanus finmarchicus*. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 575–610.
3. Jorgensen, O. M., 1933. On the marine Cladocera from the Northumbrian plankton. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 177–226.
4. Nicholls, A. G., 1933. On the biology of *Calanus finmarchicus*. I. Reproduction and seasonal distribution in the Clyde sea-area during 1932. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 83–109.
5. Marshall, S. M., 1933. *Ibid.* II. Seasonal variations in the size of *Calanus finmarchicus* in the Clyde sea-area. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 111–38.
6. Nicholls, A. G., 1933. *Ibid.* III. Vertical distribution and diurnal migration in the Clyde sea-area. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 139–64.
7. Orr, A. P., 1934. *Ibid.* IV. Seasonal changes in the weight and chemical composition in Loch Fyne. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 613–32.
8. Marshall, S. M., Nicholls, A. G. & Orr, A. P., 1934. *Ibid.* V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 793–827.
9. Marshall, S. M., Nicholls, A. G. & Orr, A. P., 1935. *Ibid.* VI. Oxygen consumption in relation to environmental conditions. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 1–27.
10. Bogorov, B. G., 1934. Seasonal changes in biomass of *Calanus finmarchicus* in the Plymouth area in 1930. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 585–612.
11. Russell, F. S., 1934. The study of copepods as a factor in oceanic economy. *Fifth Pacific Science Congress*, 1934, pp. 2023–34.
12. Leigh-Sharpe, W. H., 1933. A second list of parasitic Copepoda of Plymouth, with a description of three new species. *Parasitology*, Vol. 25, pp. 113–18.
13. Leigh-Sharpe, W. H., 1934. A third list of parasitic Copepoda of Plymouth with notes. *Parasitology*, Vol. 26, pp. 112–13.
14. Leigh-Sharpe, W. H., 1935. A list of British invertebrates with their characteristic parasitic and commensal Copepoda. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 47–8.
15. Moore, H. B., 1935. The biology of *Balanus balanoides*. IV. Relation to environmental factors. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 279–307.
16. Moore, H. B., 1936. *Ibid.* V. Distribution in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 701–16.
17. Nicholls, A. G., 1935. Copepods from the interstitial fauna of a sandy beach. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 379–405.
18. Fraser, J. H., 1936. The occurrence, ecology and life history of *Tigriopus fulvus* (Fischer). *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 523–36.
19. Crawford, G. I., 1936. Additions to the Plymouth Marine Fauna (1931) in the Crustacean orders Tanaidacea, Isopoda and Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 95–106.
20. Crawford, G. I., 1937. Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 631–46.

21. Frost, N., 1936. I. Amphipoda from Newfoundland waters. II. Decapod larvae from Newfoundland waters. *Newfoundland Dept. of Natural Resources, Division of Fish Research. Reports. Faunistic Series*, No. 1.
22. Crawford, G. I., 1937. The fauna of certain estuaries in West England and South Wales, with special reference to the Tanaidacea, Isopoda and Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 647–62.
23. Tattersall, W. M., 1938. The seasonal occurrence of mysids off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 43–56.
24. Rawlinson, R., 1938. On the occurrence of *Jaxea nocturna* (Chiereghin) Nardo off Rame Head, Devon. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 79–81.
25. Goodhart, C. B., 1939. Notes on the bionomics of the tube-building amphipod, *Leptocheirus pilosus* Zaddach. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 311–25.
26. Watkin, E. E., 1939. The pelagic phase in the life history of the amphipod genus *Bathyporeia*. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 467–81.
27. Moore, H. B. & Kitching, J. A., 1939. The biology of *Chthamalus stellatus* (Poli). *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 521–41.
28. Lebour, M. V., 1939. Decapod Crustacea associated with the ascidian *Herdmania*. *Proc. Zool. Soc. Lond.*, B, Vol. 108, pp. 649–53.
29. Elofson, O., 1940. Notes on the ostracod fauna of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 495–504.
30. Watkin, E. E., 1941. Observations on the night tidal migrant Crustacea of Kames Bay. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 81–96.
31. Williams, G. & Needham, A. E., 1941. Metric variations in populations of *Carcinus moenas*. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 261–81.
32. Sproston, N. G. & Hartley, P. H. T., 1941. The ecology of some parasitic copepods of gadoids and other fishes. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 361–92.
33. Dixon, A. Y., 1944. Notes on certain aspects of the biology of *Cumopsis goodsiri* (van Beneden) and some other cumaceans in relation to their environment. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 61–71.
34. Lloyd, A. J. & Yonge, C. M., 1947. The biology of *Crangon vulgaris* L. in the Bristol Channel and Severn Estuary. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 626–61.
35. Spooner, G. M., 1947. The distribution of *Gammarus* species in estuaries. Part I. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 1–52.
36. Jones, N. S., 1948. The ecology of the Amphipoda of the south of the Isle of Man. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 400–39.
37. Pyefinch, K. A., 1948. Notes on the biology of cirripedes. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 464–503.
38. Marshall, S. M., 1949. On the biology of the small copepods in Loch Striven. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 45–122.
39. Pyefinch, K. A., 1949. Short-period fluctuations in the numbers of barnacle larvae, with notes on comparisons between pump and net plankton hauls. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 353–69.
40. Tattersall, O. S., 1949. A rare species of mysid from the Plymouth area. *Nature, Lond.*, Vol. 163, p. 450.
41. Barnes, H., 1950. A note on the barnacle larvae of the Clyde sea area as sampled by the Hardy Continuous Plankton Recorder. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 73–80.
42. Spooner, G. M., 1950. Notes on the Plymouth marine fauna: Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 247–53.

43. Digby, P. S. B., 1950. The biology of the small planktonic copepods of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 393–438.
44. Knight-Jones, E. W. & Stevenson, J. P., 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 281–97.

See also: Vertical distribution of *Calanus*, V, 2, 7; Fungus in *Pinnotheres*, XII, 1; Protozoan parasites of *Calanus*, XVI A, 13; Pelagic animals off the S.W. coasts, XVIII D, 5; Copepod parasites of the cockle, XIX A, 6; *Hemiurus* in *Acartia*, XIX A, 7.

