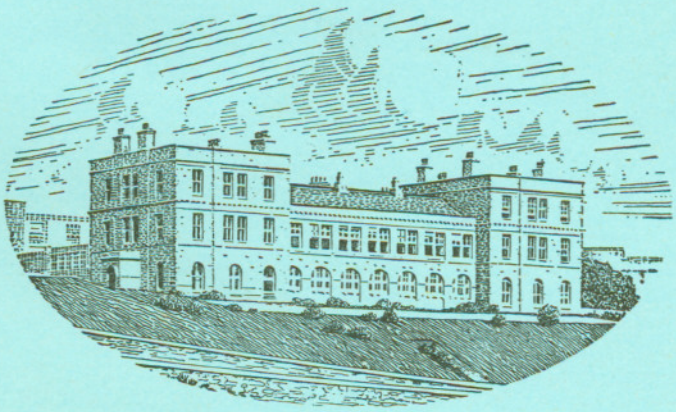
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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October, 1960

W. H. Searle

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OBITUARY

William H. Searle, B.E.M.

By the death at the age of 84 of Mr William H. Searle there passed away, on 6 April 1960, one who had served the Laboratory longer than anyone else and who, during his 63 years as fisherman-collector, had installed himself in the affections of countless biologists the world over. From December 1895 until his retirement on 30 September 1958 his assiduous and unwearied devotion to his collecting duties, year in and year out whatever the weather, on the shore or in his boats, earned him the lasting gratitude of all those innumerable research workers, teachers and students who relied on 'Bill' to procure living material for their researches or studies. He, more than anyone else, knew where the animals were to be found, how to capture them without damage and how to ensure their safe arrival at the Laboratory hours later. More than one student who had been collecting on the shore alongside Bill has later been astonished to observe the large and varied assortment of creatures emerging alive and kicking from one small and tightly packed basket. He had a keen eye for the little things—*Gromia*, praniza larvae and the like, from the rock crevices he split open with his crow-bar. These he would carefully transfer from silted rock surface to honey jar on the point of his pocket-knife. He knew well their scientific names, though foreigners would often have difficulty in recognizing them when pronounced with a strong Devonshire accent. It was usually the old names current during his youth that he knew, and he was not alone in deploring the activities of systematists in so frequently changing and re-changing so many of them.

Bill often spoke of the wonderful time he spent with the late Dr E. J. Allen, F.R.S., and the late Mr R. A. Todd exploring, for its fauna, the Salcombe estuary during the summer of 1900, when so much was excitingly new. Collecting trips to Salcombe with Bill, even thirty years later, are still as green in the memory of a younger generation as were then the acres of *Zostera* amid which Bill's fork turned up rare and fascinating things. He was largely responsible for discovering the riches of the rocky reefs at Wembury Point; in those days walking there and back from Turnchapel, no short distance when carrying a crowbar and one or two loaded collecting baskets.

Of the boats he used in Plymouth Sound and immediate environs the small sailing ship 'Anton Dohrn' was worked by him for many years single-handed. He served aboard 'Busy Bee', 'Huxley', and 'Oithona', and from 1923 onwards skippered the motor-boat 'Gammarus'. In those days 'Gammarus' had a stout mast on which with a following wind Bill would hoist sail to help her along, for in her early years she was rather underpowered.

Bill's knowledge of the bottom of Plymouth Sound was unrivalled; legend has it that caught by a sudden sea-fog he could always tell where he was by dredging up a sample of the bottom. Like so many of the older seamen he could not swim, and he chewed, not smoked, tobacco.

Well deserved honours came to Bill late. In 1953 he was elected an associate member of the M.B.A.; he received the Queen's Coronation Medal and in 1957 the British Empire Medal. When he retired he could look back with pride on a long life well spent in the service of science.

D. P. WILSON

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A MUSCLE RECEPTOR ORGAN IN *ELEDONE CIRRHOSA*

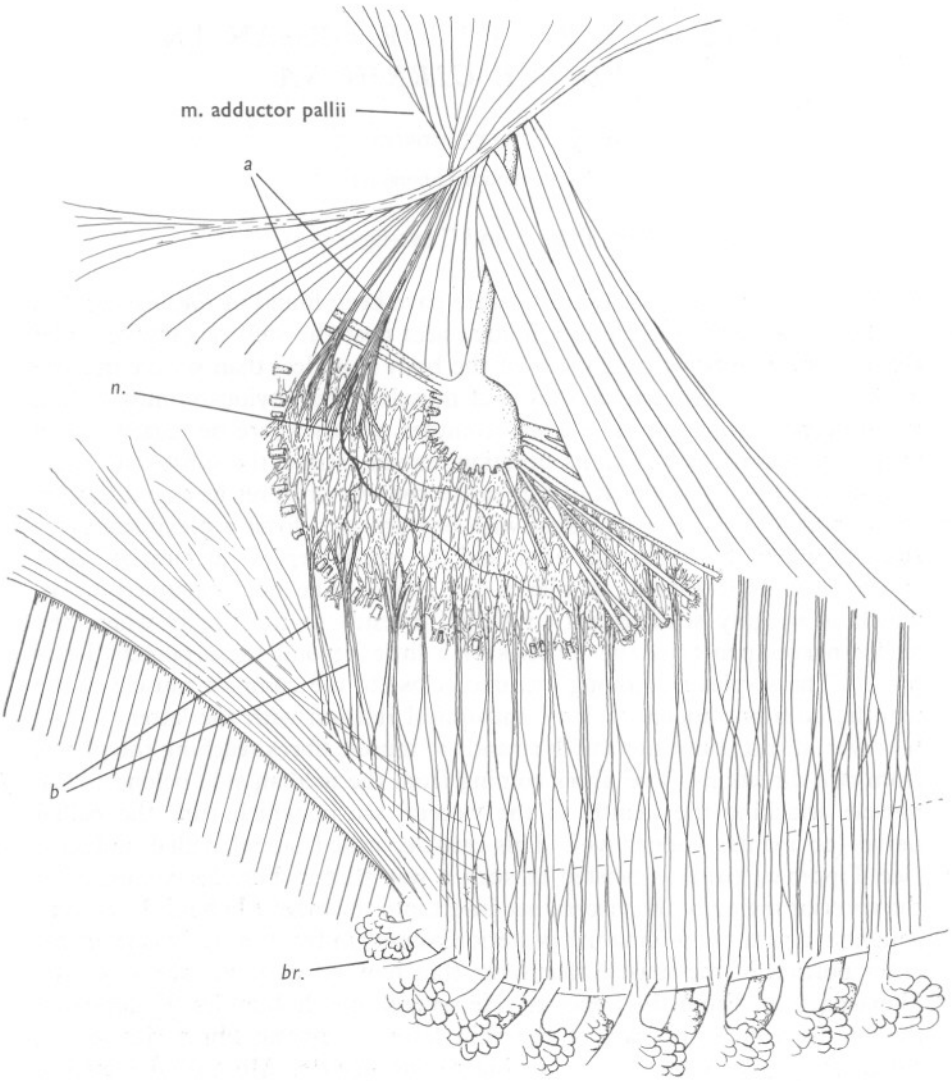
By J. S. ALEXANDROWICZ
The Plymouth Laboratory

(With Plate I and Text-figs. 1–4)

Nerve cells evidently of a sensory nature have been found in *Eledone cirrhosa* on the inside of the mantle in a limited area near the stellate ganglion. The cells, whose number on each side of the body is no less than 50, are in close association with a special thin layer of muscles, and obviously must have a proprioceptive function. The whole complex can therefore be regarded as a muscle receptor which from its situation may be termed the substellar organ.

The muscular component of this organ consists of fibres arranged in very flat bundles which, anastomosing with one another, form a plexiform layer situated under the stellate ganglion and the stellar nerves. It may be called substellar muscle plexus (ss-plexus for short). The area occupied by it, which is roughly semicircular in shape, extends to the points where the stellar nerves penetrate the muscles or a little beyond these points (Text-fig. 1). The ss-plexus, although situated close to the compact muscle of the mantle, does not appear to have anatomical relation with the latter; it has, however, direct connexions with strands of muscle fibres reaching the plexus from two directions. The fibres coming from the median side belong to the muscle attaching the mantle to the visceral sac in which runs the pallial nerve (or mantle connective). This muscle, called lateral pallial adductor (see Tippmar, 1913) is twisted in such a way that its bundles coming from the anterior region of the visceral sac insert into the mantle behind the stellate ganglion, and those originating posteriorly insert in front of it. It is from the latter portion of the muscle that some thin bundles pass into the ss-plexus (Text-fig. 1*a*). From the opposite side several muscle bundles (*b*) approach the plexus which are part of the thin layer of muscle fibres situated in the membrane attaching the branchia to the mantle. Most of the muscle fibres of this membrane run in the same direction towards the line of insertion of the pallial adductor and the area of the ss-plexus; near the free border of the branchial membrane they form a somewhat thicker band running parallel to this border.

It should be emphasized that a part only of the ss-plexus is connected with the muscle fibres of the pallial adductor and of the branchial membrane. Its other fibres spread in the connective-tissue sheet lining the mantle and terminate in this tissue independently of the neighbouring muscles. On the



Text-fig. 1. *Eledone cirrhosa*. Inside view of portion of the mantle showing the situation of substellar muscle plexus of the right side. Most of the stellar nerves have been cut out to show the plexus connecting with (*a*) the fibres of m. adductor pallii, and (*b*) the fibres of the muscle of the branchial membrane. *n*, nerve to the substellar muscle plexus; *br*., branchia.

other hand, many fibres of the branchial membrane passing on to the area of the ss-plexus do not fuse with its bundles and insert into the connective tissue in the meshes of the plexus.

The muscle fibres of the plexus which are *ca.* 3μ thick can branch and exchange anastomoses. The mode of their arrangement can be seen in Pl. I, fig. 1.

The ss-plexus is often very distinct in methylene-blue preparations. In order to facilitate its staining it is advisable to remove the epithelial layer lining the mantle cavity, to cut out the stellar nerves and to take away carefully the loose tissue beneath them. For better observation of the muscle and nerve elements the plexus can be separated from the mantle wall, but this should be done when the preparations after staining, fixing, etc., have been transferred into xylol. One must proceed from the outside, taking piece by piece the mantle muscles from the plexus and not vice versa. Preparations shown in photographs (Pl. I) were made in that way. The muscle fibres stain with methylene blue readily but unevenly. Much better pictures of the plexus structure can be obtained with Bodian's method; in such preparations, however, it is much more difficult to remove the unwanted tissues from the plexus muscles.

Nerves

The nerve supplying the plexus muscles arises from the mantle connective. It is covered at its point of origin and in its initial course by that portion of the pallial adductor which passes in front of the stellate ganglion. After giving off to this muscle several branches the nerve emerges near one of the bundles fusing with the plexus and runs across the latter in a wavy line obliquely backwards distributing branches to the muscles. In addition to this system of nerves which are doubtless of motor character there is on the plexus a second system connecting with some of the stellar nerves by thin nerves. The greatest number of the latter was four in one preparation, but how many they actually are remains uncertain. They are difficult to find for they join thinner stellar nerves situated deeper under the thick ones, and as the space between the stellar nerves is filled by loose tissue which must be removed one can never be sure whether in this operation some tiny nerves have not be torn away. On the other hand, there are here thin arteries which can easily be mistaken for nerves.

It seems very probable, as will be shown below, that this system of nerve fibres is formed by the axons of receptor neurons.

Nerve cells

Nerve cells are scattered over the ss-plexus at a distance from one another; sometimes two or, more rarely, three can be seen lying close together. They are all multipolar and can have a variety of shapes depending on the disposition

of their processes (Pl. I, figs 3–5). Owing to this feature their dimensions can only be generally defined as being in the range between 40 and 100 μ. How many nerve cells there are in all on the plexus could not be exactly determined because they are difficult to stain: sometimes they do not show at all, in other instances only a few can be spotted. The greatest number seen in one preparation was 25 in an area approximately equal to half of the plexus. Hence it may be deduced that their total number is not less than 50, but it can be higher than that. Because of their poor staining properties it has not been possible to gain a precise knowledge of their distribution. Such pictures as in Pl. I, fig. 2, showing several cells not far from one another, are not often seen, and there is no certainty whether the cells are spaced in the same way on the whole plexus. It is true that groupings with similarly or even more densely arranged cells have been observed at various points near the central region of the plexus as well as towards its periphery, but there is still not sufficient evidence whether the cells are distributed so closely everywhere or merely at certain points.

The number of processes arising from cell bodies is variable. Five or six of them are usually met with, but their true number can be greater since in addition to the thick processes some tiny ones can be frequently noticed, but they do not stain well. The processes which must be classified as dendrites project in all directions giving off branches spreading on the muscles. The thicker of them cross the muscle bundles at various angles, whilst the thin ones take their course alongside the muscle fibres. Very thin branches can arise directly from the stout cell processes, sometimes several of them close to each other. No special end-organs could be seen, and whether the nerves terminate on the muscle fibres or on the connective tissue between them I am unable to say.

The cell processes can be followed in favourable conditions for about 250 μ from the cell body, but appear not to end there, at least not all of them. Their tracing in methylene-blue preparations is uncertain because of the difficulty in distinguishing the nerves from the muscle fibres that stain readily and give off fine branches frequently looking like nerve filaments. There are, moreover, on the same muscles, motor fibres coming from the nerve mentioned above. Besides, methylene-blue preparations are often indecipherable because of deformations of fibres produced by longer immersion of tissues (8–10 h, sometimes up to 20 h) in methylene-blue solution in sea water

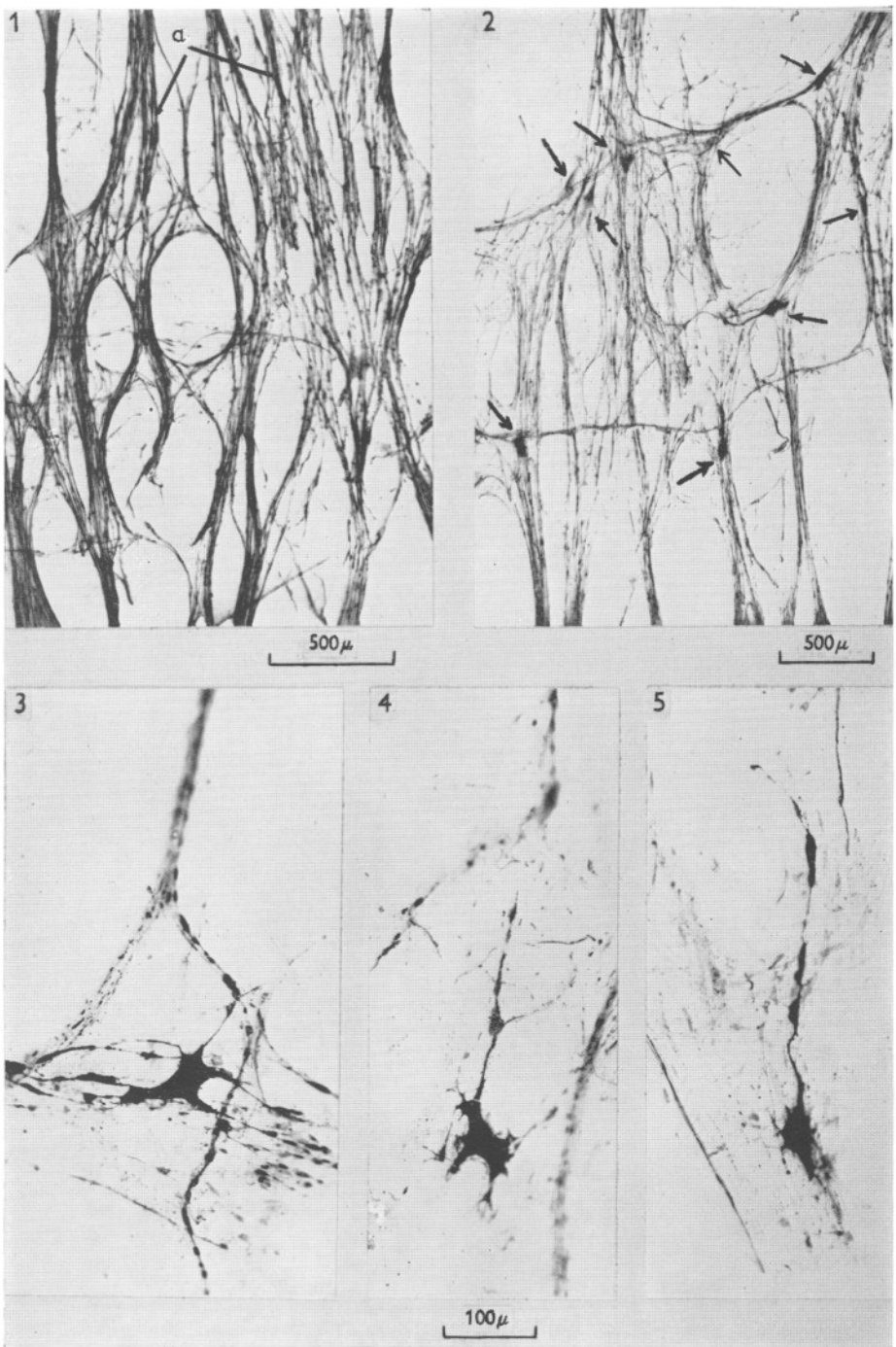
EXPLANATION OF PLATE I

All photographs were made from preparations of *Eledone cirrhosa* stained with methylene blue, fixed in ammonium molybdate and mounted in xylol-dammar.

Fig. 1. Substellar muscle plexus. *a*, bundles of fibres coming from m. adductor pallii.

Fig. 2. Receptor cells (indicated by arrows) on the substellar muscle plexus.

Figs. 3–5. Receptor cells of various shapes.



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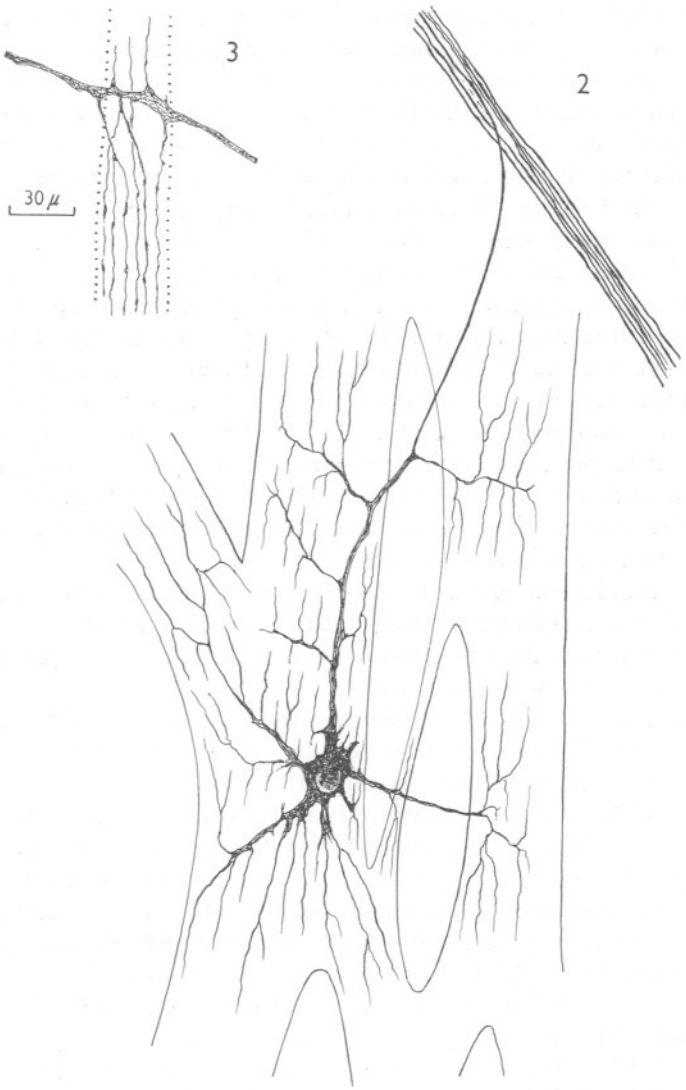


Text-fig. 2. Receptor cell of the substellar organ. Drawing compiled from several preparations.

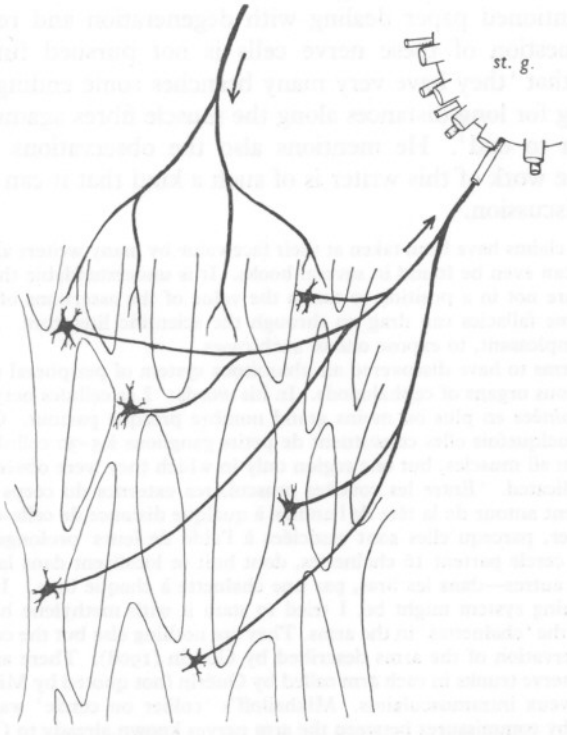
Text-fig. 3. Fine branches of a receptor cell dendrite given off to a small strip of plexus muscle (outlined by dots). From preparation stained with Bodian's method.

(1:30,000). The dendritic processes proved to be particularly susceptible to this treatment and disintegrated readily. More reliable pictures have been obtained with Bodian's method which proved to be helpful in determining (on whole mounted preparations) the course of the cell processes and their

finer branches. The representation of the receptor neuron shown in Text-fig. 2 is based on pictures obtained with both staining methods. It may be that the expansions of some dendrites reach farther than seen in this drawing, and it must be realized that the fine terminal branches are much more numerous than is shown. How dense they in fact are can be judged on the evidence of preparations in which the impregnation of some branches was more complete. In Text-fig. 3 is shown a muscle strip only 32 μ wide crossed by a cell process which sends to this muscle several branches running parallel with each other and obviously destined exclusively to this muscle strip. Although such pictures, because of uneven impregnation of nerve elements, are not of common occurrence, there is every reason to believe that in the dendritic field of each neuron the nerves fibres are in similar relations with the muscles. Furthermore, considering the length of the cell processes and the distribution of the nerve cells, it may be assumed that in those regions where the nerve cells are situated not far from one another all muscle bundles are covered by their processes. Should the cells be equally densely spaced over the whole ss-plexus then the latter would be everywhere pervaded by the ramifications of their dendrites.

The axon at its root and in its initial course is not easily discernible since it gives off branches looking exactly like those of the dendrites. Occasionally it stains better than the other processes and then can be recognized at first sight (Pl. I, fig. 5). When the processes stain equally well it can sometimes be distinguished by its greater thickness, but this is not a reliable characteristic. Thus, the identification of the axon can only be certain when it is possible to trace it for a longer distance. It can be then seen that its outlines are somewhat uneven up to the point at which branches cease to spring from it. When the last of these branches is given off (this point can be at a distance of about 500 μ from the cell body), the axon changes in appearance and proceeds farther as a smooth fibre which finally joins one of the nerves running on the plexus. Sometimes three or four axons associate and run together before entering a thicker bundle of fibres. In a few cases when such a nerve carrying the axons could be followed in its proximal course it was found to join one of the thinner stellar nerves. This observation revealed the existence of connexions, already alluded to, between the nerves of the plexus and the stellate ganglion and provided indicative evidence as to the course taken by the axons of the receptor cells. Whether they all behave in the same way is difficult to ascertain because the nerves on the ss-plexus run in all directions anastomosing occasionally with each other, and the tracing of fibres of different origin is possible in exceptional cases only. Anyhow, in view of the evidence available it seems more probable that the centripetal paths of these receptor cells are directed towards the stellate ganglion. According to this assumption the basic pattern of nerve elements in the substellar organ would be as diagrammatically represented in Text-fig. 4.