XXIV. ARACHNIDA, INSECTA

1. Mansour, K., 1930. Preliminary studies on the bacterial cell-mass (accessory cell-mass) of *Calandra oryzae* (Linn.): the rice weevil. *Quart. Journ. Micr. Sci.*, Vol. lxxiii, pp. 421–36.
2. Sen, P., 1931. Preliminary observations on the early stages of *Scatella stagnalis* Fal. (Ephydridae, Diptera). *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 847–51.
3. Lebour, M. V., 1945. Notes on the Pycnogonida of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 139–65.
4. Spooner, G. M., 1948. The British species of psenine wasps. (Hymenoptera: Sphecidae.) *Trans. Roy. Entomol. Soc.*, Vol. 99, pp. 129–72.
5. Hall, R. E., 1949. Notes on the Plymouth marine fauna: Chironomidae. (Insecta: Diptera.) *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 807–8.
6. Fountain, H. C., 1949. Notes on the Plymouth marine fauna: Halacarididae. (Arachnida: Acarina.) *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 808–9.
7. Lebour, M. V., 1949. Two new pycnogonids from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 118, pp. 929–32.
8. Théodoridès, J., 1949. Quelques publications récentes (1939–48) sur la biologie des Coléoptères des Iles Britanniques. *L'Entomologiste*, Vol. v, pp. 68–72.

See also: Physiology of muscle in *Dytiscus*, XI E, 2.

XXV. MOLLUSCA

A. *Systematics and morphology*

1. Orton, J. H., 1928. The dominant species of *Ostrea*. *Nature, Lond.*, Vol. 121, pp. 320–1.
2. Yonge, C. M., 1928. Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Phil. Trans. Roy. Soc.*, B, Vol. 216, pp. 221–63.
3. Orton, J. H., 1929. Oysters and oyster culture. *Ency. Brit.* (14th ed.).
4. Amirthalingham, C., 1929. Structure of pearls. *Nature, Lond.*, Vol. 123, p. 129.
5. Russell, L., 1929. The comparative morphology of the elysioid and æolidioid types of the molluscan nervous system, and its bearing on the relationships of the ascoglossan nudibranchs. *Proc. Zool. Soc. Lond.*, pp. 197–233.
6. Orton, J. H. & Amirthalingham, C., 1930. Giant English oysters (*O. edulis*). *Nature, Lond.*, Vol. 126, p. 309.
7. Atkins, D., 1930. On abnormal conditions of the gills in *Mytilus edulis*. Part I. On permanent natural reversal of the frontal cilia on the gill filaments of *Mytilus edulis*. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 919–70.

8. ATKINS, D., 1931. *Ibid.* Part II. Structural abnormalities, with a note on the method of division of the mantle cavity in normal individuals. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 489–543.
9. ATKINS, D., 1931. Note on some abnormalities of labial palps and foot of *Mytilus edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 545–50.
10. ATKINS, D., 1931. Note on the regeneration of the gill of *Mytilus edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 551–66.
11. BERRILL, N. J., 1931. The natural history of *Bulla hydatis* Linn. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 567–71.
12. MOORE, H. B., 1931. The systematic value of a study of molluscan faeces. *Proc. Malac. Soc.*, Vol. XIX, pp. 281–90.
13. GRAHAM, A., 1931. On the morphology, feeding mechanisms, and digestion of *Ensis siliqua* Schumacher. *Trans. Roy. Soc. Edin.*, Vol. LVI, pp. 725–51.
14. MOORE, H. B., 1932. The faecal pellets of the Trochidae. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 235–41.
14*a*. LEBOUR, M. V., 1932. Cowries. *Natural History, New York*, Vol. XXXII, pp. 188–94.
15. YONGE, C. M., 1932. Giant clams and burrowing clams. *Natural History, New York*, Vol. XXXII, pp. 244–57.
16. YONGE, C. M., 1932. On the size attained by the crystalline style in *Tridacna* and *Strombus*. *Proc. Malac. Soc.*, Vol. XX, pp. 44–5.
17. YONGE, C. M., 1932. The crystalline style of the Mollusca. *Science Progress*, April 1932.
18. GRAHAM, A., 1932. On the structure and function of the alimentary canal of the limpet. *Trans. Roy. Soc. Edin.*, Vol. LVII, pp. 287–308.
19. LEBOUR, M. V., 1933. The British species of *Trivia*: *T. arctica* and *T. monacha*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 477–84.
20. YOUNG, J. Z., 1934. Structure of nerve fibres in *Sepia*. *Proc. Physiol. Soc.*, Nov. 17, *Journ. Physiol.*, Vol. LXXXIII, pp. 27*P*–28*P*.
21. GRAHAM, A., 1934. The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proc. Roy. Soc. Edin.*, Vol. LIV, pp. 158–87.
22. ROTHSCHILD, M., 1936. Gigantism and variation in *Peringia ulvae* Pennant 1777, caused by infection with larval trematodes. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 537–46.
23. REES, W. J., 1936. Note on the ubiquitous cercaria from *Littorina rudis*, *L. obtusata* and *L. littorea*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 621–4.
24. REES, W. J., 1936. The effect of parasitism by larval trematodes on the tissues of *Littorina littorea* (Linné). *Proc. Zool. Soc. Lond.*, pp. 357–68.
24*a*. YOUNG, J. Z., 1936. The structure of nerve fibres in cephalopods and Crustacea. *Proc. Roy. Soc.*, B, Vol. 121, pp. 319–36.
25. ATKINS, D., 1936–43. On the ciliary mechanisms and interrelationships of lamellibranchs. Part I. Some new observations on sorting mechanisms in certain lamellibranchs. II. Sorting devices on the gills. III. Types of lamellibranch gills and their food currents. IV. Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs. V. Note on the gills of *Amussium pleuronectes*. VI. The pattern of the lateral ciliated cells of the gill filaments of the Lamellibranchia. VII. Latero-frontal cilia of the gill filaments and their phylogenetic value. VIII. Notes on gill musculature in the Microciliobranchia. *Quart. Journ. Micr. Sci.*, Vol. 79, pp. 181–308, 1936, 339–73, 1937, 376–421, 423–45; Vol. 80, pp. 321–9, 1938, 331–44, 345–436; Vol. 84, pp. 187–256, 1943.

26. FRETTER, V., 1937. The structure and function of the alimentary canal of some species of Polyplacophora (Mollusca). *Trans. Roy. Soc. Edin.*, Vol. LIX, pp. 119–64.
27. GRAHAM, A., 1938. The structure and function of the alimentary canal of eolid molluscs, with a discussion on their nematocysts. *Trans. Roy. Soc. Edin.*, Vol. LIX, pp. 267–307.
28. YONGE, C. M., 1939. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. *Phil. Trans. Roy. Soc.*, B, Vol. 230, pp. 79–147.
29. YONGE, C. M., 1939. On the mantle cavity and its contained organs in the Loricata (Placophora). *Quart. Journ. Micr. Sci.*, Vol. 81, pp. 367–90.
30. FRETTER, V., 1939. The structure and function of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Trans. Roy. Soc. Edin.*, Vol. LIX, pp. 599–646.
31. POPHAM, M. L., 1940. The mantle cavity of some of the Erycinidae, Montacutidae and Galeommatidae with special reference to the ciliary mechanisms. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 549–87.
32. PURCHON, R. D., 1941. On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 1–39.
33. FRETTER, V., 1941. The genital ducts of some British stenoglossan prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 173–211.
34. FRETTER, V., 1941. An abnormal male *Sepia officinalis*. *Proc. Malacol. Soc.*, Vol. XXIV, pp. 154–5.
35. HOWELLS, H. H., 1942. The structure and function of the alimentary canal of *Aplysia punctata*. *Quart. Journ. Micr. Sci.*, Vol. 83, pp. 357–97.
36. FRETTER, V., 1943. Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes & Hanley) and their bearing on its relationships. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 685–720.
37. FRETTER, V., 1946. The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a discussion on their evolution in the prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 312–51.
38. LEBOUR, M. V., 1946. The species of *Teredo* from Plymouth waters. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 381–9.
39. FRETTER, V., 1946. The pedal sucker and anal gland of some British Stenoglossa. *Proc. Malacol. Soc.*, Vol. XXVII, pp. 126–30.
40. LEBOUR, M. V., 1946–7. The oyster, I and II. *School Science Review*, Vol. XXVIII, pp. 81–6, 216–19.
41. YONGE, C. M., 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. Roy. Soc.*, B, Vol. 232, pp. 443–518.
42. FRETTER, V., 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 597–632.
43. FRETTER, V. & GRAHAM, A., 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 493–532.
44. GRAHAM, A., 1949. The molluscan stomach. *Trans. Roy. Soc. Edin.*, Vol. LXI, pp. 737–78.
45. REES, W. J., 1950. On a giant squid, *Ommastrephes caroli* Furtado, stranded at Looe, Cornwall. *Bull. Brit. Mus.* (*Nat. Hist.*), *Zool.*, Vol. I, pp. 31–41.

46. BIDDER, A. M., 1950. The digestive mechanism of the european squids, *Loligo vulgaris, Loligo forbesii, Alloteuthis media* and *Alloteuthis subulata. Quart. Journ. Micr. Sci.*, Vol. 91, pp. 1–43.
47. FRETTER, V., 1951. Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 567–86.
48. HOLME, N. A., 1951. The identification of British species of the genus *Ensis* Schumacher (Lamellibranchiata). *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 639–47.

See also: Chemical composition, X, 9, 10, 17.

B. *Reproduction and development*

1. ORTON, J. H., 1928. On rhythmic periods in shell-growth in *O. edulis* with a note on fattening. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 365–427.
2. AMIRTHALINGHAM, C., 1928. On lunar periodicity in reproduction of *Pecten opercularis* near Plymouth in 1927–28. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 605–41.
3. ORTON, J. H., 1928. Observations on *Patella vulgata*. Part I. Sex-phenomena, breeding and shell-growth. II. Rate of growth of shell. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 851–62, 863–74.
4. STEPHEN, A. C., 1929. Notes on the rate of growth of *Tellina tenuis* da Costa in the Firth of Clyde. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 117–29.
5. LEBOUR, M. V., 1931. The larval stages of *Nassarius reticulatus* and *Nassarius incrassatus*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 797–817.
6. LEBOUR, M. V., 1931. The larval stages of *Trivia europea*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 819–31.
7. ORTON, J. H. & AMIRTHALINGHAM, C., 1931. Observations and experiments on sex-change in the european oyster (*O. edulis*). Part II. On the gonad of egg-spawning individuals. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 315–24.
8. ORTON, J. H., 1933. *Ibid.* Part III. On the fate of unspawned ova. Part IV. On the change from male to female. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 1–53.
9. ORTON, J. H., 1936. *Ibid.* V. A simultaneous study of spawning in 1927 in two distinct geographical localities. *Mém. Mus. Roy. Hist. Nat. Belg.*, Ser. 2, Fasc. 3, 997–1056.
10. LEBOUR, M. V., 1932. The larval stages of *Simnia patula*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 107–15.
11. LEBOUR, M. V., 1932. The eggs and early larvae of two commensal gastropods *Stilifer stylifer* and *Odostomia eulimoides*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 117–21.
12. HOBSON, A. D., 1932. On the vitelline membrane of the egg of *Psammechinus miliaris* and of *Teredo norvegica*. *Journ. Exp. Biol.*, Vol. IX, pp. 93–106.
13. LEBOUR, M. V., 1933. The larval stages of *Erato voluta* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 485–90.
14. LEBOUR, M. V., 1933. The life-histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 491–8.
15. LEBOUR, M. V., 1933. The eggs and larvae of *Turritella communis* Lamarck and *Aporrhais pes-pelicani* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 499–506.
16. LEBOUR, M. V., 1933. The eggs and larvae of *Philbertia gracilis* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 507–10.

17. HÖRSTADIUS, S., 1933. Einige Untersuchungen über die Eiweissverdauung bei Gastropoden. *Biol. Zbl.*, Bd. LIII, pp. 645–50.
18. LEBOUR, M. V., 1933. The importance of larval Mollusca in the plankton. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 335–43.
19. LEBOUR, M. V., 1935. The Echinospira larvae (Mollusca) of Plymouth. *Proc. Zool. Soc. Lond.*, pp. 163–74.
20. LEBOUR, M. V., 1934. Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth Rissoidae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 523–39.
21. LEBOUR, M. V., 1934. The eggs and larvae of some British Turridae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 541–54.
22. LEBOUR, M. V., 1935. The larval stages of *Balcis alba* and *B. devians*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 65–9.
23. LEBOUR, M. V., 1935. The breeding of *Littorina neritoides*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 373–8.
24. SMITH, F. G. W., 1935. The development of *Patella vulgata*. *Phil. Trans. Roy. Soc.*, B, Vol. 225, pp. 95–125.
25. LEBOUR, M. V., 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 547–65.
26. LEBOUR, M. V., 1937. Larval and post-larval *Lima* from Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 705–10.
27. LEBOUR, M. V., 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 105–66.
28. MOORE, H. B., 1937. The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 721–42.
29. MOORE, H. B., 1938. The biology of *Purpura lapillus*. Part II. Growth. III. Life history and relation to environmental factors. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 57–66, 67–74.
30. LEBOUR, M. V., 1938. The life history of *Kellia suborbicularis*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 447–51.
31. COLE, H. A., 1938. The fate of the larval organs in the metamorphosis of *Ostrea edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 469–84.
32. LEBOUR, M. V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 119–44.
33. ROTHSCHILD, A. & ROTHSCHILD, M., 1939. Some observations on the growth of *Peringia ulvae* (Pennant) 1777 in the laboratory. *Novitates Zoolog.*, Vol. XLI, pp. 240–7.
34. BRUCE, J. R., KNIGHT, M. & PARKE, M. W., 1940. The rearing of oyster larvae on an algal diet. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 337–74.
35. HUGHES, E., 1940. The breeding of oysters in tanks. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 543–7.
36. HÖRSTADIUS, G. (geb. KJELLSTRÖM) & HÖRSTADIUS, S., 1940. Untersuchungen über die Eiweissverdauung in vivo und in vitro bei einigen Gastropoden. *Pubb. Staz. Zool. Napoli*, Vol. XVIII, pp. 151–249.
37. ROTHSCHILD, M., 1941. The effect of trematode parasites on the growth of *Littorina neritoides* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 69–80.
38. COLE, H. A., 1941. The fecundity of *Ostrea edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 243–60.