In *Octopus vulgaris* the structure of the ss-plexus was found to be essentially the same as described above, and the presence of nerve cells in it could be ascertained. Therefore the substellar organ in this species appears to be quite similar to that in *Eledone*, but, as I examined one specimen only and more material was not available, the present account had to be restricted to a single species of the Octopoda.



Text-fig. 4. Simplified diagram of the arrangement of nerve elements in a part of the substellar organ. *st.g.*, stellate ganglion.

DISCUSSION

It is evident that the nerve cells in the substellar organ are of a sort differing markedly from all known types of cells in other organs of cephalopods. On account of their position in a muscle layer a comparison might be made with the ganglion cells of the nerve plexus in the digestive tract and those in the auricles. However, the former are unipolar or bipolar and only rarely tripolar, and evidently it is not their dendrites, but their axons, which are spreading over the muscle fibres. The cells in the auricles are unipolar and are doubtless of a different sort (Alexandrowicz, 1928, 1960). As regards the mantle muscles there is only one reliable record of the presence of multipolar cells in them,

viz. in the paper of Sereni & Young (1932), in which a photograph is reproduced showing a section through the mantle muscles with such nerve cells stained after Cajal. If these sections were made, as seems very probable, from the region of the mantle under the stellar nerves, the cells found in them would be doubtless the same as described in the present paper, for, as Young states, they were situated 'in the thin coats of muscle cells which lie outside the main mass of muscles' which might well be the substellar muscle plexus. In the above-mentioned paper dealing with degeneration and regeneration of nerves the question of these nerve cells is not pursued further. Young briefly states that 'they have very many branches some ending near the cell others running for long distances along the muscle fibres against which some of them seem to end'. He mentions also the observations of Mikhailoff (1921), but the work of this writer is of such a kind that it can be ignored in the present discussion.[1]

[1] Mikhailoff's claims have been taken at their face value by many writers and reproductions of his drawings can even be found in several books. It is understandable that the authors of synoptic works are not in a position to assess the value of the assertions of each writer and consequently some fallacies can drag on through the scientific literature. I consider it my duty, however unpleasant, to expose one of such cases.

Mikhailoff affirms to have discovered an ubiquitous system of peripheral nerve cells in the muscles and various organs of cephalopods. In his words: 'Les cellules nerveuses périphériques sont disséminées en plus ou moins grand nombre presque partout. Quelquefois elles sont solitaires, quelquefois elles constituent de petits ganglions à 5–30 cellules.' He assumes that they occur in all muscles, but one region only in which they were observed is somewhat more exactly indicated. 'Entre les couches musculaires externes du corps ces cellules nerveuses se localisent autour de la tête de l'animal à quelque distance de celle-ci, en constituant le véritable collier, parcequ'elles sont associées à l'aide de leurs prolongements nerveux. De ce collier ou cercle partent 16 chaînettes, dont huit se localisent dans la musculature du corps et les huit autres—dans les bras, par une chaînette à chaque bras.' In order to verify what this intriguing system might be, I tried to stain it with methylene blue in *Sepia* and could easily find the 'chaînettes' in the arms. They are nothing else but the components of the complicated innervation of the arms described by Guérin (1908). There are in fact several such peripheral nerve trunks in each arm called by Guérin (not quoted by Mikhailoff) cordons (or chaînes) nerveux intramusculaires. Mikhailoff's 'collier ou cercle' was most probably the ring formed by commissures between the arm nerves known already to Cuvier and represented in all the works dealing with nervous system in cephalopods. The other eight nerves connecting with the 'collier' could have been the main arm nerves which Mikhailoff did not follow to their origin in the brachial ganglia and assumed that they pass on to the muscles of the body. If therefore, as it is evident, his belief to be a discoverer of new nerve elements in the muscles and his ideas about their structure were chiefly, or perhaps entirely, based on the observation of the peripheral trunks in the arms, they resulted from the basic ignorance of the anatomy of the animals investigated. What structures he saw in other muscles and considered them to be nerve cells is difficult to say. His statement that the size of these 'cells' was 4–9 μ makes the supposition probable that they were swellings produced on fibres during staining since the nerve cells in cephalopods are as a rule much larger and even the smallest of them measure more than 10 μ.

As regards other organs mentioned by Mikhailoff his remarks about the presence of nerve cells in the heart and 'certain glands' are very vague and hardly trustworthy. What, however, he saw in the intestine were true nerve cells, but, first, their presence in this organ was already known and, secondly, his description was inadequate.

No importance whatsoever can be attributed to Mikhailoff's classification of nerve cells (motor, sensory, trophic), based on structural differences of their processes as he saw them.

The first question which arose when the nerve cells on the ss-plexus were noticed was that of their nature and this was really puzzling as long as it was not evident how the cell processes that ended on the muscles and seemed to be all of the same kind should be classified. After it had been ascertained that each cell possesses one long projection joining a nerve trunk it became clear that the others are dendrites and that the basic structure of these neurons is that of typical units of the nervous system. Nevertheless they are remarkable in many respects.

The fact itself that such sensory cells with their dendrites terminating on muscles are present in cephalopods is interesting because elements of a similar sort have been found in a small number of animals, and in those in which their presence is known, as in crustaceans and insects, they occur in a very limited number and only in particular regions of the body.

Compared with the muscle receptors in crustaceans the substellar organ in *Eledone* shows important differences in the way in which the muscular and nervous components are connected with each other. In the former the arborizations of the nerve cells end in a special region of the muscle in which the muscle tissue is replaced by connective tissue fibres, whereas in the substellar organ the branches of the dendrites spread over the wide areas of the muscles. Perhaps the enigmatic N-cells in thoracic muscles of some crustaceans show certain points of resemblance in the behaviour of cell processes since they have processes of considerable length running in various directions and terminating between the muscle fibres; however, the pattern of distribution of their terminal branches is different and their dendritic fields are limited to a small part of the muscle unit.

The presence of branches springing from the axon, but looking and behaving like the processes of the cell body, is a striking but not unknown feature. Similar processes from the axons have been found in sensory cells of insects (Zawarzin, 1912), in the cells of muscle receptor organs and N-cells of decapod crustaceans, and in certain sensory cells of stomatopods (Alexandrowicz, 1952, 1957).

A peculiar feature of the substellar organ which puts it into a special

He obviously exercised little criticism in interpretation of methylene-blue preparations and considered various artefacts to be distinctive features of nerve elements. Artefacts in Mikhailoff's preparations were presumably even more frequent than usual since he applied very hypotonic solutions (equivalent to 0·9 % NaCl), because, as he affirms, solutions of methylene blue in sea water or isotonic liquids are unobtainable. This is proof that not a single work of various writers who applied such solutions for staining the nervous system in marine invertebrates was known to him. There is indeed no reference to any work relating to the subject of his investigations. There is instead a list of the writer's own papers concerning the nervous system of vertebrates.

Thus, there can be no doubt that all Mikhailoff's claims were unfounded. At the best he can be credited for having given, although unintentionally, pictures of peripheral nerve trunks in cephalopod arms stained with methylene blue (his fig. 1 and evidently fig. 8), whereas their previous representation by Guérin was based on Golgi preparations.

category of muscle receptors is the multitude of neurons connected with its muscular component. In crustaceans a receptor consists as a rule of one cell and one muscle. In insects a similar basic pattern of structure of muscle receptors has been found (Finlayson & Lowenstein, 1955; Slifer & Finlayson, 1956). It is true that in some instances a fusion of receptor muscles can take place, as for example, in *Leander serratus* (Alexandrowicz, 1956) and *Praunus flexuosus* (unpublished observation of the writer), so that several nerve cells (up to 4) can end on one long muscle. The fact, therefore, that several cells are in relation with one muscle is not unique, but it is their number in the substellar organ that is striking. Considering the structure of this organ it does not seem probable that it could be functionally differentiated since to the best evidence the ss-plexus appears to be an anatomical unit. This would imply that the changes in condition of the plexus such as occur during contraction or stretching must affect all its muscle elements at the same time. Consequently, whichever of these changes is eliciting the response of the receptor cells the latter must be triggered simultaneously. It follows that when the receptor organs of the two sides of the body react together, as they probably do, the impulses to higher centres are transmitted by one hundred neurons at least.

The accumulation of so many nerve units in one organ may perhaps find its explanation in the fact that in cephalopods in general the number of neurons involved in innervation of any organ is comparatively much greater than in arthropods. I have already (1960) pointed out this 'uneconomical use of nervous substance' when discussing the abundance of nerve elements in the hearts of *Sepia*.

As regards the function of the substellar organ, the only conclusion which can be drawn from the histological evidence is that just mentioned, namely, that it responds to changes affecting the plexus muscles and, since the latter are connected with the pallial adductor and the muscle of the brachial membrane, the function of the receptor must also be related to the action of these muscles. It is, however, not obvious whether the receptor cells become stimulated by the contraction or by stretching of the plexus muscles. It is equally difficult to guess whether these organs are in action only during vigorous contraction of the mantle muscles such as occur when the animal swims backwards, or play some role in adjustment of respiratory movements varying in intensity.

The assumption that the axons of the receptor cells run towards the stellate ganglion harmonizes with the results of Young's experiments (Sereni & Young, 1932) on degeneration and regeneration of fibres in the stellar nerves and the mantle connective (in *Eledone* and *Octopus*). Young came to the conclusion that there are in these nerves 'afferent fibres whose cell bodies lie at the periphery'. He even mentions that this path of afferent fibres may include possibly a few proprioceptors.

There is every reason for assuming that the axons of substellar receptors would behave like those in Young's experiments, but it is not evident whether the afferent path discovered by him consisted of these elements only. Young defines it as 'small' and referring to the afferent fibres in the stellar nerves says that 'they are very few in number compared with the motor fibres'. It is therefore possible that they could all come from the substellar organ; some other considerations, however, make this supposition questionable. My observations of the course of cell axons do not tally well with Young's results on one point. As stated in the foregoing description the axons of the receptor neurons appear to join the stellar nerves of thinner calibre, whereas the afferent fibres observed by Young were evidently running in the thick trunks, as he explicitly states: 'such fibres seem to be more numerous in the large posterior stellar nerves than in the lateral ones'. There are two possibilities: either some nerves carrying the receptor axons and joining the thick stellar nerves were not noticed by me—they could easily be torn away when removing the connective tissue between the nerves—or there is another system of fibres running into stellate ganglion from some yet unknown sensory cells. As these afferent fibres were apparently seen in many thick nerves the second alternative appears to be more probable. The conclusive evidence could possibly be provided if Young's experiments were repeated with the aim of estimating the number of afferent fibres in the stellar nerves. If it were found that this number in the stouter of these nerves surpassed their possible number from the substellar organ, there would only be the question where these other sensory cells sending their axons through the stellar nerves are situated. It would be also interesting to know where the axons of the receptor neurones of the substellar organ are ending. Young proved that there is a path of centripetal fibres in the mantle connective and concluded that the afferent fibres from the stellar nerves pass through the stellate ganglion. The question is whether or not some of them terminate in this ganglion. Here perhaps the comparison of the number of fibres entering the ganglion with the stellar nerves and leaving it with the mantle connective could provide some evidence.

Are there proprioceptors of a similar or of some different kind in other species of the Cephalopoda and in other regions of their body? Considering the high degree of development of the nervous system in these animals and the richness of nerve elements in all their organs it seems plausible that if in the neuromuscular mechanisms of vertebrates and arthropods the proprioceptors play an important role, the cephalopods should have them also.

In many attempts to solve this problem I examined various regions of the cephalopod body, paying special attention to those muscles which at certain movements of the animal become more forcibly stretched, on the supposition that in such muscles the proprioceptors are more likely to occur. This

conjecture was based on the fact that the stretch receptors in crustaceans associated with the extensor muscles must become stimulated at the flexion of the abdomen. As one sort of these receptors (MRO2) presumably responds to strong contractions of the flexor muscles, such as during the flipping of the abdomen in escape reaction, I ventured to suggest (1951) that its function may consist in inhibiting the giant fibres after each powerful contraction of the muscles produced by them. On this line of thought the occurrence of muscle receptor organs was rather to be expected in decapod Cephalopoda which have giant fibres, but the search for them in *Sepia* and *Loligo* has been as yet unsuccessful. This is not to say that they are in fact missing, and neither can it be maintained that in Octopoda they are present in that region only where they have been found. If their structure should be of a similar type as in the substellar organ this would add to the difficulties of research. A thin muscle unit with different pattern of innervation as in MRO of crustaceans can be often clearly distinguished amidst the ordinary muscle fibres even when the nerve cell does not show. If, however, the receptor organ should consist of nerve cells connected with muscles of common appearance, and these cells were refractory to staining, their discovery would depend on such a chance, as happened in the present case with *Eledone*, that a nerve cell was spotted and efforts could be concentrated on one region.

The conclusion to be made is that, since negative results have no value, the problem of the absence or presence of receptor organs in cephalopods cannot be solved until some infallible method of detecting nerve cells is found and with the aid of such a method the whole muscle system is submitted to systematic investigation.

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SUMMARY

In *Eledone cirrhosa* a muscle receptor organ has been found situated under the nerves radiating from the stellate ganglion. This organ for which the term substellar organ is proposed consists of nerve cells scattered over a plexus of muscle fibres connected with the bundles of the pallial adductor muscle and of the muscle of the branchial membrane. The nerve cells whose number is no less than 50 on each side of the body are multipolar with long dendritic processes sending many thin branches alongside the muscle fibres. The axons of these receptor neurons join the stellar nerves and run in them towards the stellate ganglion. Whether all the axons of these neurons take the same course and where they end could not be ascertained.

The motor innervation for the muscular component of the substellar organ is supplied by a nerve arising from the mantle connective (pallial nerve).

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PLANT HORMONES IN MARINE PHYTOPLANKTON, ZOOPLANKTON AND SEA WATER

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(Text-figs. 1–4)

Studies by many workers on the subtle ecological relationships of marine organisms suggest that the distribution of these organisms may be controlled, at least in part, by trace organic substances in their environment. These substances may range from 'toxins to vitamins and hormones' (Lucas, 1955). Saunders (1957) has reviewed the interrelations of dissolved organic matter and phytoplankton and considered the possible roles of organic metabolites in the growth of the algae. The presence of several vitamins, for example, B_{12}, thiamin, niacin and biotin, has been demonstrated in natural waters, but the possible occurrence of plant hormones has not previously been considered.

Work is in progress at Aberdeen on the production by algae of plant hormones of the auxin type, and detection of these auxins in algal media. Auxins are hormones which promote cell enlargement in plants. All the known auxins are indole compounds. This paper reports results of an examination of marine phytoplankton and sea water.

Many of the indole compounds known to be concerned in the bio-synthesis or degradation of indole auxins in the higher plants also occur in animals. For this reason it was decided to examine also zooplankton.

MATERIALS

The following materials have been examined:

Plankton

Marine phytoplankton and zooplankton collected by the fisheries research ships of the Department of Agriculture and Fisheries for Scotland was treated immediately on collecting with half its volume of ethanol, and stored in the deep-freeze or freeze-dried on reaching the laboratory.

Details of the phytoplankton samples, which consisted predominantly of diatoms, are given in Table 1. In addition to the species listed in Table 1, a few protozoa, silico-flagellates, small copepods and faecal pellets were present in sample I, a few faecal pellets in sample II and a few dinoflagellates in all three samples.

TABLE 1

Species	Cells/litre I	IIA	IIB	III
Leptocylindrus danicus	120	—	150	—
Chaetoceros debilis	120	195	750	—
C. decipiens	105	135	1350	—
C. convolutus	—	—	600	—
Thalassiosira gravida	75	15	—	—
Guinardia flaccida	45	—	—	—
Nitzschia seriata	45	45	1500	1080
Coscinodiscus concinnus	45	—	—	—
Thalassiothrix longissima	45	—	—	—
T. nitzschioides	30	—	—	—
Rhizosolenia hebetata (semispina)	—	90	2700	—
Rhizosolenia styliformis	—	—	—	405

All hauls were by vertical standard net. Trawling positions were as follows: sample I, 60° 35′ N., 3° 12′ E. 14. iv. 57; IIA 57° 00′ N., 1° 00° W. 31. v. 57; IIB 66° 47′ N., 16° 27′ W. 18. vii. 57; III, 60° 31′ N., 0° 40′ W. 8. vii. 58; 59° 3′ N., 2° 15′ W. 11. vii. 58.

Zooplankton sample I consisted predominantly of Copepoda (*Temora*, *Calanus*, stages I–IV and *Para/Pseudo-calanus*) and sample II predominantly of a mollusc, *Spiratella* (*Limacina*) *retroversa*. The trawling positions were as follows: sample I, 55° 5½′ N. 5° 2′ W., 2 May 1958; sample II, 61° 1′ N., 10° 0′ W., 10 July 1958.

Sea water

(I) 110 l., from 60 miles off-shore (57° 0′ N., 0° 30′ E.).

(II) 200 l., inshore sea water collected along the east coast of Scotland just south of Aberdeen.

EXPERIMENTAL TECHNIQUES

Slightly different extraction techniques were used with the different materials, and full details are given below. Attention is concentrated in this paper on the following fractions: (1) the acidic ether-soluble fraction (EA fraction), which would contain 3-indolylacetic acid (IAA) and most of the known auxins if present; (2) the acidic ether-soluble substances derived from the hydrolysed aqueous ether-insoluble fraction (SA fraction); and (3) the corresponding neutral fractions (EN and SN).

Some explanation of the reasons for examining the second set of fractions may be desirable. Recent work on plant growth hormones has shown that significant amounts of biological activity occur in the aqueous, ether-insoluble fractions of plant extracts, a fact which is of considerable interest, as the activity cannot be explained in terms of any of the known hormones. It was important therefore to analyse this fraction. Unfortunately, a direct examination is difficult, because large quantities of pigments, carbohydrates, amino acids and other substances, which may interfere with the bio-assays, are present. The following procedure was therefore adopted.

From an analysis of previous work on the aqueous, ether-insoluble hormones it is possible that these substances are unstable auxin complexes which yield ether-soluble hormones on treatment with acid or alkali (Bentley, 1960*a*). Accordingly, it was decided to treat the ether-insoluble fraction with alkali and look for any ether-soluble hormones produced. If any were found, they would be much more amenable to examination than substances in the aqueous ether-insoluble fraction, and it was hoped that any results obtained with them would help to shed light on their non-ether-soluble precursors. This fraction is referred to as the saponified fraction (SA = saponified acidic; SN = saponified neutral).

Detailed extraction techniques

Phytoplankton sample I

The material, which had been stored in the deep-freeze without filtration, was acidified to pH 5·0 and stirred for 30 min with 500 ml. absolute ethanol. The mixture was filtered through paper pulp and the alcohol extract neutralized. The alcohol was removed under vacuum leaving 70 ml. aqueous extract. This was re-acidified to pH 5·0 and extracted with ether. The ether extract was divided into acidic (EA) and neutral (EN) fractions, using 5% $NaHCO_3$. The aqueous, non-ether soluble material, was saponified with N-NaOH for 30 min at 15 lb. pressure, acidified and extracted with ether. This saponified extract was also separated into acidic (SA) and neutral (SN) fractions.

Phytoplankton sample II

The samples were freeze-dried on arrival in the laboratory (dry weight 5·4 g). A little water was added, the pH adjusted to 5·0 and the mixture stirred for 30 min with two lots of 100 ml. chloroform. The material was filtered and separated, the chloroform fraction washed free of HCl, evaporated to dryness and extracted with light petroleum 40–60 °C to remove fatty materials. The petroleum fraction was rejected. Extraction with three lots of methanol followed, the methanol extract evaporated to dryness, the residue taken up in ether and split into acidic (EA) and neutral (EN) fractions. The aqueous non-chloroform soluble fraction was extracted with petroleum, then saponified as sample I and split into acidic (SA) and neutral (SN) fractions.

Zooplankton samples I and II

The material was extracted with 80% ethanol in a Waring blendor at pH 4·0, filtered and pH adjusted to 7·0. The alcohol was removed under vacuum, the extract re-acidified (pH 5·0) and extracted first with 40–60 °C light petroleum, then with ether. The ether solution was split into acidic (EA) and neutral (EN) fractions. The aqueous non-ether soluble fraction was saponified and split into acidic (SA) and neutral (SN) fractions.

Sea water

The samples were filtered, acidified to pH 5·0 and extracted by stirring for 1 h with freshly distilled chloroform. The chloroform was separated off, distilled *in vacuo* and the residues extracted with ether. The ether from sample II was separated into acidic (EA) and neutral (EN) fractions. It was not possible to work with the aqueous non-ether soluble fractions because of their large volumes, and because of the high concentration of salts.

Chromatography

Ether extracts were evaporated to dryness on a freeze-drier and the residues dissolved in a few drops of ethanol for loading on to chromatograms. Extracts were usually purified by preliminary paper chromatography using water as eluant and applying the extracts as a broad strip on the starting line; the pigments remained on the starting line, which was rejected. The remainder of the paper was flushed with ethanol and the recovered material chromatographed in *iso*-propanol:water:ammonia (sp.gr. 0·88) (10:1:1), or water. The ammoniacal *iso*-propanol mixture is widely used in auxin chromatography, as it has been found to give good separation of acidic auxins (Stowe & Thimann, 1954). It has the disadvantage that the ammonia may cause breakdown of unstable compounds with production of artifacts (Bentley, 1958*b*, 1960*b*), but it was felt advisable to use it here for the purposes of comparison with earlier work on plant extracts. Water, which was also used, is a neutral innocuous solvent in which the extracts run very quickly, thus minimizing the possibility of breakdown of compounds during chromatography. It was used as a check on the number of active zones obtained in the ammoniacal *iso*-propanol. It has the disadvantage that it does not give good compact spots suitable for colour tests. Some experiments were also tried using *iso*-propanol-water-acetic acid, but under these conditions no separation of active zones was achieved and activity was detected only at the solvent front. Acidic solvent systems were not therefore suitable. Chromatography was carried out in a constant temperature room at 15° C. Chromatograms were examined under filtered ultra-violet light (2537 Å transmitted) and used either for indole colour tests or bio-assays. The reagents used for colour tests were Ehrlich (*p*-dimethyl aminobenzaldehyde), Salkowski and nitrous/nitric acid, using the techniques of Jepson (1958). Chromatograms to be bio-assayed were cut into ten equal portions and the portions eluted with 1 ml. water for testing. 3-Indolylacetic acid (IAA) and 3-indolyl-acetonitrile (IAN) were run as marker spots.

Assay technique

The *Avena* coleoptile straight-growth method, which is a measure of auxin activity in cell-enlargement, was used. 10 mm lengths of *Avena* coleoptiles are suspended in the solutions to be tested, and the increase in

lengths measured after 24 h. The tissues grow by cell-enlargement. 1% sucrose and phosphate-citrate buffer (10^{-2}M K_2HPO_4 and $0{\cdot}5 \times 10^{-2}$M citric acid) at pH 5·0 is used as a basic medium. For full details of the assay method see Bentley & Housley (1954). The test is specific for auxins. Other growth substances, e.g. vitamins and gibberellins, are virtually inactive. All the chromatography papers used in the bio-assays were washed in water and acetone before bio-assay, to remove impurities. Blank chromatograms, loaded with ether or alcohol but without extracts, were frequently developed and bio-assayed, and showed no biological activity.

RESULTS

Marine phytoplankton

There is an active zone (Z) on the EA chromatograms and hints of activity at two less mobile zones (X and Y, Fig. 1 A). There are also two active zones in the SA fraction (Fig. 1 B), from which all the ether-soluble hormones had been removed before saponification. Several positive Ehrlich colours were obtained with the SA fraction, as indicated, but none with the EA fraction. For the sake of clarity, the three zones of activity in both the EA and the SA fractions in all the species examined have been called X, Y and Z, as indicated on the figures. This is because they show certain points of resemblance with auxins located in other plant materials and labelled X, Y and Z. This work is considered later in this section.

Three zones of activity can also be located in the SA fraction of sample II (Fig. 1 C). It is frequently found that sometimes only one zone (X) can be located; sometimes this can be resolved into two zones (X and Y). These separations probably depend on small differences in conditions of chromatography. A pink (or purple) Ehrlich reaction at R_f 0·1–0·2 has been obtained with all the SA samples examined, as shown in Figs. 1 A and B. This colour reaction indicates the presence of an indole compound. The SA fraction of sample III gave exactly similar results to Fig. 1 C, with three clear-cut zones, X, Y and Z. Thus, it seems that there are at least two, and often three active compounds in the SA fractions of varied samples of phytoplankton, indicating that these compounds are possibly involved in basic metabolism common to a range of species.

It has been thought in the past that the plant hormones were all acidic in nature. However, evidence is accumulating that there are also neutral auxins. Fig. 1 D shows that there is activity in the EN fraction of sample II, though this has not resolved into clear-cut zones. Moreover, it is not always obtained, suggesting that, when it does occur, it comes from neutral precursors, depending on the conditions of chromatography. Figs. 1 E and F illustrate activity found in the SN zones of samples I and II, respectively. Again, this activity is not always obtained and activity in specific zones is not reproducible.

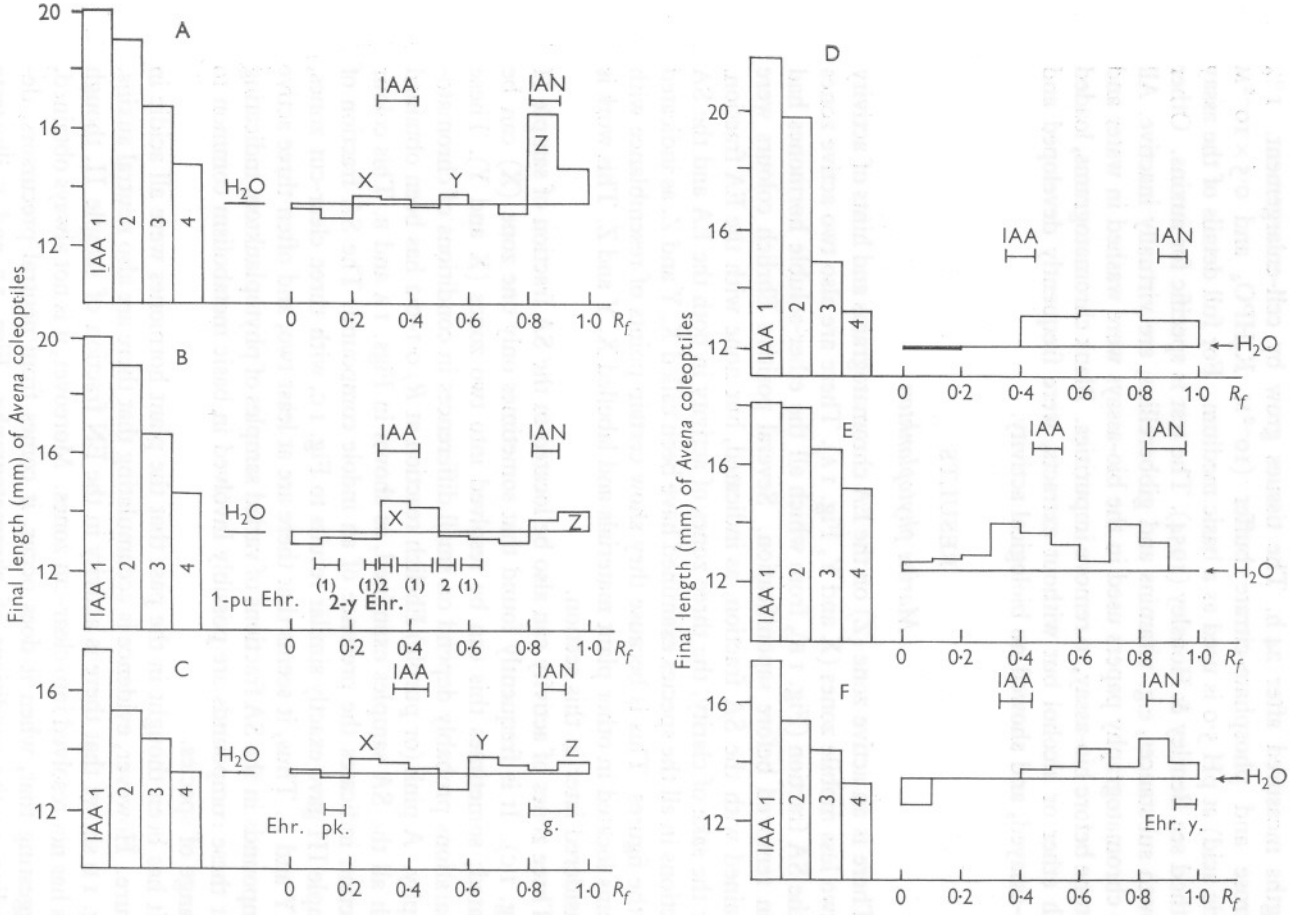

Fig. 1. Extracts of marine phytoplankton chromatographed in *iso*-propanol-ammonia. A, EA fraction of sample I; B, SA fraction of sample I; C, SA fraction of sample II; D, EN fraction of sample II; E, SN fraction of sample I; F, SN fraction of sample II. IAA controls are as follows: 1 = 1 mg/l.; 2 = 0·1 mg/l.; 3 = 0·01 mg/l.; 4 = 0·001 mg/l. Ehrlich colours are as follows: pu., purple; pk., pink; g., green; y, yellow.

The compounds located in the EA and SA fractions show some properties in common, suggesting that in fact they may be the same compounds occurring in both fractions, existing naturally in small quantities and also released possibly from precursors in the aqueous fraction by the saponification. For example, when zone Z in the EA fraction is eluted and re-chromatographed

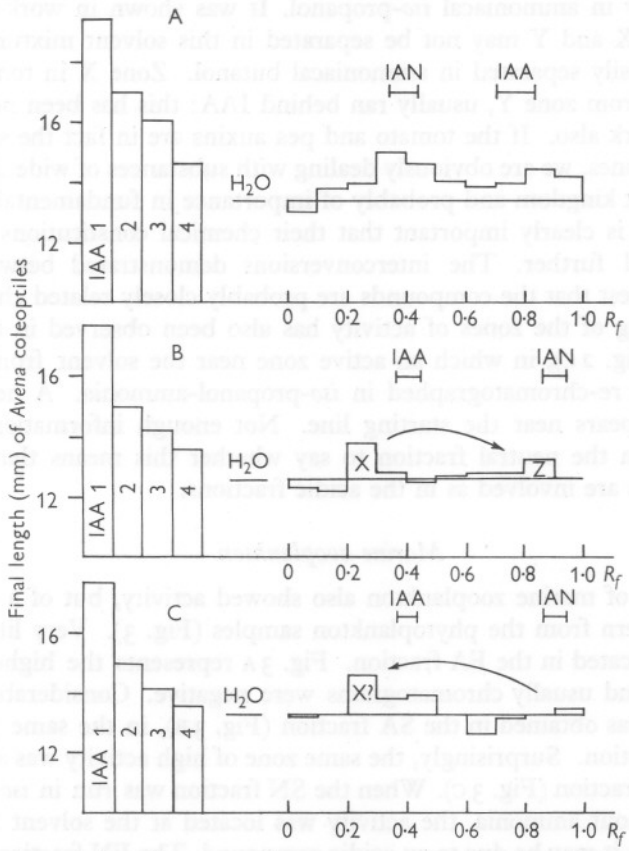

Fig. 2. Interchangeability of zones on chromatograms of marine phytoplankton. A, zone R_f 0·8–1·0 of Fig. 1A eluted and re-chromatographed in water. B, zone R_f 0·2–0·6 of Fig. 1C eluted and re-chromatographed in *iso*-propanol-ammonia. C, zone R_f 0·6–1·0 of Fig. 1F eluted and re-chromatographed in *iso*-propanol-ammonia. IAA controls are as in Fig. 1.

in *water* two active zones appear (Fig. 2A). When zone X of the SA fraction is eluted and re-chromatographed in ammoniacal *iso*-propanol, activity appears also in zone Z (Fig. 2B). This interconvertibility of the zones of activity suggests that the compounds concerned are closely related chemically and exist on the paper in a state of equilibrium with each other.

The interconvertibility of X and Z may be related to a similar phenomenon observed in extracts of tomato roots, in which three compounds, X, Y, and Z,

were shown to be mutually interconvertible (Britton *et al.*, 1956). The same phenomenon is also reported in extracts of pea roots (Audus & Gunning, 1958), and in various pure algal cultures (Bentley, 1958*a*). There is evidence on several of the algal chromatograms of the existence of zone Y, though this is only transient. This may be because chromatography in the present work was usually in ammoniacal *iso*-propanol. It was shown in work on tomato roots that X and Y may not be separated in this solvent mixture, whereas they are easily separated in ammoniacal butanol. Zone X in tomato, when separated from zone Y, usually ran behind IAA: this has been noted in the present work also. If the tomato and pea auxins are in fact the same as the algal hormones, we are obviously dealing with substances of wide distribution in the plant kingdom and probably of importance in fundamental cell metabolism. It is clearly important that their chemical constitutions should be investigated further. The interconversions demonstrated between X, Y, and Z suggest that the compounds are probably closely related chemically.

A shifting of the zones of activity has also been observed in the neutral fraction (Fig. 2 C), in which an active zone near the solvent front has been eluted and re-chromatographed in *iso*-propanol-ammonia. A new zone of activity appears near the starting line. Not enough information is as yet available on the neutral fraction to say whether this means that the same compounds are involved as in the acidic fractions.

Marine zooplankton

Extracts of marine zooplankton also showed activity, but of a rather different pattern from the phytoplankton samples (Fig. 3). Very little activity could be located in the EA fraction. Fig. 3 A represents the highest activity obtained, and usually chromatograms were negative. Considerable activity, however, was obtained in the SA fraction (Fig. 3 B), in the same position as the EA fraction. Surprisingly, the same zone of high activity was also located in the SN fraction (Fig. 3 C). When the SN fraction was run in *iso*-propanol-water, without ammonia, the activity was located at the solvent front, suggesting that it may be due to an acidic compound. The EN fraction contained no activity.

The EA and SA fractions of zooplankton sample II gave very much the same results as sample I, with a zone of activity running in the IAA position and a positive Ehrlich reaction, indicating an indole compound, at around R_f 6·0. The high activity detected in the SN fraction of sample I was not found in sample II.

Sea water

Fig 4 A shows the results of bio-assay of a chromatogram of the ether fraction of the offshore sample, run in *iso*-propanol-ammonia. There are two clear-cut zones of activity corresponding to zones X and Z located in the

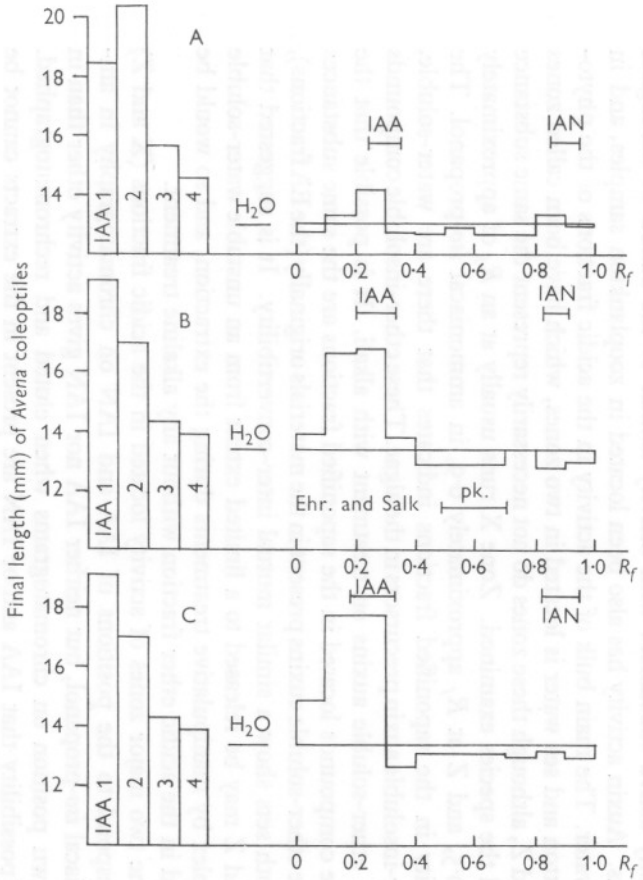

Fig. 3. Extracts of marine zooplankton chromatographed in *iso*-propanol-ammonia. A, EA fraction of sample I; B, SA fraction of sample I; C, SN fraction of sample I. IAA controls are as in Fig. 1.

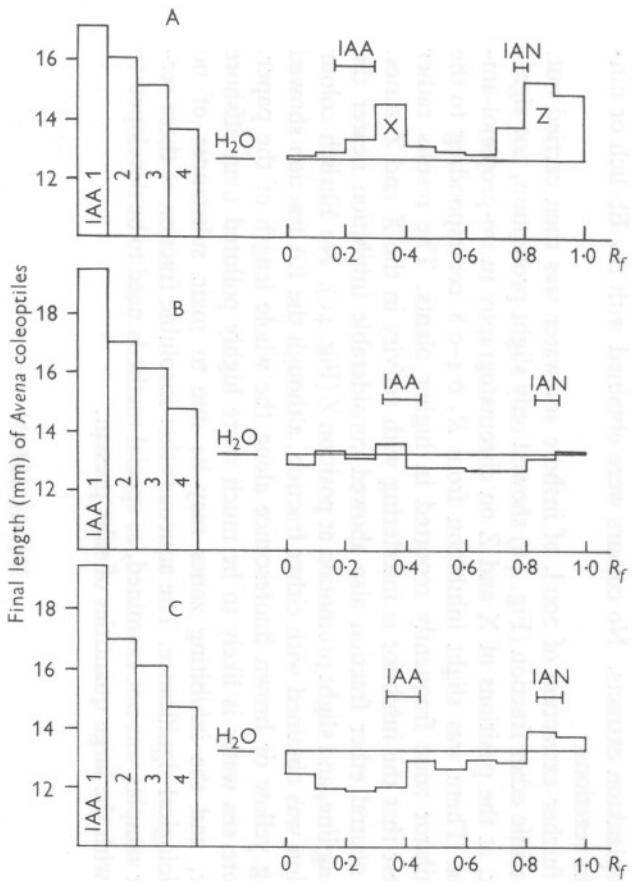

Fig. 4. Extracts of sea water chromatographed in *iso*-propanol-ammonia. A, Ether fraction of sample I; B, EA fraction of sample II; C, EN fraction of sample II. IAA controls are as in Fig. 1.

phytoplankton extracts. No colours were obtained with the Ehrlich or ninhydrin reactions.

A further extraction of 200 l. of inshore sea water was then carried out. The acidic ether fraction (Fig. 4 B) showed only slight promotion, not significant, at the positions of X and Z on chromatography in *iso*-propanol-ammonia. There was slight inhibition from R_f 0·4–0·8 corresponding to the β-inhibitor zone frequently reported in higher plants. The results rather suggest that the inhibitor is interfering with activity in the X and Z zones. The neutral ether fraction also showed considerable inhibition nearer the starting line, and slight promotion at position Z (Fig. 4 C). No Ehrlich colour reaction was obtained with either fraction, although the EA fraction showed strong yellow or brown fluorescence along the whole length of the paper. Inshore sea water is likely to be much more highly polluted than offshore water, and the inhibiting zones may be due to toxic substances of no physiological significance. The aqueous ether-insoluble fraction of these seawater samples was not examined, as special methods need to be developed to deal with the large quantities of salts present.

DISCUSSION

The foregoing results establish that marine phytoplankton contains biologically active substances with activity similar to the auxins of the higher plants. Auxin activity has also been located in zooplankton samples, and in sea water. The main bulk of the activity in the acidic fractions of the phytoplankton and sea water is located in two zones, which have been called zones X and Z, although these zones do not necessarily represent the same substance in all the species examined. Zone X runs usually at an R_f of approximately 0·3–0·5, and Z at R_f approximately 0·9, in ammoniacal *iso*-propanol. The activity in the saponified fractions indicates that there are water-soluble, ether-insoluble auxin precursors in the algae. These ether-insoluble compounds yield ether-soluble auxins on treatment with alkali. It is possible that the active compounds located in the saponified fractions are the same substances as the ether-soluble auxins present in the materials originally (the EA fractions), as both sets show a similar mutual inter-convertibility. It is suggested that X and Z may be released to a limited extent from an unstable water-soluble complex by manipulative treatments during the extraction, and so would be found in the acidic ether fraction without any alkaline treatment.

The two major zones of activity located in the acidic fractions (X and Z) correspond to the positions of IAA and IAN on chromatography in ammoniacal *iso*-propanol, but neither IAA nor IAN gives activity other than in its own position on chromatograms when eluted and rechromatographed. The possibility that IAA and/or IAN are present in the extracts cannot be dismissed, since biological activity is obtained at the position of these com-

pounds in both ammoniacal *iso*-propanol and water. One must conclude, however, that other compounds (referred to in this work as X and Z) are also present in these active zones, since they show a mutual inter-convertibility which is not shown by IAA and IAN.

The total amount of auxins (zones X and Z) located in the offshore sea water, calculated in terms of the IAA controls bio-assayed in the same experiment, is 0·375 μg in 110 l. (0·06 μg in zone X and 0·315 μg in zone Z). An improvement in the growth of a marine diatom, *Skeletonema costatum*, under the influence of IAA at a concentration of 10^{-11} to 10^{-10} g/ml. has been noted (Bentley, 1958*a*). This is equivalent to 1–10 μg in 100 l. Thus the amount of auxin detected in sea water is approximately ten times less than would be needed to have an optimum effect on the growth of *Skeletonema*. It should be borne in mind, however, that the amounts of auxin finally detected by bio-assay of extracts are probably much less than those present in the original materials due to losses in the many stages of purification and assay.

The investigations reported in this article have been carried out during the tenure of a Senior Government Research Fellowship, and I am indebted to the Director of the Department of Agriculture and Fisheries for Scotland Marine Laboratory for facilities for the work.

SUMMARY

Extracts of marine phytoplankton, marine zooplankton and sea water have been examined for plant hormones of the auxin type. The phytoplankton consisted predominantly of diatoms, in particular of *Leptocylindrus danicus*, *Chaetoceros debilis* and *C. decipiens*. The zooplankton consisted predominantly of copepods, in particular *Temora*, *Calanus* stages I–IV and *Para/Pseudocalanus*. The samples were extracted chemically and the extracts split into acidic and neutral components of (*a*) the ether-soluble fractions, and (*b*) the ether-soluble fractions of the residue after alkaline hydrolysis. The fractions were further purified by paper chromatography in water followed by chromatography in ammoniacal *iso*-propanol. They were assayed for biological activity by the *Avena* straight-growth test, which measures the activity of auxins in cell-enlargement.

Biological activity was detected in all phytoplankton fractions. Activity in the acidic fractions is mainly due to two hormones, tentatively called X and Z. These are probably closely related chemically, as they show a mutual interconvertibility.The same two zones of activity were detected in sea water. The zooplankton samples also contained active substances. Indole compounds can be detected in the extracts, but it is not clear that the biological activity is due to indolylacetic acid or any of the known indole hormones.

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THE LIGAMENT OF *COCHLODESMA PRAETENUE* (PULTENEY)

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(Text-fig. 1)

In a recent paper (Allen, 1958) the ligament of *Cochlodesma praetenue* (Pulteney) was shown to have unusual features, the significance of which was not appreciated at that time. Examination of its structure shows that a further description is necessary.

Studies by Owen, Trueman & Yonge (1953), Owen (1958, 1959), and Yonge (1953, 1957) have made clear the basic structure of the ligament of the adult bivalve. Primarily the ligament is composed of an inner layer covered by the anterior and posterior outer layers and the periostracum. The inner layer is secreted by the epithelium of the mantle isthmus, the outer layers are secreted by the outer surface of the outer mantle fold within the depths of the mantle embayments at either end of the mantle isthmus, and the periostracum is secreted by the inner surface of the outer mantle fold. This primary ligament may be secondarily extended anteriorly and/or posteriorly by fusion of the mantle margins and may involve (1) extension by periostracum, or (2) extension by fusion layer.

The ligament of *C. praetenue*, although much modified, is opisthodetic, i.e. the point of minimal growth is anterior (Owen, 1959; Allen, 1960). The primary ligament is secondarily extended anteriorly and posteriorly by fused periostracum and fusion layer. These secondary layers can be seen externally and are remarkable for the unusual paired lateral extensions of the fusion layer which follow the line of the umbonal ridge (Fig. 1). The primary ligament is internal. The ligament is best described by analysis of its various parts.

The inner layer lies below the umbo. It is held between a pair of spoon-shaped extensions of the pronounced internal ridges of each shell valve (see Allen, 1958, fig. 2). The lateral faces of the inner layer attached to the spoon-shaped extensions are concave, while the free ventral edge is grooved in the sagittal plane. Growth lines show that most of the growth takes place ventrally and posteriorly (Fig. 1 c).

The posterior outer layer is applied to the postero-dorsal sides of the inner layer. It is wedge-shaped and all growth is posterior. The growth lines are continuous with those of the inner layer. The lateral faces are slightly convex.

The posterior fusion layer covers the dorsal side of the posterior outer layer and extends to a point close to the anterior limit of the posterior adductor muscle.