39. ROTHSCHILD, M., 1941. Observations on the growth and trematode infections of *Peringia ulvae* (Pennant), 1777, in a pool in the Tamar Saltings, Plymouth. *Parasitology*, Vol. 33, pp. 406–15.
40. LEBOUR, M. V., 1945. The eggs and larvae of some prosobranchs from Bermuda. *Proc. Zool. Soc. Lond.*, Vol. 114, pp. 462–89.
41. GRAHAM, A. & FRETTER, V., 1947. The life-history of *Patina pellucida* (L). *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 590–601.

C. *Physiology*

1. YONGE, C. M., 1928. The absorption of glucose by *Ostrea edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 643–53.
2. WILSON, D. P., 1929. A habit of the common periwinkle (*Littorina littorea* Linn.). *Nature, Lond.*, Vol. 124, p. 443.
3. YONGE, C. M., 1930. The crystalline style of the Mollusca and a carnivorous habit cannot normally co-exist. *Nature, Lond.*, Vol. 125, pp. 444–5.
4. RUSSELL, F. S. & STEVEN, G. A., 1930. The swimming of cuttlefish. *Nature, Lond.*, Vol. 125, p. 893.
5. BAYLISS, L. E., BOYLAND, E. & RITCHIE, A. D., 1930. The adductor mechanism of *Pecten*. *Proc. Roy. Soc.*, B, Vol. 106, pp. 363–76.
6. SETNA, S. B., 1930. The neuro-muscular mechanism of the gill of *Pecten*. *Quart. Journ. Micr. Sci.*, Vol. 73, pp. 365–91.
7. TAKATSUKI, S., 1934. On the nature and functions of the amoebocytes of *Ostrea edulis*. *Quart. Journ. Micr. Sci.*, Vol. 76, pp. 379–431.
8. YONGE, C. M., 1938. Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 453–68.
9. NELSON, T. C., 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica*, *O. edulis* and *O. angulata*, with comparisons with other species of the genus. *Journ. Morph.*, Vol. LXIII, pp. 1–61.
10. MOORE, H. B., 1938. Algal production and the food requirements of a limpet. *Proc. Malac. Soc.*, Vol. XXIII, pp. 117–18.
11. WILSON, D. P., 1946. A note on the capture of prey by *Sepia officinalis* L. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 421–5.
12. YONGE, C. M., 1948. Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (Da Costa) and *Lutraria lutraria* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 585–96
13. JØRGENSEN, C. B., 1949. The rate of feeding by *Mytilus* in different kinds of suspension. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 333–44.

See also: Nerve physiology, XI C, 9, 16, 20, 29, 32, 34, 36, 37, 38, 51, 52; Muscle physiology, XI E, 22, 26; Colour changes in *Sepia*, XI E, 25; Yolk absorption in *Loligo*, XI J, 2; Digestion, XI J, 6; Respiration, XI K, 3, 9; Feeding, XVII, 7; XXIII C, 37.

D. *Ecology*

1. STEPHEN, A. C., 1928. Notes on the biology of *Tellina tenuis* da Costa. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 683–702.
2. ORTON, J. H., 1928. The biology of shell-fish in relation to public health. *Journ. Roy. San. Inst.*, Vol. 49, pp. 263–74.

3. ORTON, J. H. & WINCKWORTH, R., 1928. The occurrence of the American oyster pest, *Urosalpinx cinerea* (Say), on English oyster beds. *Nature, Lond.*, Vol. 122, p. 241.
4. ORTON, J. H., 1928. Transplantation of the European oyster. *Science*, Vol. LXVII, pp. 582–3.
5. ORTON, J. H., 1929. Observations on *Patella vulgata*. Part III. Habitat and habits. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 277–88.
6. ORTON, J. H., 1929. Oyster cultivation and related researches in the British Isles. *Nature, Lond.*, Vol. 123, pp. 208–10.
7. ORTON, J. H., 1929. British oyster fisheries. *Nature, Lond.*, Vol. 123, pp. 451–4.
8. ORTON, J. H. & AMIRTHALINGHAM, C., 1929. The oyster-drills in English oyster-beds. *Nature, Lond.*, Vol. 124, pp. 298–9.
9. ORTON, J. H., 1929. Habitats and feeding habits of *Ocinebra erinacea*. *Nature, Lond.*, Vol. 124, pp. 370–1.
10. ORTON, J. H., 1930. On the oyster drills in the Essex estuaries. *Essex Naturalist*, Vol. XXII, pp. 298–306.
11. STEPHEN, A. C., 1931. Notes on the biology of certain lamellibranchs on the Scottish coast. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 277–300.
12. ORTON, J. H., 1931. On the effect of the severe winter of 1928–29 on the oyster drills (with a record of five years' observations on sea-temperature on the oyster-beds) of the Blackwater estuary. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 301–13.
13. LEBOUR, M. V., 1931. *Clione limacina* in Plymouth waters. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 785–95.
14. STEPHEN, A. C., 1932. Notes on the biology of some lamellibranchs in the Clyde area. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 51–68.
15. LEBOUR, M. V., 1932. *Limacina retroversa* in Plymouth waters. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 123–9.
16. MOORE, H. B., 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 61–89.
17. YONGE, C. M., 1937. The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.). *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 687–703.
18. MOORE, H. B., 1940. The biology of *Littorina littorea*. Part II. Zonation in relation to other gastropods on stony and muddy shores. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 227–37.
19. ORTON, J. H., 1940. Fluctuations in oyster production in the Fal estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 331–5.
20. LYSAGHT, A. M., 1941. The biology and trematode parasites of the gastropod *Littorina neritoides* (L.) on the Plymouth Breakwater. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 41–67.
21. WILSON, D. P., 1941. Oyster rearing on the River Yealm. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 125–7.
22. COLE, H. A., 1942. The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 477–508.
23. YONGE, C. M., 1946. On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 358–76.
24. YONGE, C. M., 1946. On the habits of *Turritella communis* Risso. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 377–80.
25. SPOONER, G. M., 1947. Further extension of the range of *Crepidula fornicata* (L.). *Journ. Conchol.*, Vol. 22, p. 243.
26. GRIGG, U. M., 1949. The occurrence of British *Aplysia*. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 795–805.