The anterior outer layer is remarkable for its scroll-like form. It extends a short distance anterior to the posterior outer layer and fans out forming a pair of lateral wings. From the posterior edge of the wings a thin sheet of this

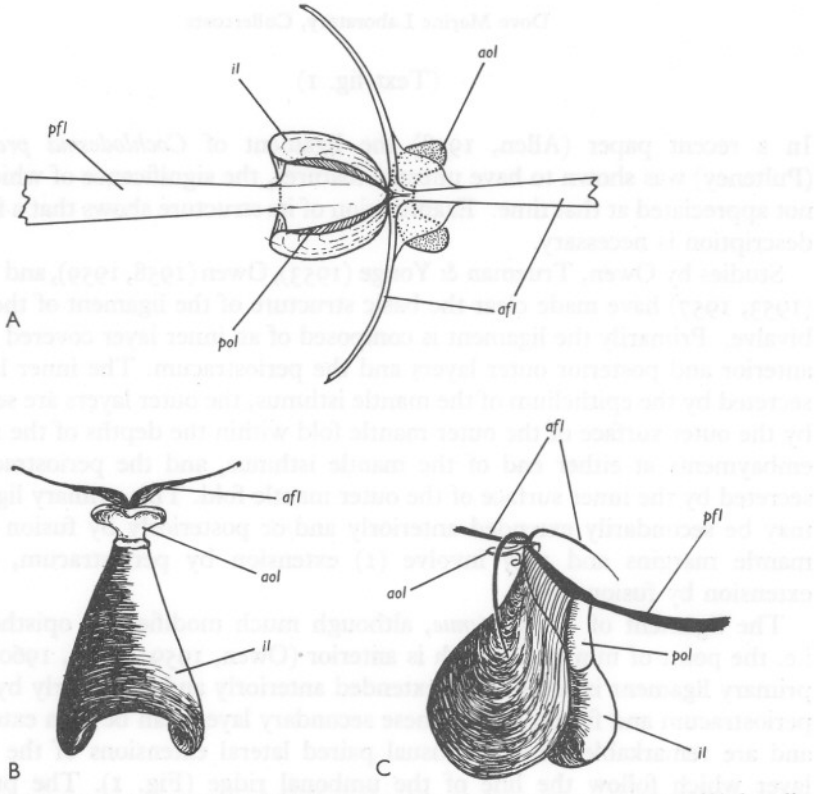

Fig. 1. Semi-diagrammatic views of the ligament of *Cochlodesma praetenue* as seen (A) dorsally, (B) anteriorly and (C) postero-laterally. *afl*, anterior fusion layer, *aol*, anterior outer layer, *il*, inner layer, *pfl*, posterior fusion layer, *pol*, posterior outer layer. The covering periostracum is not shown.

layer extends ventrally overlapping the inner layer to a slight extent (Fig. 1 B, C). This gives the erroneous impression that the anterior outer layer is merely a continuation of the inner layer (see Allen, 1958, p. 98).

The anterior fusion layer is also unusual. It extends from just posterior to the anterior adductor muscle to the posterior limit of the anterior outer layer where it divides into two lateral forks that follow the line of the umbonal ridge. The angle between each fork and the sagittal part has a thin covering

of fusion layer, which is separate from the underlying wings of the anterior outer layer (Fig. 1 A, B). A fold of epithelium extends between the two layers.

The fused periostracum covers the ligament and extends slightly beyond the anterior and posterior limits of the fusion layer.

It is clear that this ligament, although unusual, does not differ basically in its constitution from any other opisthodetic ligament. Posterior fusion layer, posterior outer layer and inner layer are normal. It is the lateral extensions of the anterior outer layer and anterior fusion layer that are atypical. It seems likely that these are formed by extension, lateral folding and fusion of the outer mantle edge in the depths of the anterior embayment.

SUMMARY

The ligament of *Cochlodesma praetenue* is described. Although unusual in form, it does not differ basically from other opisthodetic ligaments.

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ON CHANGES OF SEA TEMPERATURE IN THE ENGLISH CHANNEL

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(Text-figs. 1–5)

In a series of papers dealing with changes in the distribution of intertidal animals around Britain, and especially along the English Channel, attention was drawn to some local aspects of the general warming-up of sea and air that has taken place in the last 50 years (Southward & Crisp, 1954, 1956; Crisp and Southward, 1958). In the first of these papers smoothed values of annual mean air temperature at Plymouth Hoe, and sea surface temperature of the southern Celtic Sea were given, the latter values being based on Smed (1952). The graphs showed a rise of about 1° C in the air temperature and 0·5° C in sea temperature during 50 years.

More recently Cooper (1958) has tabulated the monthly mean sea temperatures for Plymouth Sound, based on three times a week readings taken below the Hoe by the Plymouth City Meteorologist. He interprets the figures as showing a rise of about 0·3° C, but does not give the annual means for the whole period. Annual means may not illustrate fully the effect of a very cold spring and very hot summer in the same year (e.g. 1947) but they do allow rapid comparison for biological purposes, and have considerable significance when resident or sedentary perennial species are being studied, whether they are pilchards or barnacles, for example.

In view of the increases in temperature already noted it would be surprising if a similar rise was not found at International Station E1, which has been worked, with some gaps, since 1903. Some monthly values for this station were given by Atkins & Jenkins (1952), but they showed no long-term trend. The apparent absence of any change may well have been due to the use of the integral mean of the whole water column; a dubious procedure for temperature. However, Cooper (1958), after remarking that he himself had failed to find any evidence of long-term changes at E_1, points out that there are inevitably many sources of bias in the raw data, which requires tedious treatment to make it statistically reasonable. Such treatment may be possible in the future (Cooper, personal communications), but there is an immediate need for information of use in current investigations of bottom fauna, plankton and other fields. Therefore, I have reassessed part of the E1 data, using only the observations of most interest—surface values, for comparison with the

many surface observations in other areas, and bottom values for use with studies of bottom fauna and deeper living plankton animals.

Most of the actual observations at E1 have been published by the International Council, those for the period 1921–30 in the Rapport Atlantique, and those for 1931–38 and 1947–54 in the Bulletin Hydrographique. I am indebted to the observers, Mr F. A. J. Armstrong and Mr E. I. Butler, for the later observations which have not yet been published. For each year the temperatures observed each month have been plotted on graph paper, and the points joined together with a slightly smoothed freehand curve (example in

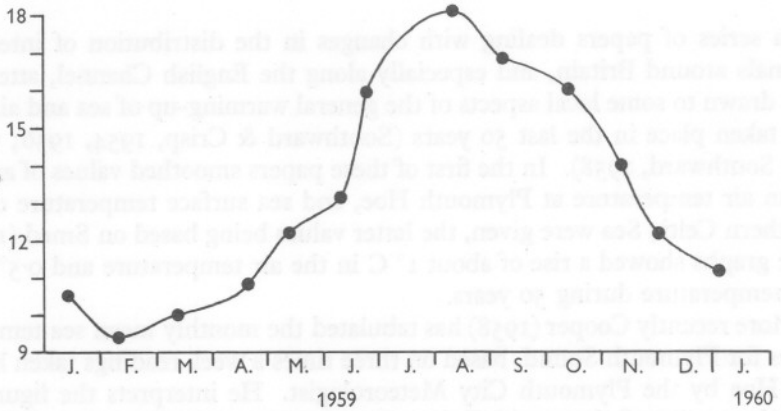

Fig. 1. An example of the method used to derive mid-monthly means from the raw data for E1. The points on the slightly smoothed curve are the actual surface temperatures observed in 1959.

Fig. 1). From the curves the mid-monthly values were read off, and additional values provided for missing months. The monthly temperatures derived in this way are presented in Table 1.

Such treatment is only a little better than use of the raw data for calculating the annual means, and as a way of deriving the monthly values has been described by a colleague as 'fudging'. However, at the moment, it is difficult to find any other manipulation to make the E1 results more presentable, except, perhaps, comparison with other stations for surface values, and I believe that it is preferable to abandoning the whole series of observations.

SURFACE TEMPERATURE AT E1

In addition to Table 1, the annual means of surface temperature are plotted in Fig. 2, which also shows the annual means for 1903–27 worked out by Lumby (1935). Lumby's method involved adjustment to make up for missing months, and there is good agreement for all but one of the overlapping years.

TABLE 1. DERIVED MID-MONTHLY VALUES OF SEA TEMPERATURE AT INTERNATIONAL STATION E1 (LONG. 50° 02′ N., LAT. 4° 22′ W.)

Surface temperatures (0–0·5 m. depth)

	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
Jan.	—	11·0	9·7	9·1	11·0	10·0	9·5	10·0	9·8	10·1	9·6	10·8	9·8	9·2	10·9	9·4
Feb.	—	9·6	9·4	8·4	9·9	9·4	9·4	9·5	8·8	9·2	9·2	10·3	9·3	8·3	9·9	9·1
Mar.	—	9·5	9·4	8·1	9·3	9·6	9·3	9·5	8·8	8·4	9·1	9·4	9·7	8·6	8·9	9·4
Apr.	—	10·6	9·9	8·3	9·6	10·2	10·4	10·0	8·9	9·3	9·6	9·1	10·2	9·6	9·6	10·0
May	12·6	12·4	10·7	10·5	10·8	10·9	12·1	12·4	11·8	11·1	10·9	11·0	10·7	11·1	11·7	12·5
June	15·0	13·8	12·4	13·5	13·8	13·4	13·2	13·4	14·8	15·2	13·9	14·4	12·4	13·4	14·1	13·7
July	15·9	13·0	16·5	15·9	16·1	17·1	15·6	17·0	17·2	15·4	15·8	17·7	14·7	15·5	16·7	14·6
Aug.	16·2	15·0	16·7	15·1	15·5	17·1	16·8	16·0	16·5	15·2	15·2	17·7	18·7	15·6	18·2	16·5
Sept	15·8	14·9	14·9	14·2	15·7	16·9	15·4	16·9	17·0	16·4	15·0	15·6	16·8	15·2	16·2	15·9
Oct	15·5	14·0	13·0	12·9	13·7	14·8	13·8	14·3	13·1	14·1	14·8	13·7	15·3	13·6	13·8	14·7
Nov.	14·2	11·9	11·5	12·4	11·6	12·8	13·4	12·8	12·5	12·8	13·4	12·6	13·2	12·3	12·2	13·3
Dec.	12·6	10·6	10·0	11·7	10·6	11·2	11·8	11·3	11·2	11·4	11·9	11·4	9·9	12·3	10·4	11·6
Year	—	12·19	12·00	11·67	12·30	12·78	12·55	12·75	12·53	12·38	12·36	12·80	12·55	12·05	12·71	12·55

	1937	1938	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Jan.	10·0	10·2	9·4	11·1	10·7	10·8	9·6	10·3	9·6	10·9	9·8	11·0	10·3	9·9	10·3
Feb.	9·7	8·9	7·7	9·9	10·0	9·4	8·8	9·1	8·5	9·1	9·5	9·1	9·7	9·4	9·4
Mar.	9·6	9·1	7·9	9·1	10·3	10·1	8·7	9·1	8·5	9·2	7·7	8·6	10·4	8·9	10·0
Apr.	10·0	9·8	9·4	10·2	10·9	10·7	9·4	9·9	8·7	9·7	8·6	9·6	10·6	9·8	10·7
May	11·5	10·8	11·6	10·2	11·9	11·3	10·5	11·7	10·8	11·7	10·6	11·9	11·5	10·4	12·3
June	15·6	12·8	13·2	12·1	14·6	14·2	12·8	14·0	13·2	14·5	13·1	14·0	14·2	13·6	13·7
July	16·2	15·6	16·8	15·8	16·6	15·7	16·4	15·9	14·9	13·3	18·5	15·5	16·1	16·4	17·5
Aug.	17·8	17·7	17·6	17·0	15·8	15·8	15·4	15·9	17·4	14·2	16·0	15·2	16·0	15·7	18·0
Sept.	16·3	15·6	16·3	15·8	17·4	15·0	14·6	15·0	16·0	14·9	14·8	15·0	14·8	14·8	16·6
Oct.	14·8	14·0	15·0	14·3	15·5	14·2	14·0	13·7	14·5	13·7	14·1	14·4	14·8	14·4	15·9
Nov.	13·3	13·0	13·7	13·7	13·3	12·7	12·9	12·4	13·0	13·0	13·1	12·9	12·7	13·7	13·7
Dec.	11·6	12·7	12·4	12·4	11·7	10·9	11·7	10·9	12·7	11·0	12·1	11·5	11·3	12·3	11·5
Year	13·03	12·51	12·58	12·63	13·22	12·56	12·06	12·32	12·31	12·10	12·32	12·39	12·70	12·41	13·30

'Bottom' temperatures (60–75 m. depth)

	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
Jan.	—	11·2	10·0	9·3	10·9	9·7	10·6	9·8	9·9	10·3	10·1	10·9	10·1	9·4	10·3	9·6
Feb.	—	10·0	9·4	8·8	10·0	9·3	9·3	9·2	8·9	9·1	9·1	9·9	9·3	8·3	9·6	9·1
Mar.	—	9·6	9·1	8·4	9·1	9·4	8·9	9·6	8·5	8·3	8·7	9·6	9·1	8·2	8·9	9·0
Apr.	—	9·7	9·6	8·4	9·3	9·7	9·4	9·8	8·9	8·9	9·2	8·7	9·5	8·7	9·1	9·1
May	10·4	10·0	10·3	9·4	10·0	10·5	10·1	10·3	9·7	9·5	9·9	9·3	10·4	9·5	9·9	9·7
June	11·7	10·6	11·0	10·3	10·3	11·1	11·0	11·2	10·7	10·8	11·6	10·1	11·1	10·6	10·6	10·5
July	12·8	12·1	11·9	11·2	11·9	11·9	11·8	12·0	12·1	11·2	13·4	10·8	11·8	11·7	11·5	11·1
Aug.	13·3	12·9	12·5	12·2	12·3	12·6	12·5	12·9	12·3	12·0	14·8	11·5	12·6	11·8	12·9	12·8
Sept.	13·8	14·0	13·3	12·6	13·3	13·3	13·5	13·3	12·9	13·3	14·9	13·0	13·9	12·3	14·0	14·1
Oct.	15·2	13·9	13·4	13·1	13·5	14·4	13·7	14·3	13·9	14·0	14·7	13·8	14·7	13·1	13·6	13·8
Nov.	14·6	11·7	11·8	12·7	12·8	12·9	13·1	12·8	12·7	12·7	13·5	12·5	13·3	12·3	13·1	12·6
Dec.	12·9	10·7	10·2	11·7	10·7	11·7	11·5	11·3	11·5	11·5	11·9	11·1	9·9	11·6	10·6	11·5
Year	—	11·36	11·04	10·67	11·17	11·37	11·28	11·37	11·00	10·96	11·81	10·93	11·30	10·62	11·17	11·07

	1937	1938	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Jan.	10·4	10·5	9·5	11·2	10·7	10·9	9·6	10·4	9·5	11·0	10·1	10·9	10·6	10·4	10·4
Feb.	9·5	8·9	7·7	9·8	10·1	9·5	8·7	9·1	8·6	9·0	9·6	9·2	10·0	9·4	9·4
Mar	9·1	9·0	7·6	8·7	9·9	9·9	8·6	9·2	8·3	8·9	7·6	8·5	10·0	9·0	9·9
Apr.	9·3	9·4	8·4	9·3	9·8	10·3	8·9	9·3	8·7	9·3	8·0	8·9	10·5	8·8	10·1
May	10·1	9·7	9·5	10·6	10·5	10·6	9·5	10·0	9·3	10·2	9·5	9·6	11·0	9·9	10·6
June	11·1	10·1	10·3	11·3	11·4	11·7	10·6	11·0	10·5	10·7	10·6	10·7	12·0	11·0	11·6
July	12·2	12·1	11·3	12·3	12·8	12·1	11·2	12·2	11·2	11·5	11·3	12·0	12·5	11·7	12·6
Aug.	13·2	13·0	12·7	13·1	13·5	13·0	12·1	12·6	12·2	12·0	13·1	12·6	13·1	12·5	13·5
Sept.	14·4	13·5	13·9	13·7	14·8	14·0	13·0	13·9	12·9	13·6	13·1	13·7	13·8	13·6	14·8
Oct.	14·4	13·4	13·7	14·3	15·4	14·1	13·5	13·7	14·3	13·8	14·0	14·1	14·6	14·4	15·3
Nov.	13·3	12·8	13·1	13·5	13·6	12·7	13·1	12·5	13·0	12·9	13·2	12·9	12·8	13·6	14·8
Dec.	11·9	12·0	12·4	12·4	11·6	10·9	11·7	10·8	12·5	11·6	12·2	11·8	11·7	12·3	11·7
Year	11·57	11·20	10·84	11·68	12·00	11·64	10·87	11·22	10·91	11·20	11·02	11·24	11·88	11·38	12·05

The general trend is obviously upwards. Compared with 1903–27, the period mean for 1928–59 is 0·46° C higher, an increase of the same order as that found further west in the Celtic Sea (see p. 449). A distinct interruption of the rise occurred in 1951–56: during this 'little cold spell' there was a slight return of the northern barnacle, *Balanus balanoides*, at many stations in south-west England and elsewhere (Southward & Crisp, 1956; and unpublished records). However, even in this period the annual means were as

high as, or higher than, those of the warmest years of 1903–11. The upward trend is also displayed in the very warm years. The year 1921 was regarded as exceptionally warm for the time (Le Danois, 1923; Harvey, 1923), but since then we have had at least two warmer years, 1949 and 1959. Looking at the graph, one might say that 1921 was the first major sign of the warm spell that set in a few years later, and which appears to be continuing still.

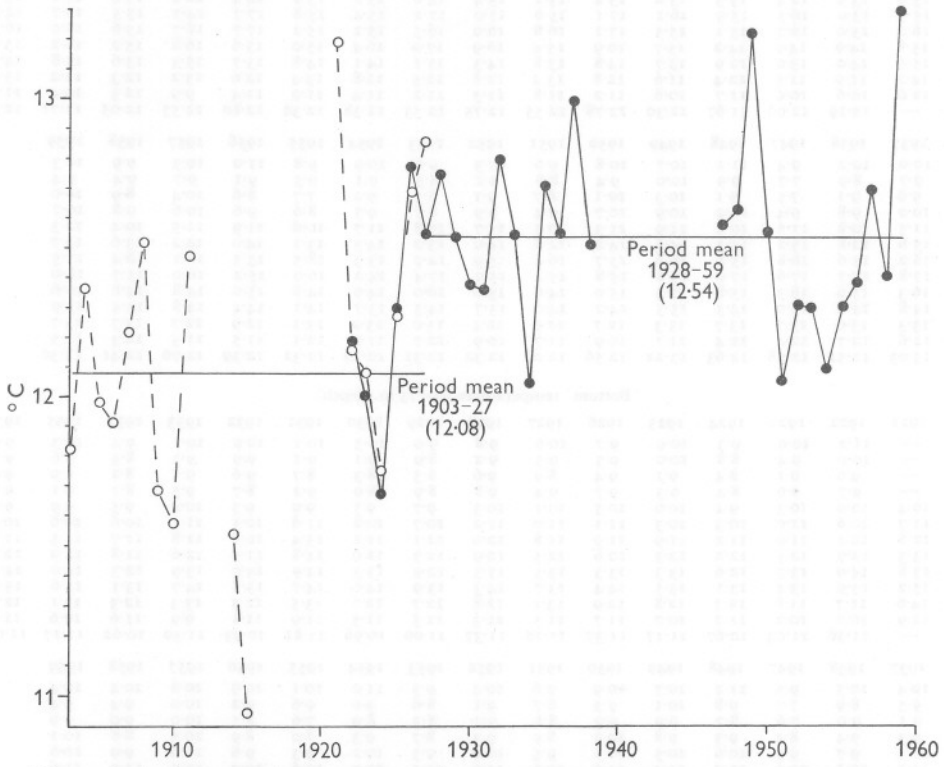

Fig. 2. Annual mean surface temperature at E1 1903–59. The black circles and solid lines are those from Table 1, while the open circles and broken line are the means calculated by Lumby (1935). Some period means are also shown.

If we examine the monthly values, the changes do not seem to have been quite so clear cut as with the annual means. The little cold spell mentioned above was marked by a sequence of cold winters (temperatures below 10° C from February to April), but in some of these years the summer was hot, which suggests a more continental, or less oceanic, marine climate than in earlier years. A similar trend since the late 1920's might be inferred from the monthly bottom temperatures also (Table 1). To contrast with this suggestion we have the generally warm years (e.g. 1949, 1959) when the surface tem-

peratures in winter (Feb.–Apr.) were higher than the temperatures found in every year before 1939.

Probably the steadiest trend can be shown in the autumn months. There has been a slow rise in October, November and December, clearly demonstrated by grouping the figures into three periods:

	October (° C)		November (° C)		December (° C)	
	Mean	Minimum	Mean	Minimum	Mean	Minimum
1921–30	13·92	12·9	12·59	11·5	11·24	10·0
1931–38	14·33	13·6	12·91	12·2	11·45	9·9
1947–59	14·50	13·7	13·13	12·4	11·72	10·9

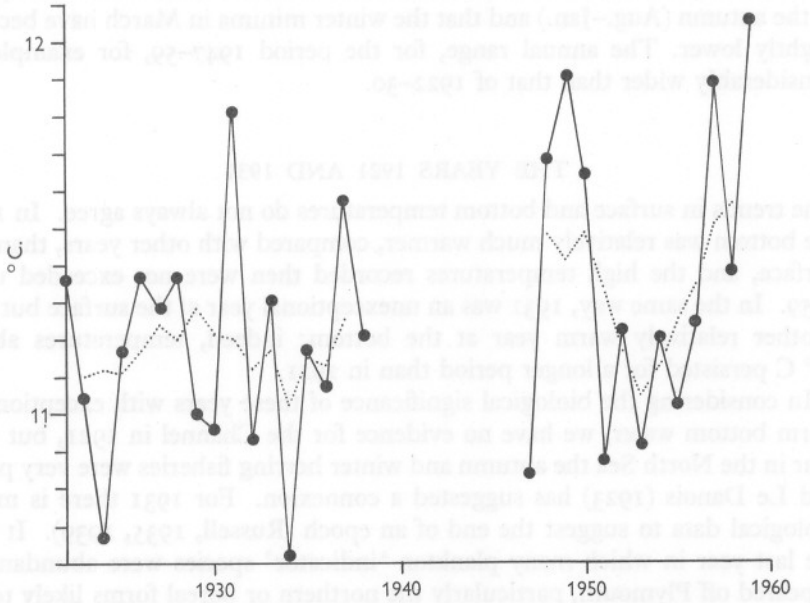

Fig. 3. Annual mean bottom temperature at E1, 1922–59.
The dotted line shows the 5-year smoothed averages.

Thus there has been a rise of half a degree in the autumn means, and nearly twice this amount in the period minima. This autumn trend appears to be carried over into January, the monthly figures for which also show rises, but only about 0·2–0·3° C in this case. The cumulative effect of these increases on winter-spawning fish (the spring-spawners of Russell, 1935, 1939) can only be guessed at, but it is worth noting that Ford (1929) deduced a link between falling sea temperatures at E1 in the autumn and a successful herring fishery off Plymouth.

BOTTOM TEMPERATURE AT E1

From 1921 to 1959 the recorded depth of the lowest water sample at E1 has varied from 60 to 75 m. This is not, of course, due to variation in the sea-bed, but to combinations of inaccurate stationing of the ships, tide, wire angle and observers' idiosyncrasies. The derived monthly values for this 'bottom' are given in Table 1, and the annual means shown on Fig. 3, together with 5-year smoothed averages. The trends to be detected from the shorter period available are, of course, less marked compared with the surface. Nevertheless, the graph suggests part of a long-term rise, of the order of 0·25° C over 40 years. The monthly values, however, indicate that most of this rise has taken place in the autumn (Aug.–Jan.) and that the winter minima in March have become slightly lower. The annual range, for the period 1947–59, for example, is considerably wider than that of 1922–30.

THE YEARS 1921 AND 1931

The trends in surface and bottom temperatures do not always agree. In 1921 the bottom was relatively much warmer, compared with other years, than the surface, and the high temperatures recorded then were not exceeded until 1959. In the same way, 1931 was an unexceptional year at the surface but was another relatively warm year at the bottom: indeed, temperatures above 14° C persisted for a longer period than in 1921.

In considering the biological significance of these years with exceptionally warm bottom water, we have no evidence for the Channel in 1921, but that year in the North Sea the autumn and winter herring fisheries were very poor, and Le Danois (1923) has suggested a connexion. For 1931 there is much biological data to suggest the end of an epoch (Russell, 1935, 1939). It was the last year in which many plankton 'indicator' species were abundant or appeared off Plymouth, particularly the northern or boreal forms likely to be adversely influenced by warmer conditions—*Aglantha*, *Sagitta elegans*, and *Meganyctiphanes*, for example. To judge from the evidence obtained by Ford (to be found in Ford, 1933; Kemp, 1938) there was a practically total failure of recruitment of herring in the Plymouth area in the winter of 1931–32. This was not due to absence of adults, for considerable landings occurred, though 'running' herring were scarce (Ford, 1933). Herring are also northern forms and are likely to be adversely affected, not necessarily directly, by warmer conditions (cf. Russell, 1939). A thorough study of the recorded hydrographical conditions in the second half of 1931, in relation to the biological changes, would be very rewarding.

COMPARISON WITH OTHER REGIONS OF THE CHANNEL

Bowden (1955) has tabulated some annual means and period monthly means of the surface temperatures taken at the Seven Stones Light Vessel, and has shown graphically the annual means for the English Channel as a whole from 1903 to 1951. Mr A. J. Lee of the Fisheries Laboratory, Lowestoft, has

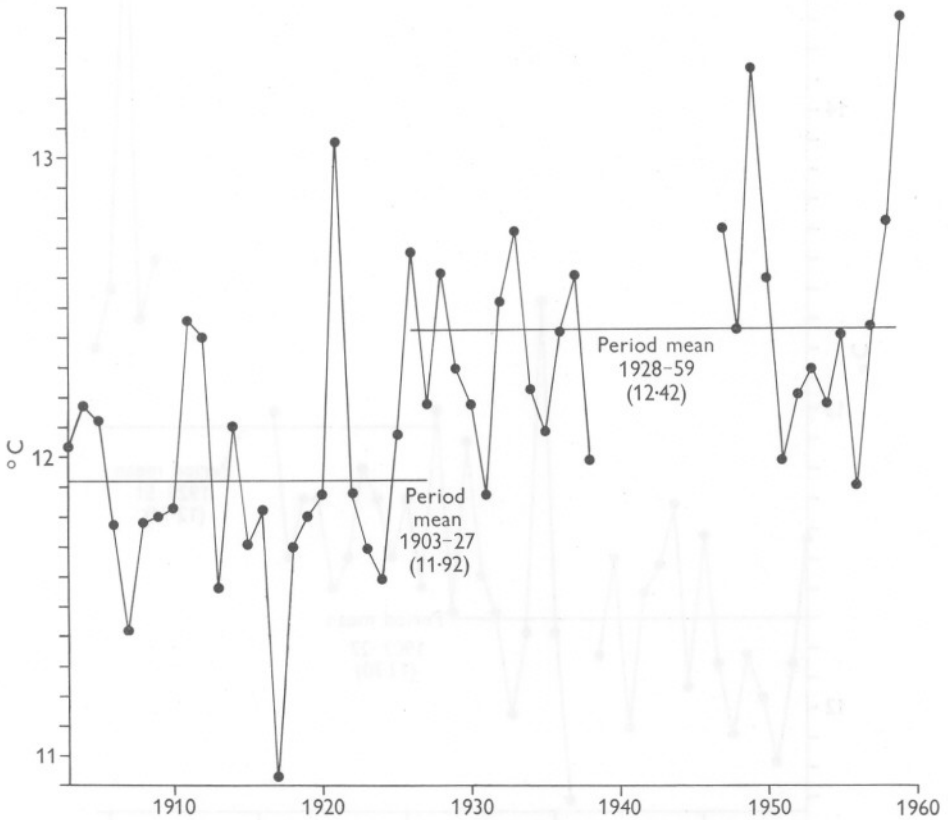

Fig. 4. Annual mean surface temperature at the Seven Stones Light Vessel, 1905–59. From Lumby (1935) and Bowden (1955), with means to 1959 supplied by Mr A. J. Lee.

kindly supplied me with further annual means for the Seven Stones to 1959. He has also supplied additional annual means to 1951 for Lumby area 9, for which Lumby (1935) has already published the means from 1903 to 1927. The annual means for these two stations are shown in Figs. 4 and 5, and it is obvious that the trends already shown for E1 are closely paralleled. At the Seven Stones the rise over 50 years has been about 0·5° C, though the peak

in 1921 was less marked, and the little cold spell of 1951–56 relatively less cold than off Plymouth.

North of Ushant (area 9) the period means show a rise of 0·64° C, somewhat more than at E1 or the Seven Stones. A larger increase than elsewhere is not

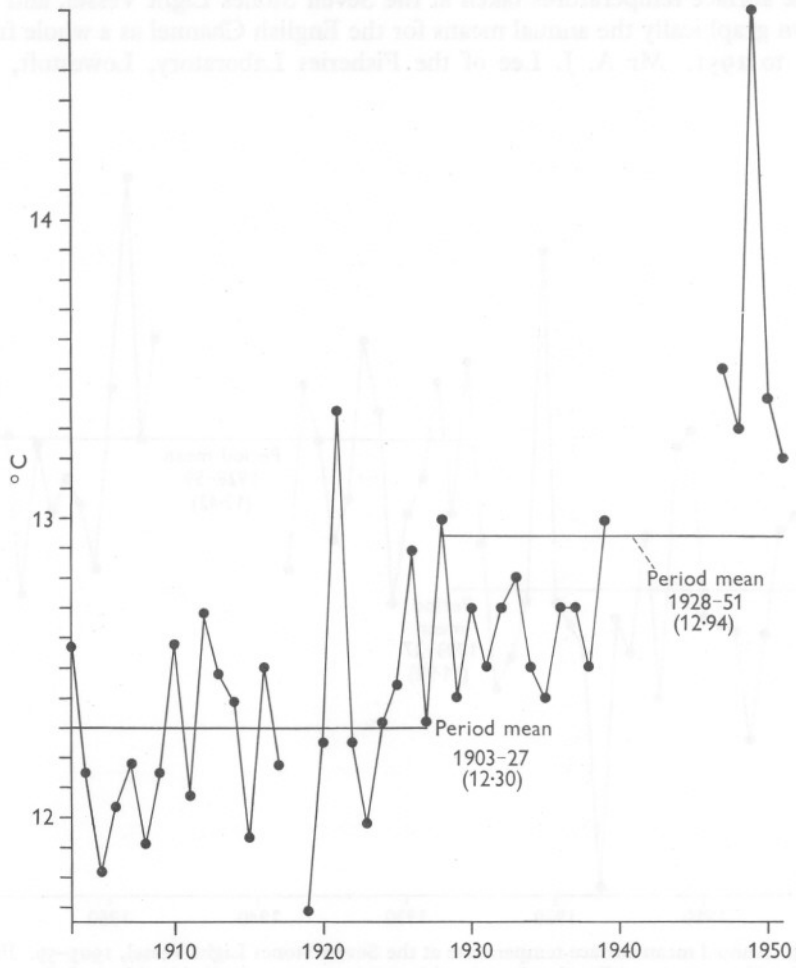

Fig. 5. Annual mean surface temperature in Lumby area 9 (area centred on long. 48° 40′ N., lat. 5° 20′ W.) north of Ushant (Ile d'Ouessant). From Lumby (1935) with additional means supplied by Mr A. J. Lee.

surprising if we remember that much of the warm water flow into the English Channel in summer (i.e. Aug.–Sept.) appears to be concentrated on the southern side (Lumby, 1925; Harvey, 1930; cf. also Dietrich, 1950). This area also shows a steadier trend than at the other two stations: it is not as coastal, and is less likely to be influenced by a flow of colder water in the winter (cf. Dietrich, 1950).

SUMMARY

Mid-monthly values of sea surface and bottom temperature, 1921–59, have been derived graphically from the raw data for International Station E1, and annual and other means calculated. The results are presented graphically and in tables, and discussed briefly in relation to faunistic and other changes in the English Channel.

Comparison with data from other areas suggests that in the Western Channel the annual mean surface temperature has risen about 0·5° C in the last 50 years. At station E1 the bottom temperature has also risen, about 0·25° C since the 1920's. The steadiest rise, in both surface and bottom temperatures, seems to have taken place in the autumn months.

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THE CILIARY FEEDING MECHANISM OF THE MEGATHYRIDAE (BRACHIOPODA), AND THE GROWTH STAGES OF THE LOPHOPHORE

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From the Plymouth Laboratory

(Text-figs. 1–11)

The Megathyridae Allan 1940 is a family of brachiopods in which the adult lophophore is of simple design, bilobed (schizolophous) in *Argyrotheca* and four-lobed (ptycholophous) in *Megathyris*. Little is known of feeding mechanisms in the family. Hérouard (1877), finding it difficult or impossible to observe the feeding currents of living brachiopods, constructed artificial lophophores of lead piping with fine perforations corresponding to the position of attachment of the filaments. Through these he forced water, while the artificial lophophores were immersed in a bowl of water. He assumed, wrongly, that the result would be similar to the action produced by cilia vibrating in water. His remarks on the working of an artificial lophophore resembling that of *Megathyris* (= *Argiope*) were transcribed by Morgan (1883) without making it clear that the observations were not his own and were not made on the living animal. Apart from Hérouard's work on artificial lophophores, the only reference to feeding in a member of the Megathyridae is that of Shipley (1883) who merely mentioned that in *Argyrotheca* the arrangement of the cilia is adapted to bring particles into the ciliated groove and thence to the mouth. Thus an examination of the method of feeding of the Megathyridae was considered desirable, and was made possible in the first instance through the kindness of M. Paul Bourgis, then, in 1955, on the staff of the Laboratoire Arago, Banyuls-sur-Mer. He sent two small consignments of living *Argyrotheca cordata* (Risso), *A. cuneata* (Risso) and *Megathyris detruncata* (Gmelin), received on the 28 October and 24 December 1955. They were taken on 'fonds coralligènes (construits par des Lithothamnides)', the first being dredged off Cap d'Aseille at a depth of 30–40 m, and the second from the Baie de Banyuls at a depth of 20–40 m. The successful method of sending these small brachiopods may be of interest. Each was rolled in damp filter-paper, and about a dozen packed in a little bag of thick polythene, which was then sealed and placed in a small (4 × 5 in.) flat case of a special kind of papier mâché. The case was enclosed in a tough envelope and sent by air mail. All the brachiopods arrived in good condition, although those received in December had been out of water for five days.

Further *Megathyris* were dredged by R. V. 'Sarsia' in May 1958 somewhat

to the south-east of La Chapelle Bank (47° 25′ N., 6° 30′ W.) at a depth of 320–490 fathoms,[1] so that the exact depth is unknown, except that it was at least 320 fathoms. They were attached to the coral *Lophelia prolifera* (L.). These deep water *Megathyris* were of the transverse type. They did not attain the maximum size of those from Banyuls, the largest being 3·2 mm long and 4·6 mm wide, but they appear to be the same species, the only recent one of the genus. From these the growth stages have been worked out.

The Megathyridae withstand laboratory conditions well. Two *Megathyris* received from Banyuls in December 1955 lived until some time in 1958, when they disappeared after the entry of a crab from an adjoining tank. Specimens collected by R.V. 'Sarsia' in May 1958 lived in the tanks to April 1960, but there is evidently not sufficient food for them in the circulating water, for one opened in March 1960 was in a starved condition with very short filaments. Most of the few *Argyrotheca* were used within a few weeks of their arrival. One *A. cordata*, however, lived for over 6 months, but was in a starved condition when opened; the filaments were short and had dark orange coloured tips.

All figures, except Fig. 8, have been drawn with the aid of a camera lucida.

THE ADULT LOPHOPHORE

In *Argyrotheca* the invagination of the schizolophous lophophore (Figs. 1, 2) is occupied by a triangular septum, with its apex just in front of the mouth. In the young the septum has the shape of an isosceles triangle; in the adult it rises gradually from the anterior margin of the valve to its apex, then drops steeply to the valve floor, with a slight concavity facing posteriorly. At a length and width of 3·6 mm—the largest seen—the septum of *A. cordata* was not connected by a ridge with the cardinalia, but was followed posteriorly by a slight groove, with a low rounded ridge on each side. It is apparently in larger specimens than those seen that it is continued as a ridge to the cardinalia, as described and figured by Davidson (1887). The crest of the septum is toothed in *A. cordata*, smooth in *A. cuneata*.

The lophophore is supported by descending branches of the loop, which in *A. cordata* was said by Davidson (1887, p. 132) to be 'two-lobed, attached to the base of the hinge-plate and again to the anterior extremity of the submarginal septum, and more or less confluent with the valve'. His largest specimen was 2½ lines long and 2 lines wide, that is about 5·3 by 4·2 mm. Schulgin (1885) figured, under the name *Argiope kowalevskii*, incomplete descending branches in an individual of which the size was not given. Shipley (1883) figured and described them as incomplete at a shell length and width of 3 mm. He stated 'although these plates do not form a continuous support in front, there are traces of them in the anterior border, in the form of small

[1] Given previously (Atkins, 1959*a*) as 400–405 fathoms and since corrected.

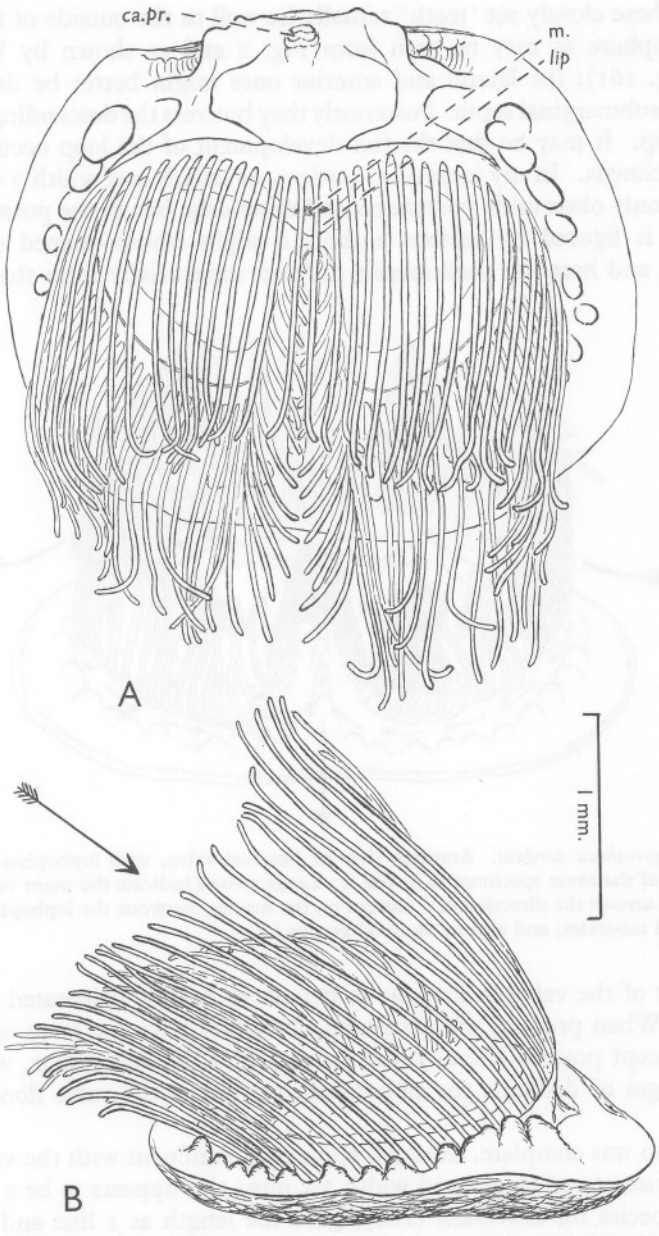

Fig. 1. *Argyrotheca cordata* of shell-length 3·0 mm and width 2·9 mm. Brachial valve with adult schizolophous lophophore, drawn living after narcotizing. A, ventral; and B, lateral view. *ca.pr.*, cardinal process; *lip*, lip of the food groove; *m.*, mouth. The arrow shows the direction of the inhalant current.

teeth'. These closely set 'teeth' actually lie well to the outside of the base of the lophophore as may be seen from Fig. 2 and as shown by Woodward (1880, fig. 161); the lateral and anterior ones might better be described as incipient submarginal septa. Posteriorly they buttress the descending branches of the loop. It may be that the full development of the loop occurs only in large specimens. In my largest *A. cordata*, of length and width 3·6 mm, the loop was only observable posteriorly and anteriorly, but in the position where the loop is figured by various authors a slight ribbon-shaped depression occurred, and here the shell mosaic differed superficially from that over the

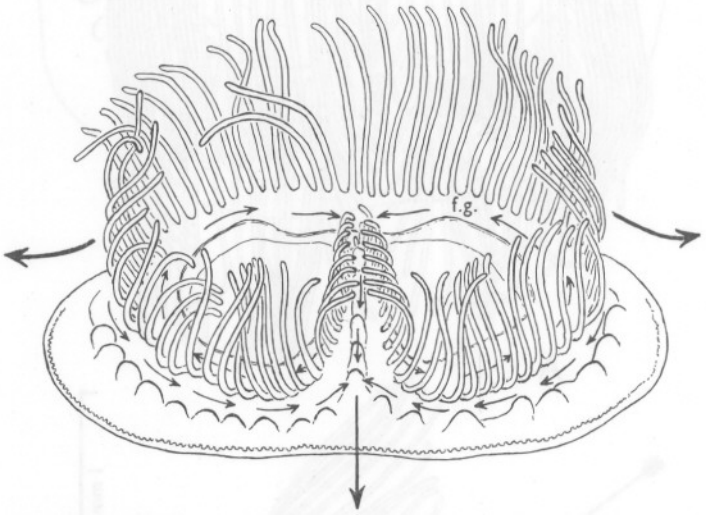

Fig. 2. *Argyrotheca cordata*. Anterior view of brachial valve, with lophophore somewhat contracted, of the same specimen as in Fig. 1. Large arrows indicate the main exhalant currents; small arrows the direction of a current on the mantle, between the lophophore and the submarginal tubercles, and also in the food groove (*f.g.*).

remainder of the valve in that the leaflets were radially orientated and more elongate. When present, the descending branches have the form of ribbons, which, except postero-laterally, are parallel with the valve floor, whereas in young stages of dallinids the ribbons are vertical to the valve floor (Atkins, 1959*b*).

The loop was complete, although apparently confluent with the valve floor, in an *A. cuneata* of length and width 3·3 mm: this appears to be a good size for this species for Davidson (1887) gave the length as 1 line and width as 2 lines. Schulgin's (1885) measurements cannot be relied on as he confused the various dimensions of the brachiopod shell. It is to be noted that Blochmann (1910) described an incomplete loop in *A. australis* of length and width 3 mm.

Postero-laterally the descending branches of the loop support the lophophore as it passes from body to mantle. The filaments lining the sides of the median invagination are carried just below the anterior face of the septum, and as this runs at an angle to the valve floor, so does the line of filaments; the latest formed filaments arise near the apex of the septum, almost on a level with the mouth. By this arrangement the lophophore slopes both from the crest of the septum to the lateral mantle margins and from a high position posteriorly to the anterior mantle margin as shown by Shipley (1883, figs. 2, 3) and Schulgin (1885, figs. 15–18).

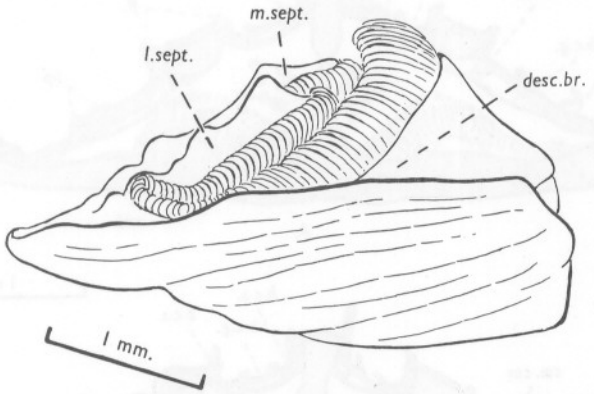

Fig. 3. *Megathyris detruncata* of shell length 4·8 mm and width 5·5 mm. Side view of brachial valve with ptycholophous lophophore strongly contracted, to show the postero-anterior slope of the lophophore. *desc.br.*, descending branch of the loop; *l.sept.*, lateral septum (right); *m. sept.*, median septum.

In *Megathyris detruncata* the adult lophophore is ptycholophous, there being a lateral invagination occupied by a septum on each side of the median septum. The lateral septa usually are not as high or as long as the median one, which has its apex just in front of the mouth. Occasionally five septa are present (Fischer & Oehlert, 1891, p. 104), but the additional two may be small and rudimentary, no doubt resembling the small submarginal septa of *Argyrotheca cordata*. The septa have sloping anterior faces, whilst posteriorly they drop steeply to the valve floor, with a slight backward-facing concavity; this was shown by Morgan (1883, figs. 6, 7). The crests of the septa are toothed. Morgan (1918) suggested that the schizolophe of *Argyrotheca* is derived from the ptycholophe of *Megathyris* by atrophy of the lateral septa. Thomson (1927, pp. 211–12) discussed this and concluded that the reverse was true, *Megathyris* passing through a schizolophous stage in its development. At the time he was writing the growth stages of the lophophore of *Megathyris* were unknown; the present work on them supports his conclusions. In the *Megathyris* examined, the descending branches of the loop could be clearly traced in some adults.

The filaments forming the sides of the invaginations arise just below the crests of the septa, and the brachial membrane, or floor of the lophophore, slopes to the frontal and lateral margins of the valves (figs. 3, 4).

On each side of the lophophore a small brachial canal, arising from a peri-oesophageal space, runs at the bases of the filaments and gives off a branch to each. In *Megathyris* a large brachial canal underlies the brachial membrane (Fig. 4, *b.c.g.*): this canal is most probably present in *Argyrotheca*, but in the

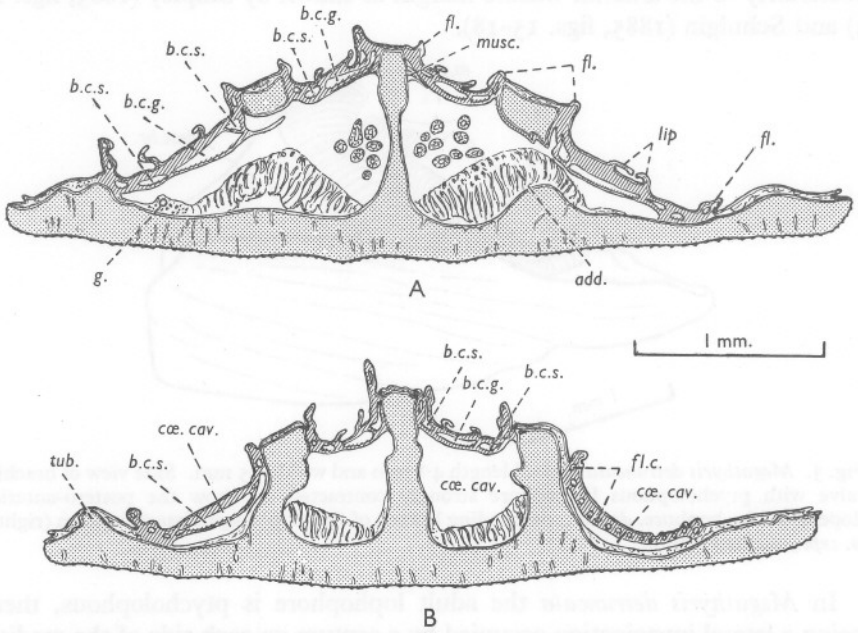

Fig. 4. *Megathyris detruncata*. Transverse sections of a specimen of shell length 3·8 mm and width 5·2 mm. A, through the posterior region of the lophophore, the backwardly projecting crests only of the lateral septa being cut; B, through the anterior region of the lophophore, near to the anterior ends of the lateral lobes. *add.*, adductor muscles; *b.c.g.*, great and *b.c.s.*, small brachial canals; *coe.cav.*, coelomic cavity; *fl.*, filament and filament base; *fl.c.*, filamentar canals; *g.*, gonad; *lip* of the food groove; *musc.*, muscle fibres; *tub.*, tubercle.

small specimen sectioned, of length 2·6 mm and width 2·2 mm, it was most difficult to trace owing to collapse of its wall. In *Argyrotheca* the coelomic cavity, divided into two by mesentery and septum, underlies the lophophore to its anterior edge. In *Megathyris* the cavity is divided anteriorly into four by the three septa and these branches extend to the anterior extremities of the lobes of the lophophore (Fig. 4). Muscle fibres attached near the crests of the septa run under the great brachial canals.