27. HOLME, N. A., 1950. Population-dispersion in *Tellina tenuis* da Costa. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 267–80.
28. REES, W. J., 1950. The distribution of *Octopus vulgaris* Lamarck in British waters. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 361–78.

See also: Parasites, XVI A, 5; XIX A, 1, 3, 6, 8, 10, 12, 17, 18, 22; XIX D, 4; Pelagic animals off the S.W. coasts, XVIII D, 5.

XXVI. POLYZOA

1. ATKINS, D., 1932. The Loxosomatidae of the Plymouth area, including *L. obesum*, sp.nov. *Quart. Journ. Micr. Sci.*, Vol. 75, pp. 321–91.
2. ATKINS, D., 1932. The ciliary feeding mechanism of the entoproct Polyzoa, and a comparison with that of the ectoproct Polyzoa. *Quart. Journ. Micr. Sci.*, Vol. 75, pp. 393–423.
3. FAULKNER, G. H., 1933. The relation between somatic and germ cells in the asexually produced polyps of the polyzoon *Alcyonidium gelatinosum*. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. 11, pp. 255–69.

XXVII. ECHINODERMATA

1. FRAENKEL, G., 1928. Ueber den Auslösungsreiz des Umdreheflexes bei Seesternen und Schlangensternen. *Zeit. vergl. Physiol.*, Bd. 7, pp. 365–78.
2. ORTON, J. H., 1929. On the occurrence of *Echinus esculentus* on the foreshore in the British Isles. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 289–96.
3. HOBSON, A. D., 1930. Regeneration of the spines in sea-urchins. *Nature, Lond.*, Vol. 125, p. 168.
4. BULL, H. O., 1932. Note on an unusual specimen of *Asterias rubens* L. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 225–7.
5. RAWLINSON, R., 1932. Specific differences in the gonadial spicules of *Echinus esculentus* (Linnaeus) and *Psammechinus miliaris* (Gmelin). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 229–34.
6. HOBSON, A. D., 1932. The effect of fertilisation on the permeability to water and on certain other properties of the surface of the egg of *Psammechinus miliaris*. *Journ. Exp. Biol.*, Vol. IX, pp. 69–92.
7. NARASIMHAMURTI, N., 1933. The development of *Ophiocoma nigra*. *Quart. Journ. Micr. Sci.*, Vol. 76, pp. 63–88.
8. MOORE, H. B., 1934–7. A comparison of the biology of *Echinus esculentus* in different habitats. Parts I–III. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 869–85, 1934; Vol. XX, pp. 109–28, 1935; Vol. XXI, pp. 711–19, 1937.
9. MOORE, H. B., 1935. A case of hermaphroditism and viviparity in *Echinocardium cordatum*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 103–7.
10. MOORE, H. B., 1936. The biology of *Echinocardium cordatum*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 655–71.
11. SMITH, J. E., 1937. The structure and function of the tube feet in certain echinoderms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 345–57.
12. SMITH, J. E., 1937. On the nervous system of the starfish *Marthasterias glacialis* (L.). *Phil. Trans. Roy. Soc.*, B, Vol. 227, pp. 111–73.
13. SMITH, J. E., 1938. Occurrence of young *Ophiothrix fragilis* within the genital bursa of the adult. *Nature, Lond.*, Vol. 141, p. 554.
14. SMITH, J. E., 1940. The reproductive system and associated organs of the brittle-star *Ophiothrix fragilis*. *Quart. Journ. Micr. Sci.*, Vol. 82, pp. 267–309.
15. LOWNDES, A. G., 1944. Densities of the embryonic stages of sea-urchins. *Nature, Lond.*, Vol. 154, pp. 55–6.

16. Lowndes, A. G., 1944. Shape of sea-urchins. *Nature, Lond.*, Vol. 154, pp. 675–6.
17. Smith, J. E., 1946. The mechanics and innervation of the starfish tube foot-ampulla system. *Phil. Trans. Roy. Soc.*, B, Vol. 232, pp. 279–310.
18. Vevers, H. G., 1949. The biology of *Asterias rubens* L.: growth and reproduction. *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 165–87.
19. Bacci, G., 1949. Ricerche su *Asterina gibbosa* (Penn.). I. La migrazione delle gonadi. II. L'ermafroditismo in una popolazione di Plymouth. *Arch. Zool. Ital.*, Vol. xxiv, pp. 23–9, 47–74.
20. Vevers, H. G., 1950. *Ophiopsila annulosa* (M. Sars) in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. xxix, p. 81.
21. Vevers, H. G., 1951. The biology of *Asterias rubens* L. II. Parasitization of the gonads by the ciliate *Orchitophrya stellarum* Cépède. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 619–24.

See also: Experimental embryology and inheritance, VII, 7, 11, 13, 14; Phosphagen in Echinodermata, X, 19; Muscle physiology, XI E, 26; Gregarines of *Cucumaria*, XVI A, 1; Vitelline membrane of egg of *Psammechinus*, XXV B, 12.

XXVIII. PROTOCHORDATA

1. Berrill, N. J., 1928. The identification and validity of certain species of ascidians. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 159–75.
2. Berrill, N. J., 1928. The ascidian fauna of the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 177–81.
3. Garstang, S. L. & Garstang, W., 1928. On the development of *Botrylloides*. *Quart. Journ. Micr. Sci.*, Vol. 72, pp. 1–50.
4. Berrill, N. J., 1929. Studies in tunicate development. Part I. General physiology of development of simple ascidians. *Phil. Trans. Roy. Soc.*, B, Vol. 218, pp. 37–78.
5. Berrill, N. J., 1931. *Ibid.* Part II. Abbreviation of development in the Molgulidæ. *Phil. Trans. Roy. Soc.*, B, Vol. 219, pp. 281–346.
6. Berrill, N. J., 1935. *Ibid.* Part III. Differential retardation and acceleration. IV. Asexual reproduction. *Phil. Trans. Roy. Soc.*, B, Vol. 225, pp. 255–379.
7. Berrill, N. J., 1936. *Ibid.* Part V. The evolution and classification of ascidians. *Phil. Trans. Roy. Soc.*, B, Vol. 226, pp. 43–70.
8. Lindsay, S. T. & Thompson, H., 1930. The determination of specific characters for the identification of certain ascidians. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 1–51.
9. Russell, F. S. & Hastings, A. B., 1933. On the occurrence of pelagic tunicates (Thaliacea) in the waters of the English Channel off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 635–40.
10. Fischer, E., 1934. Kontrakturen der bindegewebsfreien Schwanzmuskulator der Cionalarvæ. *Pflüger Arch. Physiol.*, Bd. ccxxxv, pp. 126–8.
11. Cohen, A. & Berrill, N. J., 1936. The early development of ascidian eggs. *Biol. Bull. Woods Hole*, Vol. 70, pp. 78–88.
12. Berrill, N. J. & Cohen, A., 1936. Regeneration in *Clavelina lepadiformis*. *Journ. Exp. Biol.*, Vol. xiii, pp. 352–62.
13. Vanderbroek, G., 1937. Les mouvements protoplasmiques au cours de la fécondation de l'œuf Ascidie. *Arch. exp. Zellforsch.*, Bd. xix, pp. 411–19.