The section illustrated in Fig. 4B passes on the left anterior to the great brachial canal and on the right anterior to both small and great canals.

Shipley (1883, p. 507) described nerves passing to the lophophore; unfortunately the fixation of the specimens I sectioned was not good and the position and distribution of the nerves could not be determined.

In both *Argyrotheca* and *Megathyris* the filaments are all in a single series, an arrangement I have so far found only in these genera, but it probably occurs in *Lacazella* (= *Thecidea*) *mediterranea* (Risso), judging from the figure in Davidson's paper of 1852. It was noted by Dall (1871, p. 22) in *Argyrotheca lutea* (Dall) and both Shipley (1883) and Schulgin (1885) figured a single row in *Argyrotheca*: Thomson (1927) seems to have overlooked this fact. All the filaments have rounded or ridged frontal surfaces, resembling

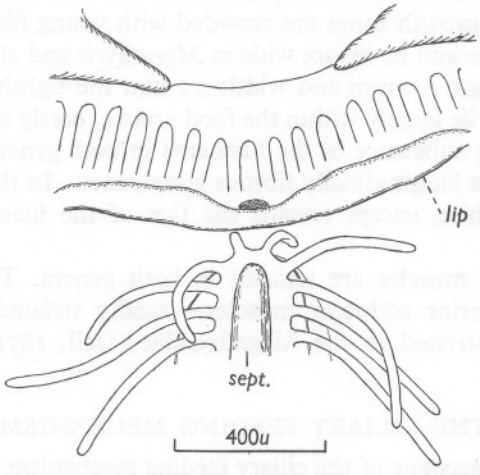

Fig. 5. *Argyrotheca cordata* of shell length and width 2·7 mm. To show the uninterrupted base of the lophophore and the uncrowded growth zone with two filament buds only. The filaments on the side of the septum are turned outward, as when the lophophore is partly contracted. This figure also shows the proximity of the mouth to the excurrent channel formed when the filaments bordering the septum are turned toward each other in the feeding animal. The lip of the food groove is turned outward. *lip*, edge of lip; *sept.*, septum.

the inner filaments of other brachiopods (Atkins, 1958, fig. 13A). This arrangement and type of filament is possibly primitive, for in the brachiopods examined, including the inarticulate *Crania*, a certain number of the first formed filaments, which come to lie behind the mouth in the adult, are in a single series and are of the inner series type, although all other filaments are in a double alternating series of two types. The inarticulates *Lingula* and *Glottidia* differ in having all filaments in a double series.

Thomson (1927, p. 204) considered that the Megathyrinae Dall 1870 (= Megathyridae Allan 1940) were not ancestral to the Dallininae or Magellaniinae Beecher 1893 (= Terebratellinae Davidson 1886), but that *Megathyris* represents the highest development of a stock which branched off

at an early stage of terebratellid development and was one of the two main divisions of the original terebratellid stock. The arrangement of the filaments in a single series supports Thomson's view.

In the Megathyridae the posterior and lateral filaments are long (Figs. 1B and 7); they gradually decrease in length anteriorly and bordering the septa, the shortest occurring at the posterior edge of the median septum where new filaments arise. The base of the lophophore is continuous in the adult, as in the trocholophous stage, and filament buds are usually no more than two, of unequal length (Fig. 5). This is in contrast with the condition in those articulates with plectolophes or with spirolophes in the adult and in which the base of the lophophore becomes interrupted in the mid-line in the schizolophous stage and the two growth zones are crowded with young filaments and buds.

The food groove and its lip are wide in *Megathyris* and *Argyrotheca*. In an *A. cordata* of length 2·0 mm and width 2·2 mm the tightly coiled filaments were once seen to lie largely within the food groove, partly covered by the lip.

The supporting substance of the filaments in both genera is thick, especially basally, with a longitudinally fibrous appearance. In the living animal it shows shining white, except toward the tips of the filaments where it is attenuated.

The filamentar muscles are striated in both genera. This is of interest because the posterior adductor muscles—usually striated in articulates—appear to be unstriated in the Megathyridae (Dall, 1871; Shipley, 1883; Atkins, 1958)

THE CILIARY FEEDING MECHANISM

The following account of the ciliary feeding mechanism of the Megathyridae is based on an investigation of *Argyrotheca cordata*, *A. cuneata*, and *Megathyris detruncata*: the water currents were observed chiefly on *Megathyris* and proved exceptionally interesting because of the surprising reversal of the water currents, not so far seen in a brachiopod outside this family.

The Megathyridae were amongst the most difficult brachiopods studied; not only were they particularly sensitive to the slightest vibration, which caused them to close and remain closed for varying, but long periods, but after separation of the valves the filaments relaxed only slightly after 24 h, and attempts to relax them with 1% stovaine and with $7\frac{1}{2}$% magnesium chloride proved only partially successful: the latter was the more effective of the two.

Argyrotheca and *Megathyris* are attached by a short pedicle in a position almost at right angles to the substratum, and their beaks therefore suffer attrition. The valves gape to an angle of 40–45°, but this was only seen to occur after the animals had been in the laboratory tanks for some weeks. One *Argyrotheca cordata* extended the filaments well beyond the shell edge, as in Schulgin's (1885) figure 5. Observations on feeding were mostly made on *Megathyris*

and most successfully on animals which had been in the tanks for 4 months, and when the temperature of the water was rising in April.

The position of the filaments during feeding was observed in a large *Megathyris*, about 6 mm long and 8 mm wide, which had been stood almost upright and was gaping widely so that the posterior ends of the three septa and the mouth could be seen. The filaments behind the mouth were erect except distally where they curved forward and touched on the anterior edge of the pedicle valve, extending beyond it slightly. The lateral filaments stood nearly erect, but slanting slightly forward, as did those at the anterior ends of the lobes—and curved slightly outward at their tips. The filaments on each side of a septum generally curved toward each other at their tips, but otherwise were nearly erect. Flocculent matter from the peridinian culture was seen to travel up the posterior filaments to their tips, where it remained. The tiny square-sided lappets edging the mantle lobes project at right angles to the valves. They probably interdigitate when the valves are closed, or nearly closed.

The ciliation of the lophophore

The single series of filaments have ciliated cells in three tracts, frontal and paired lateral.

The frontal cilia are long, about 20 μ, and, as in other brachiopods examined (Atkins, 1956, 1958, 1959*a*, *b*, *c*), are capable of reversal, beating either toward the base or toward the tip according to the quantity and size of particles impinging on the frontal surfaces of the filaments. In *Phoronis* also similar reversal of the frontal currents has been observed (Atkins, unpublished).

The lateral cilia, about 30 μ long, beat across the length of the filaments and have a well-marked dexioplectic metachronal wave. The lateral cilia, as well as the frontal, are able to reverse their beat (seen in *Megathyris*).

Abfrontal cilia could not be distinguished living and no abfrontal current could be detected: the abfrontal surface of the filament is small.

Shipley (1883, pl. 39, fig. 13) figured the cilia on the lateral and frontal surfaces of the filaments as all of the same length, while Schulgin (1885, pl. 9, fig. 26) showed the frontal cilia longer than the lateral, whereas the reverse occurs.

The brachial membrane is ciliated as shown by the movement of particles adhering to the tips of cilia: such currents as were observed passed toward and over the lip and into the food groove present at the bases of the filaments. The groove is interrupted near the posterior edge of the median septum, that is at the growth zone, and particles entering the groove on each side of it pass in opposite directions to the mouth. It is evident that on one side of a lobe the current in the groove is anteriorly directed and on the opposite side posteriorly directed (Fig. 8). The mouth, a large transverse slit, opens, as is usual, within the food groove in the mid-line posteriorly.

The ciliation of the mantle

In both species of *Argyrotheca* the mantle is ciliated: this is evident from the occasional movement of particles adhering to cilia, but although the animals were in good condition clear currents could rarely be demonstrated. On the posterior region of the pedicle valve a general anterior movement of particles was observed, as also along the crest of the median septum. The lophophore occupies much of the brachial valve: over the posterior region of the valve currents passed anteriorly and laterally. In *A. cordata* at the bases of the filaments, a broad current, between them and the submarginal tubercles, passed anteriorly and medianly and swept upward on to the median septum, joining the anteriorly directed current along its ventral edge (Fig. 2). This latter current is on the floor of the excurrent channel. No currents could be demonstrated between the submarginal tubercles and the mantle edge, although it seems probable that such exist. Submarginal tubercles are absent in *A. cuneata*.

In *Megathyris*, as in *Argyrotheca*, mantle currents were most difficult to demonstrate, although the movement of particles adhering to the tips of cilia, is evidence that the mantle is ciliated. In one specimen, on the third day after separation of the valves, feeble currents on the pedicle valve passed anteriorly to the free edge of the mantle. As in *Argyrotheca* the great extent of brachial valve occupied by the lophophore leaves only a small area of mantle exposed, and currents were not observed, except for an anteriorly directed current along the crest of the median septum.

The water currents (Figs. 1, 2, 5–8)

In *Megathyris* with valves gaping naturally, unnarcotized, the broad inhalant current is median and as it closely approaches the lophophore is drawn into the four lobes (two in *Argyrotheca*); the main part of the current, however, appears to pass into the posterior region of the lophophore where the posterior and lateral filaments are particularly long and so play a major part in creating the current. The filaments bordering the three septa generally curve toward each other over the septa—this is especially apparent over the median septum—their tips approaching or interdigitating, thus forming three excurrent channels. The exhalant current escapes between the filaments, and is strongest at the postero-lateral angles of the shell where it is fed by currents passing between the long posterior filaments and which can only escape here. Three antero-dorsal exhalant currents pass from the three excurrent channels floored by the septa and bordered by filaments. In both genera the median dorsal excurrent channel has its origin in front of the mouth where the filaments are short (Fig. 5). It is possible that this channel may carry away material voided from the mouth, although this has not been seen to occur. On one occasion in *Argyrotheca* the lip in front of the mouth was

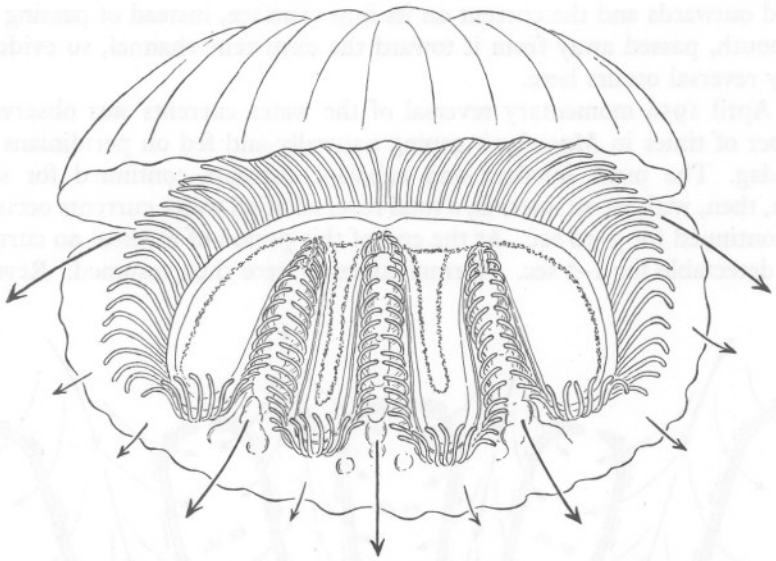

Fig. 6. *Megathyris detruncata*, View through the anterior gape of a feeding animal (unnarcotized), somewhat diagrammatic; filaments foreshortened. The exhalant currents only can be shown, for the inhalant currents enter the lophophore from the direction of the observer. Tracts of mucous glands on the brachial membrane are indicated.

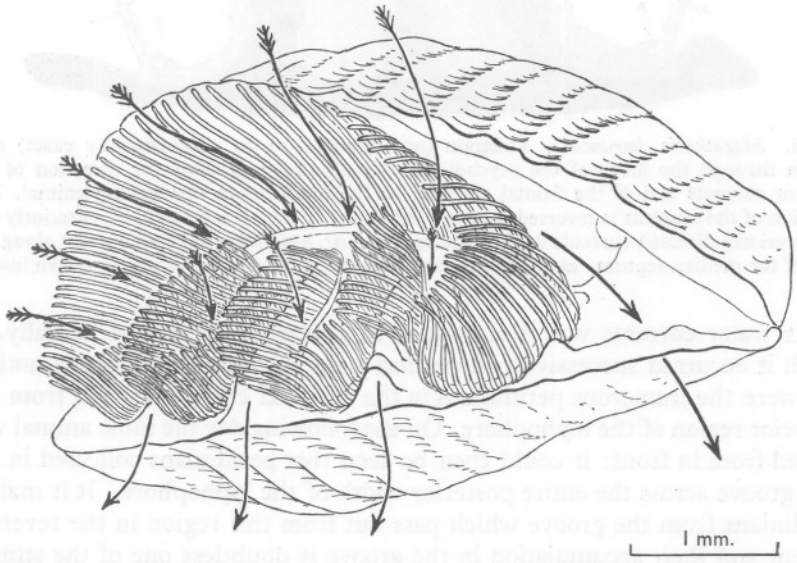

Fig. 7. *Megathyris detruncata*. Obliquely lateral view of a feeding animal to show the usual inhalant (feathered arrows) and exhalant (plain arrows) currents. Currents are reversed when strong cleansing action is needed.

turned outwards and the current on its inner surface, instead of passing into the mouth, passed away from it toward the excurrent channel, so evidently ciliary reversal occurs here.

In April 1956 momentary reversal of the water currents was observed a number of times in *Megathyris* gaping naturally and fed on peridinians and Aquadag. The usual inhalant and exhalant currents continued for some 5 min, then, without an interval, a total reversal of all water currents occurred and continued for 3–10 sec. At the end of this period of reversal no currents were detectable for 1–2 sec. Normal currents were then resumed. Reversal

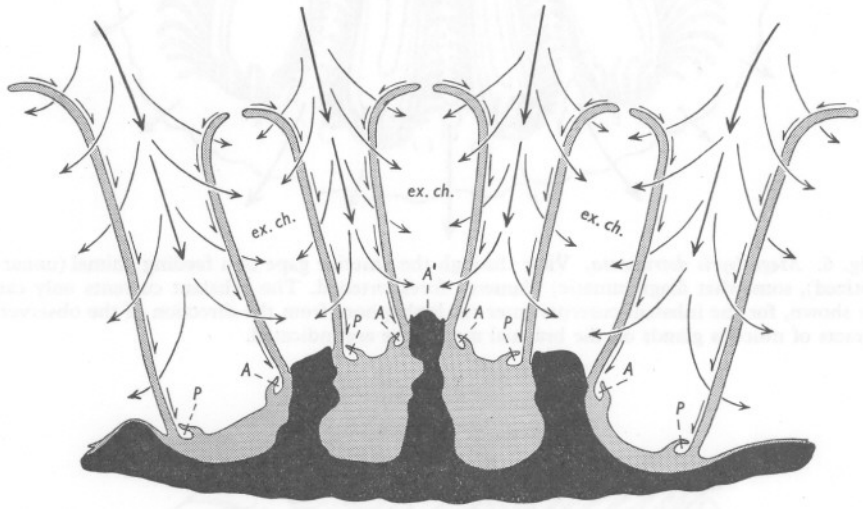

Fig. 8. *Megathyris detruncata*. Diagram (not intended to be proportionally exact) of a section through the lobes of the ptycholophous lophophore to show the direction of the inhalant currents and of the frontal currents on the filaments in the feeding animal. The direction of the currents is reversed when strong cleansing action is needed. A, anteriorly and P, posteriorly directed currents in the food grooves. A^1, anteriorly directed current along the crest of the median septum. *ex.ch.*, excurrent channel. The shell with the septa shown black.

of the water currents was first noticed in a *Megathyris* viewed laterally, in which it occurred successively more than a dozen times. Particularly noticeable were the numerous peridinians in the reversed current leaving from the posterior region of the lophophore. On the following day the same animal was viewed from in front: it could then be seen that peridinians collected in the food groove across the entire posterior width of the lophophore. It is mainly peridinians from the groove which pass out from this region in the reversed current and their accumulation in the groove is doubtless one of the stimuli which sets off the reversal. The peridinians passing out were separate and not bound together by mucus.

The reversed water current is almost certainly due to reversal of the beat of

the lateral cilia, although this could not be seen owing to the opacity of the valves and the low magnification which had to be used, nor could the metachronal wave be seen which might have given some indication of change of direction of beat. The valves were gaping widely, as in Figs. 6 and 7, and no movement of them or of the lips of the food groove could be detected, in fact no muscular movement whatever could be detected which might account for the reversal. On the third day the same animal, still in front view with valves gaping widely, but now with the filaments curved inwards and no water current detectable, suddenly showed slight reversed current.

Another *Megathyris* with valves gaping, but with filaments curved inwards at about half their length, showed no water currents or frontal currents on the filaments. A little Aquadag in sea water was dropped on to the lophophore and fell mostly into the two inner lobes. With the filaments still curved inwards, the reversed current began, and this apparently before any material had reached the mouth region. In this instance also a careful watch revealed no muscular movements.

On all occasions the reversed current was a steady continuous stream for the short while it lasted, and, judging from the movement of particles, quite as strong as the usual current. It would not appear possible that the frontal cilia beating toward the tips of the filaments could produce so strong a current, although *Megathyris* is a small animal: moreover, reversal of the water current seems to be set off by the collection of particles in the food grooves, whereas reversal of the frontal currents is caused by material impinging on the frontal surfaces of the filaments. Evidently the direction of the water current is reversed when strong cleansing action is called for.

Many Aquadag particles and peridinians passed out between the filaments all around the lophophore, yet a surprising number of the latter accumulated in the food groove across the posterior region of the lophophore.

Slight transverse movement occurred of particles on to the crests of the lateral septa, whence they were removed by the water current. The median septum had an anteriorly directed current along its crest, but the lateral septa appeared to be without such a current.

The frontal currents on the filaments

The frontal cilia of the filaments as mentioned previously (p. 467) are able to reverse their beat. Small particles impinging on the frontal surfaces are carried basally into the food grooves and thence to the mouth. The reversed currents toward the tips of the filaments are rejection currents and are seen when large or too many small particles are supplied. From the tips of the filaments rejected material drops off into the exhalant current. The rejection currents on the frontal surfaces of the filaments can occur without reversal of the inhalant and exhalant currents.

THE BEHAVIOUR OF *ARGYROTHECA CORDATA* DURING THE ESCAPE OF LARVAE

It is known from the work of Senn (1934) that *Argyrotheca cordata* and *A. cuneata* are hermaphrodite. They have paired brood pouches in which the ova develop and from which the free-swimming larvae escape (Kovalevsky, 1874, 1883; Shipley, 1883; Schulgin, 1885; Plenk, 1913). Larvae of both species were seen during October to January while the adults lived in the tanks.

Two *A. cordata* were watched under a dissecting microscope whilst liberating larvae. They opened widely, kept the filaments tightly folded inwards and at intervals snapped the valves together. The larger specimen (shell length 2·9 mm and width 3·0 mm) was watched for ½ h, during which time eight larvae escaped at varying intervals. The anterior commissure of the shell was facing upwards and the posteriorly situated brood pouches were visible through the gape. Part of the left lobe of the lophophore was wanting: the filaments of the right lobe were kept folded inwards, the posterior filaments were at times extended. Five of the larvae left the parent rapidly, swimming from the brood pouches and keeping near the pedicle valve; they swam toward the light and the surface of the water. Of these, four came from the left and one from the right pouch. When the valves first gaped a larva was seen caught in the filaments of the right side; it failed to escape during the ½ h the animal was watched. The first two larvae from the left pouch swam out in quick succession; the third after a long interval and the fourth near the end of the period of watching. They all left the shell ventrally and laterally. A fifth left this brood pouch, but failed to escape before the valves closed indefinitely. The first larvae to leave the right brood pouch swam out and away rapidly. The second nosed about, finally passed to the left side, escaping near the hinge and dropping to the bottom of the dish. The third behaved in the same manner, but was three times caught by the edges of the valve closing on it, the anterior lobe being outside. Finally, snapping of the valves shot it outside. On examination it appeared that this treatment had done it little harm. A fourth on leaving the brood pouch nosed about and was eventually shot out of the shell by closing of the valves. Judging by their behaviour these larvae were either unhealthy or had escaped prematurely. It is probable that larvae normally leave the parent rapidly, and during their escape the filaments are kept folded inwards so as not to interfere with their movements.

Larvae escaping naturally from these and other *A. cordata* in November 1955 lived some 10 days, but failed to attach themselves to the glass of the dish. Shipley (1883, pl. 40, figs. 28, 29) showed clearly the appearance of the ring of long and powerful swimming cilia when at rest and distinguished between them and the shorter, less active, cilia clothing the anterior lobe. He made certain observations on the behaviour of the free-swimming larvae.

THE IMMATURE SHELL OF *MEGATHYRIS DETRUNCATA*

Certain immature shells of *Megathyris detruncata* are figured (Figs. 9B, C, D and 10) to show the change in shape with age from elongate to transverse. The three smallest found were from Banyuls, attached near to or on adults. It cannot be altogether certain that these minute brachiopods, the largest 0·69 mm long, are *Megathyris*, for *Argyrotheca cordata* and *A. cuneata* were received at the same time, and all three megathyrids were probably dredged together. At this size it is doubtful if the three species could be distinguished with certainty. However, it is clear from the growth lines on the shell of the smallest *Megathyris*, length and width 0·97 mm, dredged by R.V. 'Sarsia' that when younger the shell was longer than wide. At a length of about 1 mm, width becomes greater than length and it is near this size that the first two rounded plicae are evident, with, between them a gentle indentation of the anterior shell edge (Fig. 10A, B); this becomes deeper with age (Fig. 10F). *Terebratalia transversa* (Sowerby), markedly transverse in the adult, is also elongate in the early stages (Atkins, 1959*c*), but this change in shape is of particular interest in the Megathyridae because of discussions by Jeffreys (1880), Davidson (1887), Fischer & Oehlert (1891) and Dall (1921) as to whether *Gwynia capsula* (Jeffreys) is an adult or an immature form of another species of megathyrid, such as *Argyrotheca cistellula* (Searles Wood) with which it is found. Thomson's (1927, p. 208) statement that it 'cannot be the young of that species from its more elongate form' is thus questionable. Jeffreys (1880), Davidson (1887) and Fischer & Oehlert (1891) were unable to find septum or loop in *Gwynia capsula* about 1·75 mm long and 1·3 mm wide. This is perhaps not altogether surprising as Jeffreys for one soaked the minute shells for several days in 'dilute potash water'. Such treatment is apt to cause disintegration of the shell in adult brachiopods before the flesh is sufficiently dissolved to brush or blow out of the shell. This is no doubt because organic matter enters into the shell substance. Dall (1921, p. 325), in the larger specimens he examined, found a distinct loop with its lower edge cemented to the valve, and thought the species sufficiently distinct though very near to *Argyrotheca cistellula*.

As *Megathyris* passes through a schizolophous stage at a shell length of 1–2 mm, where it is found together with *Argyrotheca* it may in some instances be somewhat difficult to distinguish between the two genera at that size, although *Megathyris* is likely to have greater width.