14. BARRINGTON, E. J. W., 1937. The digestive system of *Amphioxus* (*Branchiostoma*) *lanceolatus*. *Phil. Trans. Roy. Soc.*, B, Vol. 228, pp. 269–312.
15. BRAMBELL, F. W. ROGERS & GOODHART, C. B., 1941. *Saccoglossus horsti* sp.n., an enteropneust occurring in the Solent. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 283–301.
16. BERRILL, N. J., 1947. The ascidians *Tridemnum alleni* and *Distaplia garstangi*, new species from the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 609–15.
17. BERRILL, N. J., 1947. The development and growth of *Ciona*. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 616–25.
18. BERRILL, N. J., 1947. The structure, tadpole and budding of the ascidian *Pycnoclavella aurilucens* Garstang. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 245–51.
19. BERRILL, N. J., 1948. Structure, tadpole and bud formation in the ascidian *Archidistoma*. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 380–8.
20. BERRILL, N. J., 1948. The development, morphology and budding of the ascidian *Diazona*. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 389–99.
21. BERRILL, N. J., 1948. The gonads, larvae, and budding of the polystyelid ascidians *Stolonica* and *Distomus*. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 633–50.
22. MILLAR, R. H., 1949. The larva of a didemnid ascidian, with notes on the structure of the colony and the adult. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 583–6.
23. MILLAR, R. H., 1950. *Lissoclinum argyllense* n.sp., a new ascidian from Scotland. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 389–92.
24. HAYWOOD, C. A. & MOON, H. P., 1950. The mechanics of the blood vascular system of *Ascidiella aspersa*. *Journ. Exp. Biol.*, Vol. XXVII, pp. 14–28.
25. BURDON-JONES, C., 1951. Observations on the spawning behaviour of *Saccoglossus horsti* Brambell & Goodhart and of other Enteropneusta. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 625–38.

See also: Development of isolated blastomeres of ascidian egg, VII, 10; Phosphagen in Protochordata, X, 19; Amoeba from an ascidian, XVI A, 6; Feeding-rate of ascidians, XVII, 7; Pelagic animals off the S.W. coasts, XVIII D, 5; Decapods associated with *Herdmania*, XXIII D, 28; Myenteric nerve-plexus of lower chordates, XXIX A, 12.

XXIX. PISCES

A. *Systematics and morphology*

1. YONGE, C. M., 1928. *Queer Fish*. London.
2. DAWES, B., 1929. The histology of the alimentary tract of the plaice (*Pleuronectes platessa*). *Quart. Journ. Micr. Sci.*, Vol. 73, pp. 243–74.
3. FORD, E., 1930. Some abnormal fishes received at the Plymouth Laboratory. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 53–64.
4. STEVEN, G. A., 1931. Rays and skates of Devon and Cornwall. Methods of rapid identification on the fishmarket. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 367–77.
5. FORD, E., 1933. The number of vertebrae in the herring and its variation. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 211–22.
6. LISSNER, H., 1934. On races of herrings. *Journ. Cons. Int. Explor. Mer*, Vol. IX, pp. 346–64.

7. STEVEN, G. A., 1934–5. King Herring. *Trans. Proc. Torquay Nat. Hist. Soc.*, Vol. VII, pp. 31–8.
8. HOWES, N. H., 1936. A study of the histology of the pituitary gland of the skate. *Quart. Journ. Micr. Sci.*, Vol. 78, pp. 637–51.
9. FORD, E., 1937. Vertebral variation in teleostean fishes. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 1–60.
10. FORD, E., 1941. *Ibid.* II. The herring (*Clupea harengus* L.). *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 151–72.
11. FORD, E., 1946. *Ibid.* III. Isospondyli. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 390–7.
12. KIRTISINGHE, P., 1940. The myenteric nerve-plexus in some lower chordates. *Quart. Journ. Micr. Sci.*, Vol. 81, pp. 521–39.
13. STEVEN, G. A., 1947. The British Raiidae. *Science Progress*, Vol. XXXV, pp. 220–36.
14. THOMAS, P. K. & YOUNG, J. Z., 1949. Internode lengths in the nerves of fishes. *Journ. Anat., Lond.*, Vol. 83, pp. 336–50.
15. AL-HUSSAINI, A. H., 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: Anatomy and histology. *Quart. Journ. Micr. Sci.*, Vol. 90, pp. 109–39.
16. AL-HUSSAINI, A. H., 1949. *Ibid.* Cytology and physiology. *Quart. Journ. Micr. Sci.*, Vol. 90, pp. 323–54.
17. CORBIN, P. G., 1950. *Ammodytes immaculatus*, a new species of sand-eel found in European seas. *Nature, Lond.*, Vol. 166, pp. 525–6.
18. NICOL, J. A. C., 1950. The autonomic nervous system of the chimaeroid fish, *Hydrolagus colliei*. *Quart. Journ. Micr. Sci.*, Vol. 91, pp. 379–99.
19. NICOL, J. A. C., 1950. Autonomic nervous system of the ratfish. *Nature, Lond.*, Vol. 165, p. 584.

See also: Chemical constituents, X, 1.

B. *Reproduction and development*

1. BULL, H. O., 1928. The relationship between state of maturity and chemical composition of the whiting, *Gadus merlangus* L. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 207–18.
2. WYNNE-EDWARDS, V. C., 1929. The reproductive organs of the herring in relation to growth. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 49–65.
3. ORTON, J. H., 1929. Reproduction and death in invertebrates and fishes. *Nature, Lond.*, Vol. 123, pp. 14–15.
4. HICKLING, C. F., 1930. A contribution towards the life-history of the spur-dog. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 529–76.
5. HOBSON, A. D., 1930. A note on the formation of the egg case of the skate. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 577–81.
6. DAWES, B., 1930–1. Growth and maintenance in the plaice (*Pleuronectes platessa* L.). Parts I and II. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 103–74, 877–947.
7. DAWES, B., 1931. A statistical study of growth and maintenance in the plaice (*Pleuronectes platessa* L.). *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 949–75.
8. FORD, E., 1931. Growth in length during the transition from larva to adolescent in the pilchard and sprat. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 977–85.
9. FORD, E., 1931. Changes in length during the larval life and metamorphosis of the freshwater eel (*Anguilla vulgaris* Turt.). *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 987–1000.

10. Beer, G. R. de, 1931. The development of the skull of *Scyllium* (*Scyliorhinus*) *canicula* L. *Quart. Journ. Micr. Sci.*, Vol. lxxiv, pp. 591–645.
11. Steven, G. A., 1934. Observations on the growth of the claspers and cloaca in *Raia clavata* Linnaeus. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 887–99.
12. Schindler, O., 1934. Beiträge zur Kenntnis der Niere mariner Fischlarven. *Sitzber. Akad. Wissensch. Wien Math.-Nat. Kl.*, Abt. 1, Bd. cxliii, pp. 265–83.
13. Hickling, C. F., 1935. Seasonal changes in the ovary of the immature hake, *Merlucius merluccius* L. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 443–62.
14. Hickling, C. F. & Rutenberg, E., 1936. The ovary as an indicator of the spawning period in fishes. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 311–17.
15. Marshall, S. M., Nicholls, A. G. & Orr, A. P., 1937. On the growth and feeding of the larval and post-larval stages of the Clyde herring. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 245–67.
16. Marshall, S. M., Nicholls, A. G. & Orr, A. P., 1939. On the growth and feeding of young herring in the Clyde. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 427–55.
17. Metten, H., 1940. Studies on the reproduction of the dogfish. *Phil. Trans. Roy. Soc.*, B, Vol. 230, pp. 217–38.
18. Corbin, P. G., 1947. The spawning of mackerel, *Scomber scombrus* L., and pilchard, *Clupea pilchardus* Walbaum, in the Celtic Sea in 1937–39. With observations on the zooplankton indicator species, *Sagitta* and *Muggiaea*. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 65–132.
19. Gross, F., 1949. Further observations on fish growth in a fertilized sea loch (Loch Craiglin). *Journ. Mar. Biol. Assoc.*, Vol. xxviii, pp. 1–8.
20. Corbin, P. G., 1950. Records of pilchard spawning in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. xxix, pp. 91–5.
21. Menon, M. D. (with an appendix by T. J. Hart), 1950. The use of bones, other than otoliths, in determining the age and growth-rate of fishes. *Journ. Cons. Int. Explor. Mer*, Vol. xvi, pp. 311–35, appendix, pp. 335–40.

C. *Physiology*

1. Lebour, M. V., 1927. The food of *Sardina pilchardus* (Walbaum). *Bull. Soc. Sci. Nat. Maroc*, T. 7, pp. 220–3.
2. Yoffey, J. M., 1929. A contribution to the study of the comparative histology and physiology of the spleen, with special reference to its cellular constituents. I. In fishes. *Journ. Anat., Lond.*, Vol. 80, pp. 314–44.
3. Fraser, A. H. H., 1929. Lipin secretion in elasmobranch interrenal. *Quart. Journ. Micr. Sci.*, Vol. 83, pp. 121–34.
4. Regnart, H. C., 1931. The lower limits of perception of electrical currents by fish. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 415–20.
5. Spooner, G. M., 1931. Some observations on schooling in fish. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 421–48.
6. Bayliss, L. E., 1935. Digestion in the plaice (*Pleuronectes platessa*). *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 73–91.
7. Newell, G. E. & Roper, H. D. G., 1935. A note on the feeding habits of *Chimaera monstrosa*. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 99–102.
8. Grafflin, A., 1935. Chloride and total osmotic pressure in the blood of marine teleosts. *Biol. Bull. Woods Hole*, Vol. 69, pp. 245–58.
9. Wilson, D. P., 1937. The habits of the angler-fish *Lophius piscatorius* L. in the Plymouth aquarium. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 477–96.

10. SPOONER, G. M., 1937. The learning of detours by wrasse (*Ctenolabrus rupestris* L.). *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 497–570.
11. LOVERN, J. A. & WOOD, H., 1937. Variations in the chemical composition of herring. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 281–93.
12. WILSON, D. P., 1939. Seasonal variations in the fat content of the flounder, *Pleuronectes flesus* L. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 361–79.
13. EALES, N. B., 1949. The food of the dogfish, *Scyliorhinus caniculus* L. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 791–3.

See also: Vertical migration of young fish, V, 3, 4; Nerve physiology, XI C, 6, 14, 24; Sense-organs, XI D, 1–5, 7, 10, 12–15; Luminescence, XI E, 9; Colour changes, XI E, 10, 18, 20, 21; Muscle physiology, XI E, 13, 17, 19; Physiology of the iris, XI E, 14; Electric organs, XI E, 24; Behaviour, XI F, 1–5, 7–11; Excretion, XI H, 3; Absorption, XI J, 3; Digestion, XI J, 5; Respiration, XI K, 4; Food of young herring, XXV B, 20.

D. *Ecology*

1. FORD, E., 1928–30. Herring investigations at Plymouth. I. Methods of collection and treatment of data. II. The average number of vertebrae for herrings from the English Channel and south-east of Ireland. III. The Plymouth winter fishery during the seasons 1924–5, 1925–6, and 1926–7. IV. The growth of young herrings in the neighbourhood of Plymouth. V. The Plymouth winter fishery during the season 1927–8. VI. Winter herrings caught off the Sussex coast and in the Great West Bay during the years 1924 to 1927. VII. On the artificial fertilisation and hatching of herring eggs under known conditions of salinity, with some observations on the specific gravity of the larvae. VIII. The transition from larva to adolescent. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 237–66, 267–78, 279–304, 305–19; Vol. XVI, pp. 1–24, 25–42, 43–8, 723–52.
2. NORMAN, J. R., 1929. Note on a sailfish *Istiophorus americanus* Cuvier and Valenciennes, new to the British fauna. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 67–71.
3. RUSSELL, F. S., 1930–47. The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring-trawl in offshore waters in the Plymouth area. Parts I–VIII. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 707–22, 1930; Vol. XX, pp. 147–79, 1935; pp. 595–604, 1936; Vol. XXI, pp. 679–86, 1937; Vol. XXII, pp. 493–500, 1938; Vol. XXIII, pp. 381–6, 1939; Vol. XXIV, pp. 265–70, 1940; Vol. XXVI, pp. 605–8, 1947.
4. CORBIN, P. G., 1948–9. On the seasonal abundance of young fish. Parts IX and X. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 718–22; Vol. XXVIII, pp. 707–12.
5. STEVEN, G. A., 1932. Rays and skates of Devon and Cornwall. II. A study of the fishery; with notes on the occurrence, migrations and habits of the species. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 1–33.
6. STEVEN, G. A., 1933. *Ibid.* III. The proportion of the sexes in nature and in commercial landings, and their significance to the fishery. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 611–25.
7. BAYLIS, H. A. & JONES, E. I., 1933. Some records of parasitic worms from marine fishes at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 627–34.
8. FORD, E., 1933. An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 305–84.