THE GROWTH STAGES OF THE LOPHOPHORE AND LOOP

Two minute brachiopods, 0·34 and 0·72 mm long were found attached to an adult *Argyrotheca cordata* and were possibly or probably the young of that species. In both the lophophore was completely circular. The smaller had

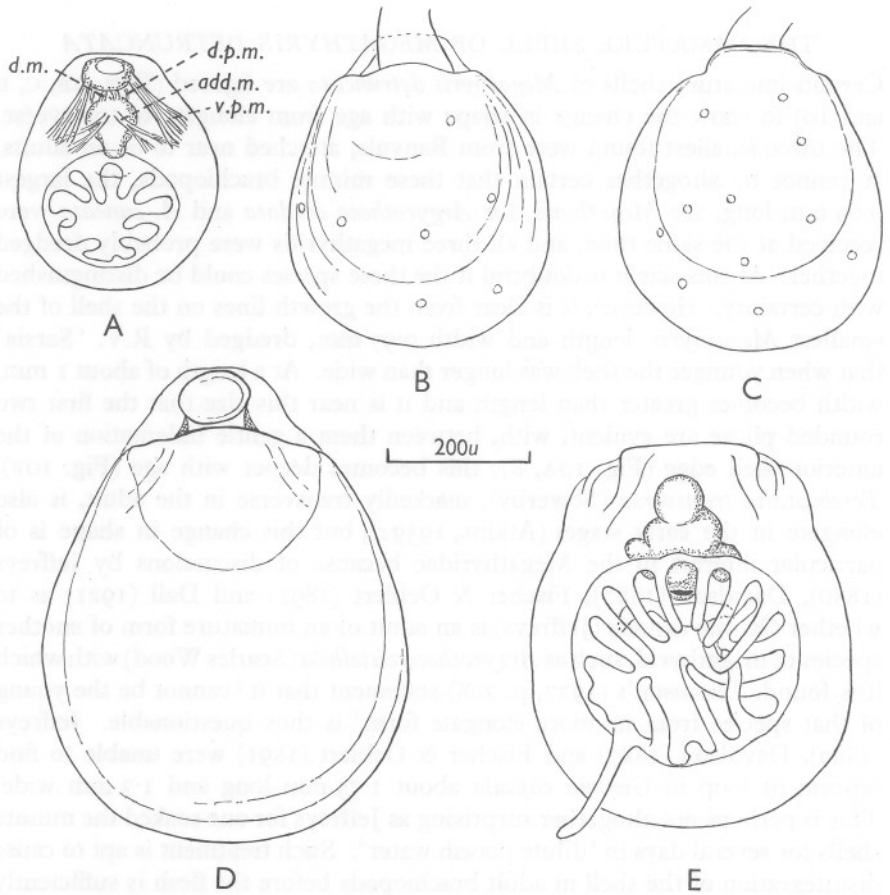

Fig. 9. A, *Argyrotheca cordata*: ventral view of a specimen of shell length 0·34 mm and width 0·29 mm, which was attached to an adult of that species; pedicle retracted. B–E, *Megathyris detruncata* from Banyuls-sur-Mer, two of which (B–D) were attached near to, and one (E) on an adult of that species. B, dorsal and C, ventral view of specimen of shell length 0·44 mm and width 0·38 mm; D, dorsal view of specimen of shell length 0·69 mm and width 0·52 mm; E, brachial valve with trocholophe of a specimen of shell length 0·62 and 0·46 mm. *add.m.*, adductor muscle; *d.m.*, diductor muscle; *d.p.m.*, dorsal and *v.p.m.*, ventral pedicle muscles.

four pairs of filaments and a bud; a small pre-oral lobe was present (Fig. 9A). Intestine and digestive diverticulata were as yet undifferentiated. This is a somewhat younger stage than that illustrated by Kovalevsky (1874) and reproduced by Oehlert & Deniker (1883) as their figure 11, for it has fewer filaments. Kovalevsky showed 10 filaments, but probably at least 12 were present, those behind the mouth being omitted, no doubt because they were obscured by the oesophagus and digestive diverticula. (In this figure

the adductor muscles were apparently labelled diductors by Kovalevsky, although they are correctly identified in a figure of an older stage—Oehlert & Deniker 1883, fig. 13.) The larger specimen had nine pairs of filaments and a bud; the lobe in front of the mouth had extended laterally to about the base of the second or third filament on each side. Intestine and digestive diverticula were differentiated. This is about the same stage as that shown in Kovalevsky's figure reproduced by Oehlert & Deniker (1883) as their figure 13. In this figure only 14 filaments are shown, those behind the mouth—probably numbering four—again being omitted. I found no intermediate stages between these tiny individuals and the adult.

The growth stages of the lophophore of *Megathyris detruncata* have been worked out chiefly from material dredged by R.V. 'Sarsia', the youngest, however, were from Banyuls, attached near or on adults. The two attached near an adult *Megathyris* were 0·44 mm long and 0·38 mm wide (Fig. 9B, C) and 0·62 mm long and 0·46 mm wide. Although the smaller remained attached to the substratum, the tissue had deteriorated and the lophophore could not be distinguished: a few mantle pits were present. The lophophore of the larger was trocholophous, of the broad based terebratellacean type set low on the dorsal mantle, with eight pairs of filaments, the last on the right being a bud: two filaments on the left were abnormal (Fig. 9E). The lip of the food groove extended only a short distance on each side of the mouth. A third specimen 0·69 mm long and 0·52 mm wide (Fig. 9D) was attached to an adult *Megathyris*. It had a trocholophous lophophore with nine pairs of filaments: the lip of the food groove extended less than half way around the lophophore.

In the contracted condition the tips of the filaments were pointed inwards. When narcotized and expanded they extended upwards, outwards and forwards. Particles passed down the filaments and toward the mouth following the position of the food groove, although it was as yet unprovided with a complete lip. Reversal of the frontal cilia was not obtained on these tiny brachiopods because of the difficulty of dealing with them. The usual inhalant current would set into the circle of filaments and out between them, as described for the trocholophous stage of the lophophore in *Terebratulina retusa* by Atkins (1956).

The young *Megathyris* now to be described were dredged by R.V. 'Sarsia'. That shown in Fig. 10A–E had a length and width of 0·97 mm with the frontal edge of the shell slightly indented. The lophophore was damaged anteriorly, it was probably still trocholophous. Descending branches had grown from the crura (Fig. 10D). The dorsal septum was represented by a slight ridge in the mid-line. In the ventral valve a septum was present: the pedicle collar was fairly deep and had longitudinal pits (Fig. 10E).

A transverse individual of shell length 1·0 and 1·2 mm had a well-developed median septum and the lophophore, with about 14 pairs of filaments, slightly invaginated in the mid-anterior line. Descending branches from the crura

had increased in length; their anterior ends could not be distinguished on the septum, but might have been hidden by filaments.

In a slightly larger, but less transverse individual, 1·2 mm long and 1·3 mm wide, the anterior invagination of the lophophore had deepened and

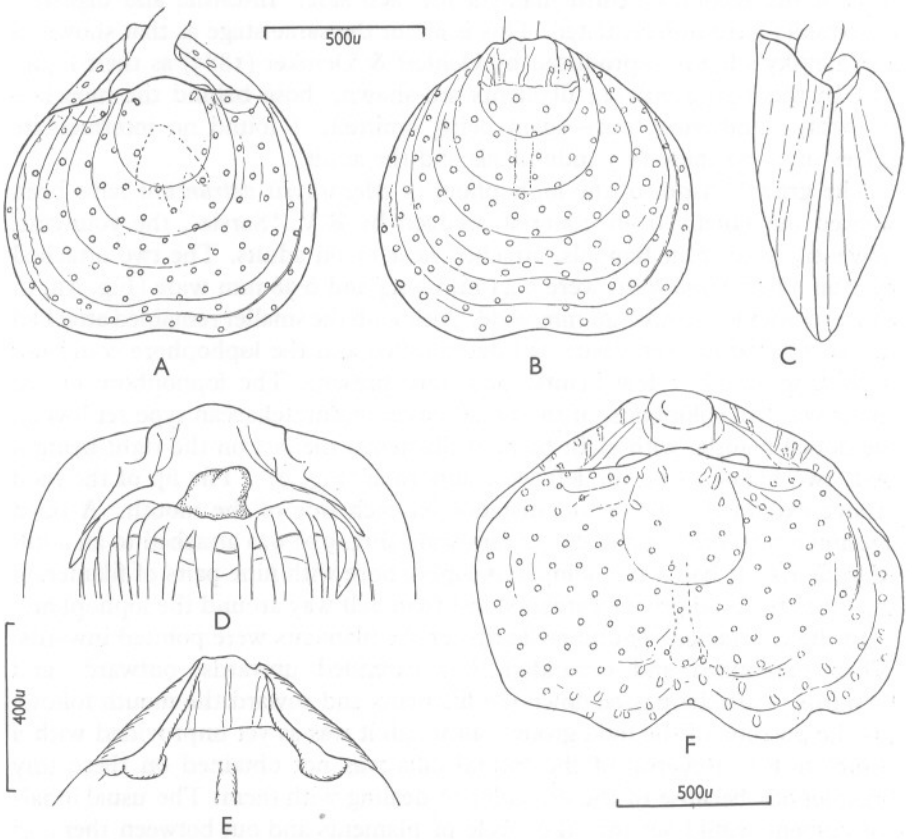

Fig. 10. *Megathyris detruncata* from near La Chapelle Bank, one (A–E) of shell length and width 0·97 mm and the other (F) of shell length 1·1 mm and width 1·4 mm. A, dorsal; B, ventral (ventral septum indicated by a broken line); C, lateral views; D, posterior region of the brachial valve to show the cardinalia and descending branches of the loop; E, umbonal region of pedicle valve to show the pedicle collar and the teeth; F, dorsal view with dorsal septum indicated by broken line.

descending branches had grown from near the ventral surface of the median septum (Fig. 11). The filaments in this individual were somewhat shorter than normal: it was possibly not entirely healthy, as it, and the previous specimen, had lived in the laboratory tanks for 16 months. These three individuals of length 0·97, 1·0 and 1·2 mm all had a gentle indentation of the anterior edge of the shell, due to the development of the first two plicae. Another two,

of shell length 1·1 and 1·4 mm with early schizolophes, had in addition lateral indentations (Fig. 10F). The test of these small specimens was fairly thick.

At a shell length of 1·8 mm and width of 2·65 mm the lophophore was late schizolophous. No lateral septa were as yet present, and marginal tuberculation was absent. At length of 2·2 mm and width of 3·2 mm the lophophore was still in the same stage. Lateral septa were tiny and the lophophore only slightly indented, or rather flattened where these occurred. The margin had

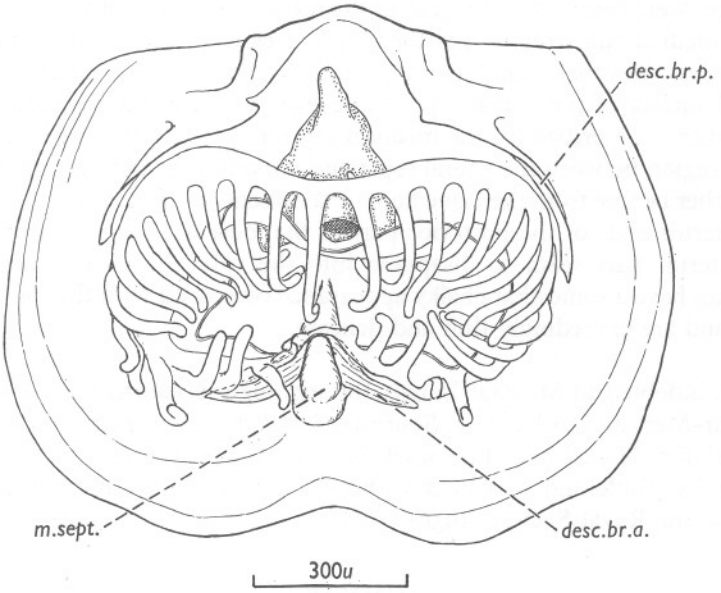

Fig. 11. *Megathyris detruncata* of shell length 1·2 mm and width 1·3 mm. Brachial valve with early schizolophe. The anterior ends of the descending branches (*desc.br.a.*) have grown from the median septum (*m.sept.*,) which alone is present. *desc.br.p.*, posterior end of descending branch of the loop. The filaments are shorter than normal. Drawn living, but not successfully relaxed.

slight tuberculations postero-laterally. At a length of 2·4 mm and width of 2·7 mm the lateral septa were larger and the lophophore was ptycholophous.

Thomson's (1927, p. 214) description of the loop of *Megathyris* was as follows 'loop consisting of two descending branches which are free only near the crura, but descend (dorsally) to join the floor of the valve, rising over the two lateral septa, descending again to the floor of the valve, and attached to the sides of the median septum'. In *Argyrotheca* he described the descending branches as joining the anterior end of the median septum: according to him (p. 212) the loop-development of *Megathyris* had not then been clearly established. A loop which may disappear or be adherent to the valve floor in parts is puzzling, but I think it can be stated that in *Megathyris* the descending branches of the loop grow both from the crura and the median septum,

and the junction of the two parts occurs in the region between the lateral septa and the crura. The anterior ends of the branches appear to arise at the crest of the median septum, in fact to overlie it, and run down its sides, with the anterior edges projecting as flanges all around the anterior face of the septum. This was seen at a shell length of 3·5 mm and width of 4·7 mm. *Megathyris* did not give good sections, owing to the large proportion of shelly matter, however, in the two individuals sectioned, it appeared that the descending branches were fused with the sides of the medium septum. Between the bases of the median and lateral septa the loop is free from the valve floor in some *Megathyris*, in others confluent with it. The loop appears to run over the ventral surface of the lateral septa while these are still tiny, its anterior edge projecting as described for the medium septum, yet may be fused with them. In the region between the lateral septa and the crura the descending branches may either be free from the valve floor or confluent with it, in the latter instance the anterior ends of the posterior part of the loop and the posterior ends of the anterior part seem to disappear into the valve floor. The descending branches have a somewhat chalky appearance compared with that of the valve floor, and are exceedingly thin and delicate.

I am indebted to M. Paul Bougis for sending me megathyrids from Banyuls-sur-Mer, and to Dr A. J. Southward and the Captain and crew of R.V. 'Sarsia' for *Megathyris*. The work was done whilst occupying a London University Table and part of it with assistance from the Browne Research Fund of the Royal Society, 1956–57.

SUMMARY

The structure of the adult lophophores of *Argyrotheca* and *Megathyris* is described. In megathyrids the filaments are in a single series and all of the same type. The ciliary feeding mechanism differs from that previously described by the writer in brachiopods in that in addition to reversal of the frontal cilia, reversal of the inhalant and exhalant currents occurs.

The behaviour of *Argyrotheca cordata* during the escape of larvae from the brood pouches is briefly described.

Certain of the growth stages of the shell and of the lophophore and loop of *Megathyris* are described and figured. *Megathyris* passes through a schizolophous stage resembling the adult lophophore of *Argyrotheca*.

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ON THE BIOLOGY OF *CRANGON ALLMANI* KINAHAN IN NORTHUMBERLAND WATERS

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(Text-figs. 1–15)

Since November 1954, the natant epifauna in depths greater than 20 fm. off the Northumberland coast has been sampled at a number of stations with the object of obtaining information on its constitution and fluctuations. The survey has been limited to those species caught with a net of $\frac{3}{4}$ in. mesh. Seasonal and yearly fluctuations in this fauna must have a considerable effect on the inshore fisheries, for these animals form an important part of the food of marketable fish, yet, this fauna has never been subject to a detailed analysis over a number of years.

Samples have been taken as regularly as weather and other laboratory commitments have allowed. In practice this has been of the order of one sample each month, but at times sampling has been more frequent than this (Table 8). Although sampling is being continued, the material collected so far gives much information on the epifauna as a whole and the biology of the constituent natant Crustacea and Mollusca.

It was soon clear that the best method for dealing with the samples was to analyse the biology of each of the commoner species in turn before reviewing the data as a whole. *Pandalus borealis* was the first species to be so considered (Allen, 1959). The second choice is *Crangon allmani* Kinahan*. *C. allmani* has been chosen for the following reasons: (1) it is one of the more common offshore species of natant decapod in Northumberland waters; (2) in contrast to *Pandalus borealis* (Allen, 1959) it occurs throughout the area below 10 fm.; (3) it forms an important item of food for many marketable fish including the Whiting (Todd, 1907; Jones, 1954); Haddock (Ritchie, 1937; Jones, 1954); Thornback Ray and Long Rough Dab (Todd, 1907) and others; and (4) virtually nothing is known of its biology.

While earlier authors doubt whether *Crangon allmani* is more than a subspecies of *C. vulgaris* (Doflein, 1900; Ortmann, 1891) observations by Wollebaek (1908) on the adult and by Sars (1890) and Lebour (1931) on the larvae show that it is a distinct species. This study gives further emphasis to the differences between the two species and presents an opportunity to correct

* Kinahan (1857) named this shrimp *Crangon allmanni*. This is clearly a *lapsus calami* and the specific name should be spelt *allmani*.

the original descriptions of Kinahan (1857, 1861) and to figure the external anatomy more fully than hitherto.

I wish to thank Mr R. Harrison and the crew of the research vessel 'Alexander Meek' for collecting in all weathers. I am also grateful to Dr H. O. Bull for the use of his hydrographic data and for the helpful discussions during the course of the work, and to Dr R. B. Pike for information on the Clyde populations.

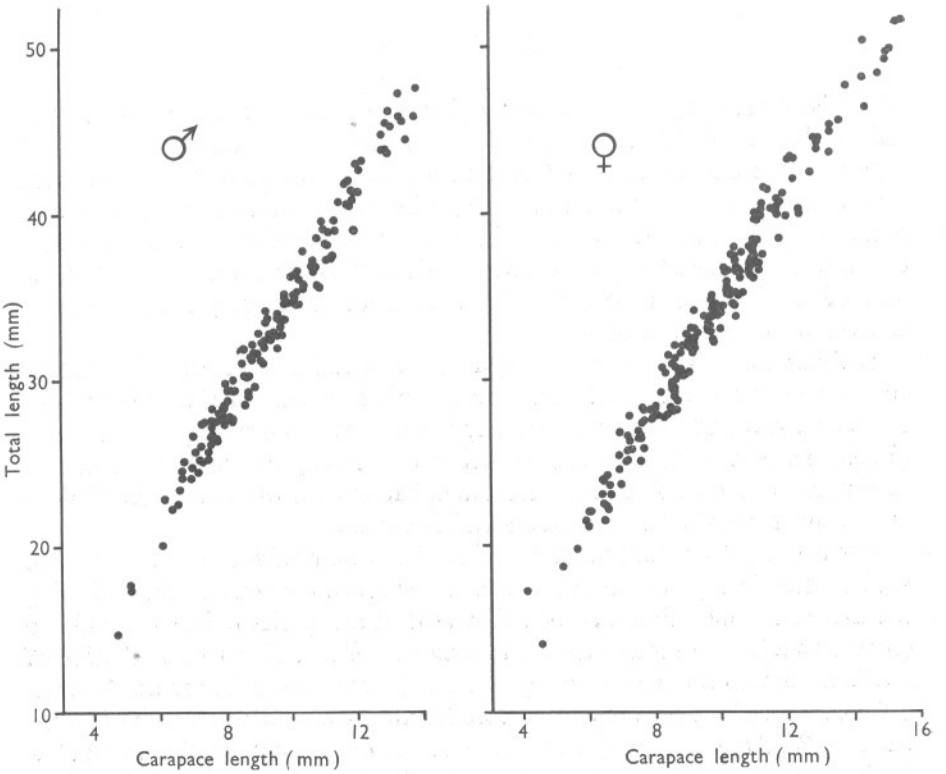

Fig. 1. Relationship between carapace length and total length in male and female *Crangon allmani*.

MATERIAL AND METHODS

Throughout this work a 9 ft. trawl has been used. Until March 1956 a beam Trawl was used, but since that date an Agassiz trawl has been preferred. Each haul was of 20 min duration. The catch was sorted and, apart from a few specimens retained for observations in the aquarium, narcotized in fresh water, fixed in 4% neutral formalin for approximately 12 h and then transferred to 90% alcohol.

Later, length measurements were taken, sex determined and when eggs were present these were classified under one of the following four groups: *a*, early blastoderm; *b*, late blastoderm and early segmentation of the body; *c*, eye visible but abdomen not free from the head; *d*, well-developed abdomen and little yolk present. Specimens with egg remains and the larvae recently released, those in breeding dress and recently moulted shrimps were all recorded. Approximately 5% (over 400) of the total number of *C. allmani* caught were retained for further examination. These animals were representative of the size range, sex and maturity within each sample. Each animal of the subsample was remeasured, pleopods examined and usually drawn to scale, gut contents examined, and maximum ova length recorded. Eggs were classified, counted and measured. Drawings were made of the appendages and body of males and females of varying sizes. The ratio of carapace length (tip of the lateral carapace spine to the posterior limit of carapace, see Fig. 12) to total length (tip of the rostrum to the tip of the uropod setae) was calculated (average 3·49, limits 3·23–3·71). This relationship was found to be linear, there being no significant difference between males and females (Fig. 1). It was found that the lateral spine of the carapace (Fig. 12) was a far more accessible anterior point of reference for measuring carapace length than the more usual posterior limit of the eye socket; only rarely was the spine found broken. Measurements were carried out with a vernier caliper and taken to the nearest 0·1 mm.

DISTRIBUTION

C. allmani is restricted to the eastern boreal region of the Atlantic. According to the literature, it extends from the White Sea to the northern part of the Bay of Biscay. It has been recorded for Iceland, it is present throughout the North Sea and the Kattegat and is found off all the coasts of Great Britain. It is apparently least plentiful off the south coasts of England and Ireland. In Danish waters and occasionally elsewhere it occurs in as little as 5 fm. of water, but its normal range extends from 10 to 100 fm. Off the Northumberland coast *C. allmani* has been taken at all depths below 9 fm. on every type of bottom with the exception of rock. The density of the population at any particular point may vary enormously. The 10 fm. contour line (see Fig. 2) is the approximate offshore limit of *C. vulgaris* and, at certain times mixed populations occur at this depth. There has never been the slightest difficulty in separating the two species; colour, body shape and the bicarinate dorsal side of the sixth abdominal segment of *C. allmani* being infallible diagnostic characters.

During this study three main stations, A and B (inshore) and C (offshore), were sampled (Fig. 2). Originally sampling started inshore (St. A) two miles due east of Blyth Harbour in 25 fm. Soon after, the offshore station (St. C)

13 miles due east of this harbour in 50 fm. was sampled. By the autumn of 1955 hopper refuse had fouled the 2 miles station, even though this was a mile inshore of the dumping grounds. This colliery refuse virtually wiped out the fauna and the ground became impossible to trawl over, so that a second inshore station (St. B) was sampled 1·9 miles, 050° from Newbiggin Church in 22 fm. Additional samples have been taken throughout the area indicated in Fig. 2, but unless otherwise stated the data presented are from samples collected at the three stations.