9. FORD, E., 1933. Marine biology and the sea fisheries. *Brit. Sea Angl. Soc. Quarterly*, Vol. XXVI, pp. 23–7, 50–6.
10. RUSSELL, F. S., 1933. Tunny in the North Sea. *Nature, Lond.*, Vol. 132, p. 786.
11. RUSSELL, F. S., 1934. Tunny investigations made in the North Sea on Col. E. T. Peel's yacht, *St George*, summer 1933. Part I. Biometric data. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 503–22.
12. RUSSELL, F. S., 1934. The tunny, *Thunnus thynnus* Linnæus. An account of its distribution and biology. *Sci. Progress*, No. 112, pp. 634–49.
13. F(ORD), E., 1934. Science and state regulation of the sea fisheries. *Nature, Lond.*, Vol. 134, pp. 593–4.
14. RUSSELL, F. S., 1935. On the occurrence of post-larval stages of the bass, *Morone labrax* (L.) in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 71–2.
15. STEVEN, G. A., 1935. Some friends and foes of the fisherman. *Brit. Sea Angl. Soc. Quart.* Vol. XXVIII, pp. 42–5.
16. FORD, E., 1935. The advance of herring research. *Nature, Lond.*, Vol. 136, pp. 896–7.
17. STEVEN, G. A., 1936. Migrations and growth of the thornback ray (*Raia clavata* L.). *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 605–14.
18. WILSON, D. P., 1937. Fishes of a rocky sea-shore. *The Aquarist and Pond-keeper*, Vol. VII, pp. 240–2.
19. FORD, E., 1937. *The Nation's Sea-fish Supply*. Buckland Lectures for 1936. London.
20. ATKINS, W. R. G., 1938. British fisheries, phosphate and the solar radiation constant. *Nature, Lond.*, Vol. 141, pp. 77–8.
21. STEVEN, G. A. & CORBIN, P. G., 1939. Mackerel investigation at Plymouth. *Rapp. Cons. Int. Explor. Mer*, Vol. CXI, App. 2, pp. 15–18.
22. HARTLEY, P. H. T., 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 1–68.
23. HICKLING, C. F., 1940. The fecundity of the herring of the southern North Sea. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 619–32.
24. HICKLING, C. F., 1945. The seasonal cycle in the Cornish pilchard, *Sardina pilchardus* Walbaum. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 115–38.
25. HICKLING, C. F., 1946. Haddock on the Porcupine Bank, September 1944. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 398–407.
26. HICKLING, C. F., 1946. The herring fisheries at Milford Haven. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 408–20.
27. HART, T. J., 1946. Report on trawling surveys on the Patagonian continental shelf. *Discovery Reports*, Vol. XXIII, pp. 223–408.
28. HARTLEY, P. H. T., 1947. Observations on flounders, *Pleuronectes flesus* L. marked in the estuaries of the Tamar and Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 53–64.
29. STEVEN, G. A., 1947. *Report on the sea fisheries of Sierra Leone*. (Freetown, 1945.) Crown Agents for the Colonies, Millbank, London, 1947. 66 pp.
30. STEVEN, G. A., 1948. Contributions to the biology of the mackerel, *Scomber scombrus* L. Mackerel migrations in the English Channel and Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 517–39.
31. STEVEN, G. A., 1949. *Ibid.* II. A study of the fishery in the south-west of England, with special reference to spawning, feeding and 'fishermen's signs'. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 555–81.

32. HART, T. J., 1948. The distribution and biology of hake. *Biol. Rev.*, Vol. 23, pp. 62–80.
33. COOPER, L. H. N. & STEVEN, G. A., 1948. An experiment in marine fish cultivation. *Nature, Lond.*, Vol. 161, p. 631.
34. GROSS, F., 1948. Marine fish cultivation. *Nature, Lond.*, Vol. 162, p. 378.
35. COOPER, L. H. N. & STEVEN, G. A., 1948. Marine fish cultivation. *Nature, Lond.*, Vol. 162, p. 378.
36. CORBIN, P. G. & VATI, V., 1949. The post-larval sand eels (Ammodytidae) of the Celtic sea and Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 287–313.
37. KELLEY, D. F., 1949. The mystery of the bass: a report on three years' study of its habits. *Angling*, Vol. XI, pp. 79–83.
38. STEVEN, G. A., 1949. The mackerel: new light on its migrations and habits. *Discovery*, March 1949, 3 pp.
39. CORBIN, P. G., 1950. The occurrence of the smooth sand-eel, *Gymnammodytes semisquamatus* (Jourdain), in the Plymouth area, with notes on *G. cicerelus* (Rafinesque), and *G. capensis* (Barnard). *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 83–9.
40. MENON, M. D., 1950. Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 185–239.
41. STEVEN, G. A., 1950. Notes on Plymouth marine fauna: Pisces. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 254–5.

See also: Bottom fauna and the food of fishes, II, 3; Vertical distribution of young teleosts, V, 3, 4; Herring and plankton, V, 26–9; Marking fish, VIII, 11; Variability in trawl catches, VIII, 14; Phosphate and fisheries, IX E, 28; Parasites, XII, 3, 4; XVI A, 19; XIX A, 4, 9, 23; XXIII A, 2, 22, B, 17, D, 32; Jelly fish and catches of herring, XVIII D, 8.

XXX. REPTILIA, AVES, MAMMALIA

1. STEVEN, G. A., 1933. The food consumed by shags and cormorants around the shores of Cornwall (England). *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 277–92.
2. STEVEN, G. A., 1934. A short investigation into the habits, abundance and species of seals on the North Cornwall coast. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 489–501.
3. STEVEN, G. A., 1936. Seals (*Halichoerus grypus*) of Cornwall coasts. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 493–506.
4. STEVEN, G. A., 1937. The common or brown seal. *The Romance of Nature*, Pt. 6.
5. RUSSELL, F. S., 1939. Turtles in the English Channel. *Nature, Lond.*, Vol. 143, pp. 206–7.
6. ROTHSCHILD, M., 1942. A note on immunity reaction in the black-headed gull (*Larus ridibundus*) infected with *Maritrema oocysta* Lebour 1907. *Journ. Parasit.*, Vol. XXVIII, pp. 423–4.
7. STEVEN, G. A., 1950. Swimming of dolphins. *Sci. Progress*, Vol. 151, pp. 524–5.
8. SERGEANT, D. E., 1951. The status of the common seal (*Phoca vitulina* L.) on the East Anglian coast. *Journ. Mar. Biol. Assoc.*, Vol. XXIX, pp. 707–17.

See also: Physiology of heart of turtle, XI C, 24; Osmotic relations in hen's egg, XI G, 3; Permeability of erythrocytes, XI G, 5; Trematode parasites of black-headed gull, XIX B, 2.

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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