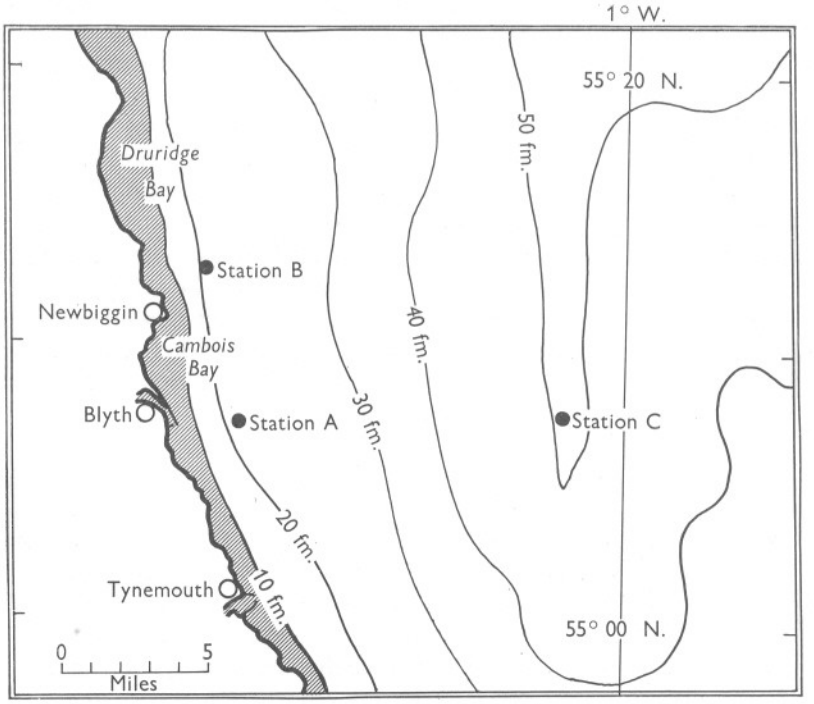

Fig. 2. The area investigated with the position of the Stations A, B, and C indicated. *Crangon vulgaris* is restricted to the hatched area and *C. allmani* to the non-hatched area.

Samples taken inshore during the first year showed a marked drop in the numbers of *C. allmani* caught during April and May (Fig. 3). This drop in numbers persisted throughout the summer and autumn months (May-October) and has proved to be a constant yearly occurrence at the inshore stations and elsewhere between 10 and 30 fm. Offshore *C. allmani* did not disappear during the summer months but it is clear that shrimps in 40–50 fm. are not evenly distributed and hauls without or with very few shrimps were taken throughout the year (Table 8). That the trawl was fishing on these occasions is indicated by the presence of normal numbers of other members of this

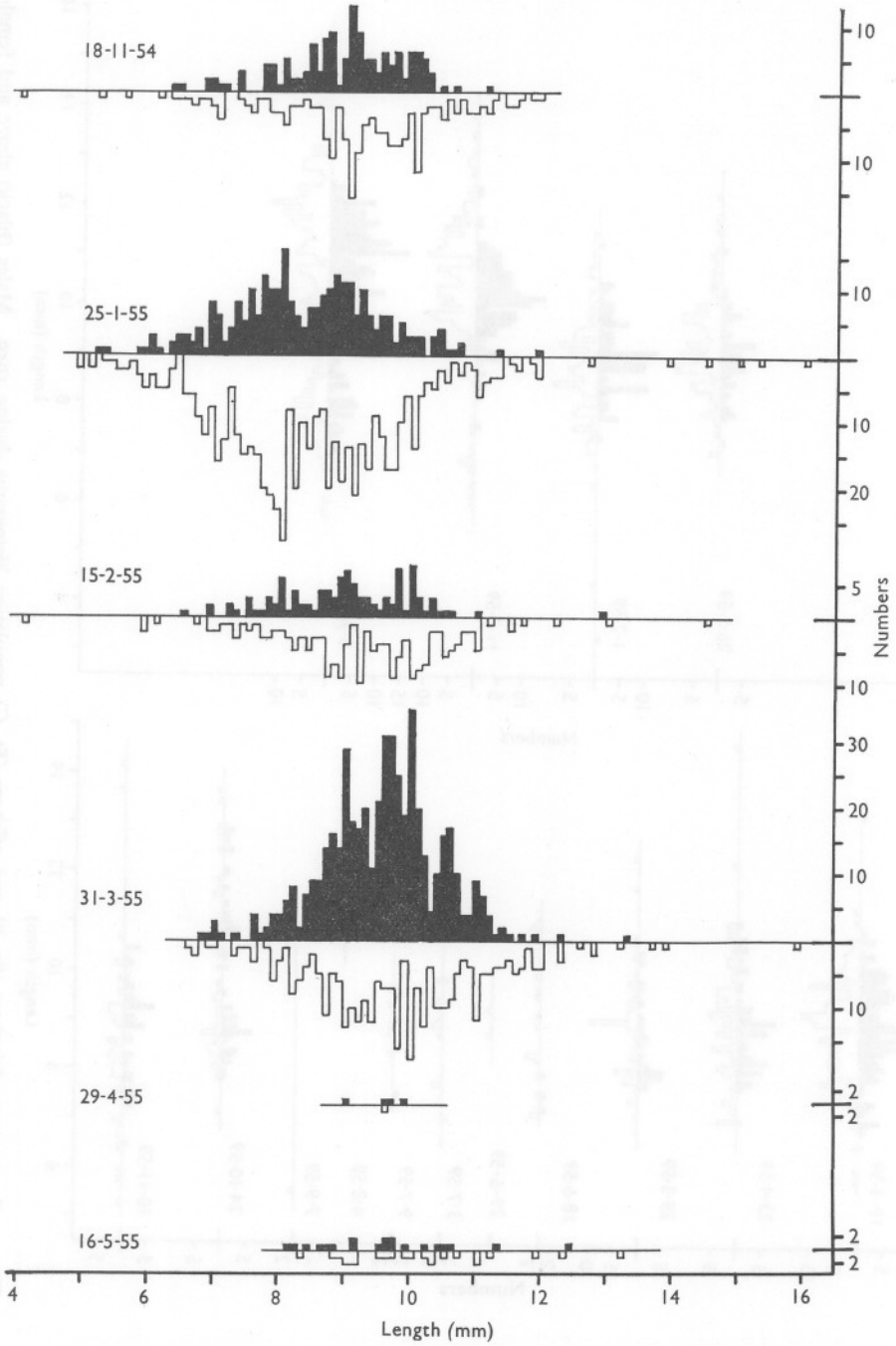

Fig. 3. Population histograms, in carapace-length groups, of the samples taken from Station A between November 1954 and May 1955 Males (black) above and females (outlined) below the line.

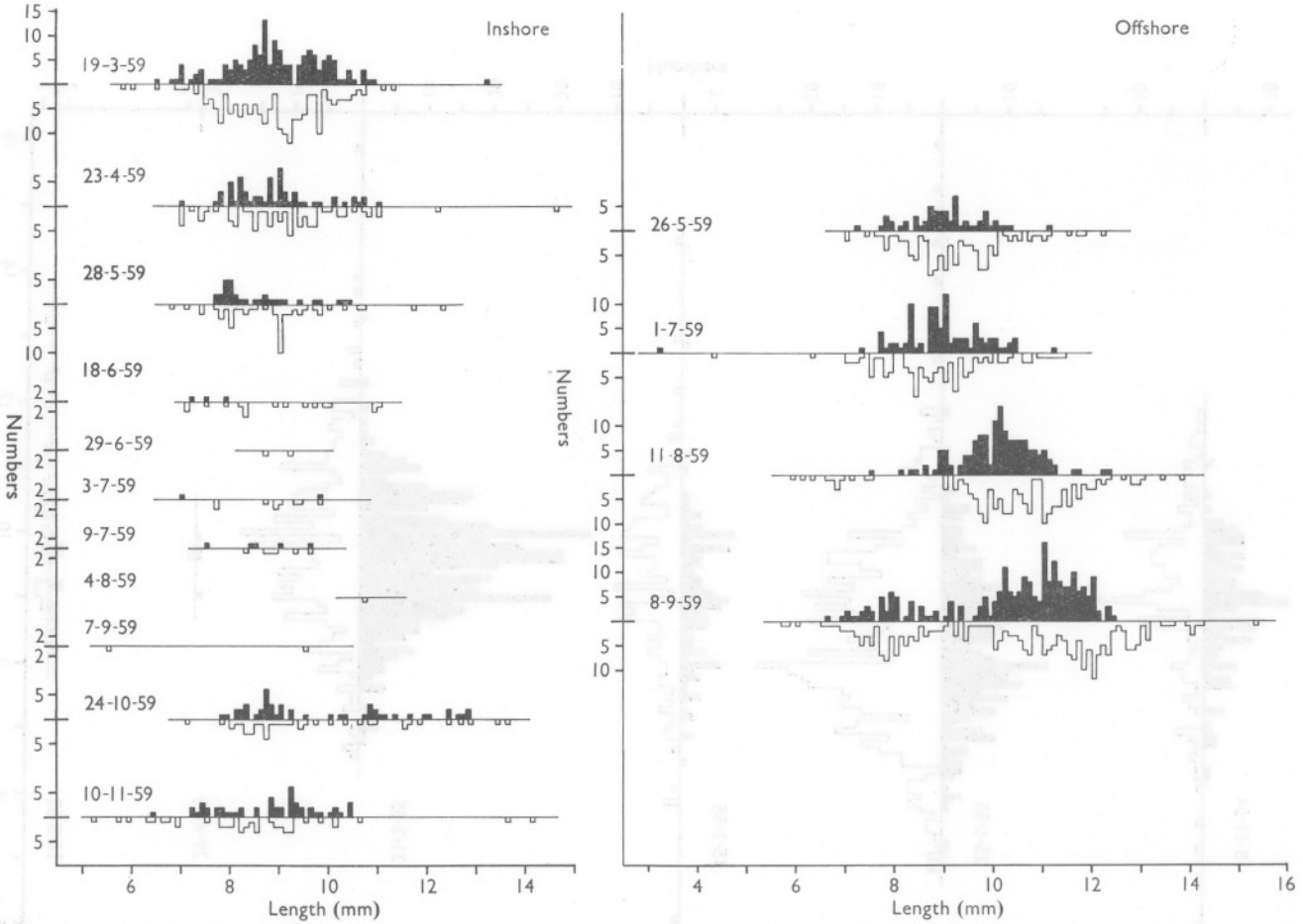

Fig. 4. Comparison of inshore (St. B) and offshore (St. C) population histograms during 1959. Males (black) above and females (outlined) below the line. The length given is that of the carapace.

epifauna. This difference between inshore and offshore populations was closely observed in 1959 (Fig. 4) when the trawling effort was increased in order to make sure that the inshore population had largely disappeared. Sampling outside the main stations indicates that this seasonal change can be observed in depths up to 35 fm. In this connexion it is of interest that examination of stomach contents of Whiting caught in the same area during 1953 to 1955 from depths of 20 to 30 fm. shows that while the fish are feeding predominantly on *C. allmani* during the months October to April few shrimps are present in the stomach contents from May to September (Goonewardene, unpublished*). Although there is lack of direct evidence, there can be little doubt that the disappearance is the result of a migration. This will be assumed in the pages preceding the discussion of this point.

BREEDING

C. allmani is a dioecious species. Offshore, the average ratio of males to females was 0·98–1·00 but with a wide range of 0·49–1·12 to 1·00. Inshore, there are on the average far fewer males than females, the ratio being 0·62–1·00, with the range being even wider than offshore 0·15–1·38 to 1·00. This point will be further discussed when evidence for migration is presented (p. 503).

TABLE 1. AVERAGE MONTHLY PERCENTAGES OF THOSE FEMALE *CRANGON ALLMANI* IN BREEDING DRESS (*bd*), THOSE BEARING EGGS AT STAGES *a–d* AND THOSE WITH EGG REMAINS FOLLOWING THE RELEASE OF THE LARVAE (*lr*)

	bd	*a*	*b*	*c*	*d*	*lr*
Nov.	—	—	—	—	—	—
Dec.	6·0	1·5	—	—	—	—
Jan.	0·8	13·8	6·0	0·9	—	—
Feb.	0·5	4·6	4·9	0·7	1·8	—
Mar.	1·0	12·4	11·9	6·1	2·8	2·7
Apr.	—	26·6	34·7	4·7	—	7·6
May	1·0	26·7	13·9	9·3	2·1	11·8
June	—	14·3	21·4	7·1	14·3	28·6
July	—	31·0	1·7	—	—	0·4
Aug.	—	—	—	—	—	0·9
Sept.	—	—	—	—	—	—

The percentages are calculated on total number of females per haul, i.e. no account is taken of immature females (see below).

Females bearing eggs first appear in small numbers (1·5% of all females†) by the end of the first week in December. All the eggs are at stage *a*. By

* University of Durham, Ph.D. Thesis, 1956. 'The biology of the Whiting (*Gadus merlangus* Linn.).

† The percentages, unless otherwise stated, including those of Table 1 are based on the total number of females in the catch, i.e. including immature females less than 7·5 mm carapace length. The percentage of immature females is small (Table 2) and does not affect the results presented.

TABLE 2. THE AVERAGE MONTHLY PERCENTAGE OF IMMATURE FEMALE *CRANGON ALLMANI* (LESS THAN 7·5 MM CARAPACE LENGTH) AND AVERAGE MONTHLY PERCENTAGE OF FEMALES GREATER THAN 7·5 MM CARAPACE LENGTH THAT ARE OVIGEROUS: INCLUDING THOSE IN BREEDING DRESS AND WITH EGG REMAINS AS WELL AS THOSE BEARING EGGS.

	(%) Immature females	(%) Ovigerous females		(%) Immature females	(%) Ovigerous females
Dec.	1·5	7·6	June	10·0*	55·0*
Jan.	12·1	24·2	July	2·9	31·4
Feb.	6·3	11·1	Aug.	7·2	1·9
Mar.	4·2	31·9	Sept.	8·6	—
Apr.	6·1	55·9	Oct.	7·4	—
May	2·9	49·1	Nov.	12·3	—

* Percentage calculated on less than thirty specimens.

the end of January 13·8% of all females bear eggs at stage *a*, 6·0% at stage *b* and a few, less than 1%, are eyed and at stage *c*. Advanced larvae at stage *d* are present (1·8%) in the mid-February samples but females that have released their larvae are not seen until the first week in March (Table 1). It appears that eggs laid at the beginning of the breeding season are carried for about 10–12 weeks. During February there is a decrease in the number of females with recently laid eggs. The percentage of females bearing stage *a* eggs increases during March and reaches a peak of more than 26% during April and May. There is a decrease in June and another peak is recorded in the offshore population in July. No females bearing stage *a* eggs have been recorded after mid-July. In fact no egg-bearing females have been taken after July although a small number of females with egg remains were taken in August (Table 1). Thus it would appear that eggs laid early in July hatch 5 or 6 weeks later, i.e. their development is twice as fast as those laid at the beginning of the breeding season. This increase in the rate of egg development as the breeding season advances is supported by the fact that while the greatest percentage of eggs at stage *a* is reached in April and May, it is the June samples that show the greatest percentage of females bearing stage *d* eggs and newly hatched larvae (14·3 and 28·6%, respectively). This indicates a development time of about 7 weeks. Such a decrease in development time has been recorded by Havinga (1930) in the case of *C. vulgaris*. He calculated that the winter (October–November) brood of *C. vulgaris* at a temperature of about 9° C take about 9 weeks for development while the summer eggs (May–June) at a temperature of about 18° C develop in half that time. This relationship to temperature is by no means so clear in Northumberland waters. From December to March there is an average drop in the temperature of the offshore water close to the bottom of 9·0–5·5° C and inshore 9·0–5·0° C (Fig. 5). From March to July there is a corresponding increase in temperature from 5–10° C inshore and from 5·5–7·5° C offshore. The range in

temperature is much the same for the two halves of the breeding season, even though the population that is inshore at the beginning of the breeding season has moved offshore during the second half of the season. That the temperature is falling in the first period and rising in the last may be

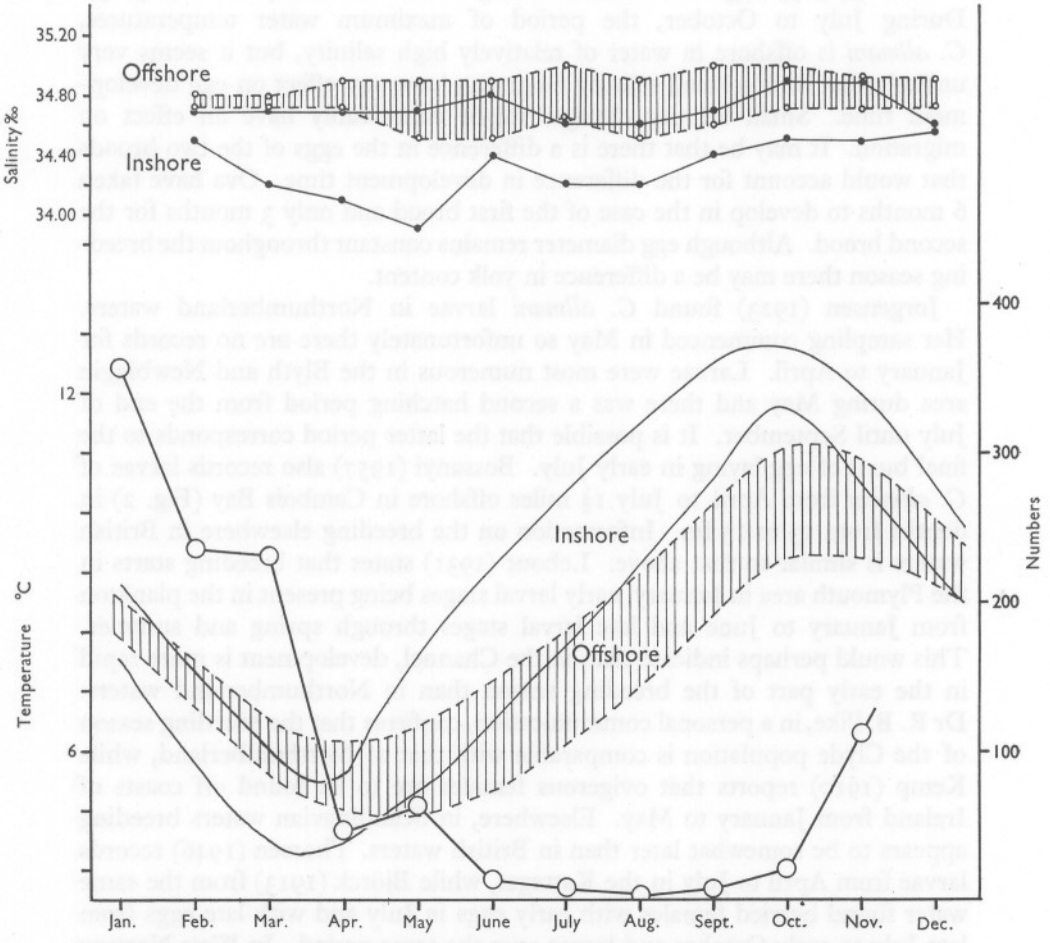

Fig. 5. The limits of salinity and temperature records from deep water inshore (25–30 fm) and offshore (45–50 fm.) during the years 1953–58. The inshore average monthly catch per 20 min haul of *C. allmani* is superimposed on the hydrographic data.

of significance. Broekema (1941) finds that salinity is related to egg development time in *C. vulgaris*, but in the case of *C. allmani* salinity changes during the breeding season cannot compare with those experienced by *C. vulgaris* in shallow and estuarine waters. Broekema finds that development may be twice as long in salinity of 16‰ as compared with 35‰ in the case of

C. vulgaris and that with increasing temperature the salinity optimum shifts towards less saline water. The maximum range in salinity of the bottom water at the inshore stations is 34–35‰, with minimum salinities in May and June and maximum in November and December. Offshore the range is less—34·5–35·0‰ and seasonal changes are not clearly seen (Fig. 5). During July to October, the period of maximum water temperatures, *C. allmani* is offshore in water of relatively high salinity, but it seems very unlikely that such a small salinity range can have any effect on egg development time. Small salinity changes might conceivably have an effect on migration. It may be that there is a difference in the eggs of the two broods that would account for the difference in development time. Ova have taken 6 months to develop in the case of the first brood and only 3 months for the second brood. Although egg diameter remains constant throughout the breeding season there may be a difference in yolk content.

Jørgensen (1923) found *C. allmani* larvae in Northumberland waters. Her sampling commenced in May so unfortunately there are no records for January to April. Larvae were most numerous in the Blyth and Newbiggin area during May and there was a second hatching period from the end of July until September. It is possible that the latter period corresponds to the final burst of egg laying in early July. Bossanyi (1957) also records larvae of *C. allmani* from April to July 1½ miles offshore in Cambois Bay (Fig. 2) in depths from 13 to 15 fm. Information on the breeding elsewhere in British waters is similar to that above. Lebour (1931) states that breeding starts in the Plymouth area in January, early larval stages being present in the plankton from January to June and late larval stages through spring and summer. This would perhaps indicate that, in the Channel, development is more rapid in the early part of the breeding season than in Northumberland waters. Dr R. B. Pike, in a personal communication, confirms that the breeding season of the Clyde population is comparable with that of Northumberland, while Kemp (1910) reports that ovigerous females are to be found off coasts of Ireland from January to May. Elsewhere, in Scandinavian waters breeding appears to be somewhat later than in British waters. Thorsen (1946) records larvae from April to July in the Kattegat, while Björck (1913) from the same water found berried females with early eggs in July and with late eggs from late July to early October and larvae over the same period. In West Norway (Wollebaek, 1908) berried females are found in March and throughout the summer, the larvae hatching during the summer months.

Analysis of the length measurements of the egg bearing females shows a decrease in average length over the breeding season although the overall size range does not differ over the season (Table 3). Only three specimens with a carapace length of less than 7·5 mm (one at 7·1 mm and two at 7·4 mm) were found carrying eggs. The majority of shrimps between 7·0 and 7·5 mm carapace length were obviously immature and this was confirmed when ovum

length was plotted against carapace length in non-ovigerous females (Fig. 6). Examination of the testes shows that the male matures at about the same size as the females, so that for purposes of calculation shrimps below 7·5 mm carapace length are classified as immature.

TABLE 3. THE CARAPACE LENGTH IN MM OF FEMALE *CRANGON ALLMANI* BEARING EGGS FOR EACH MONTH OF THE BREEDING SEASON

	Average	Range		Average	Range
Dec.	10·5	(10·5)	Apr.	9·8	(6·9–12·1)
Jan.	11·3	(8·0–16·0)	May	9·3	(7·7–13·2)
Feb.	10·1	(7·4–14·8)	June	9·6*	(7·1–11·1)
Mar.	10·3	(7·9–16·9)	July	9·6	(7·9–12·4)

* Calculated on less than thirty specimens.

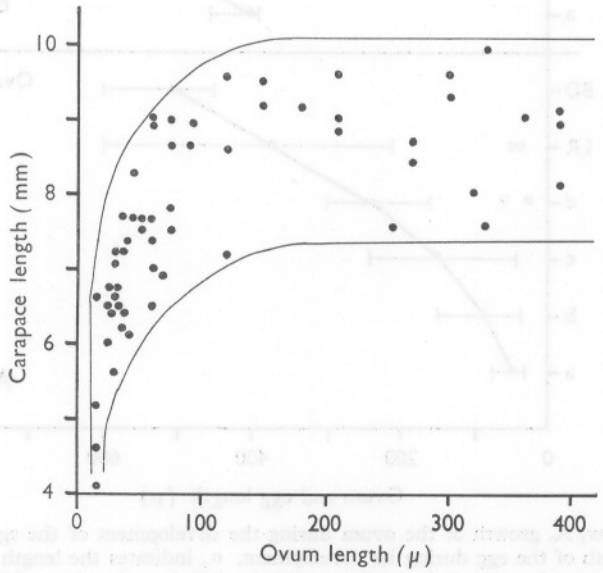

Fig. 6. Carapace length plotted against ovum length in females that have yet to lay eggs.

Little growth of the ova occurs before *C. allmani* reaches 5·5 mm carapace length. There is a marked increase in the rate of growth of the ova after the shrimp has grown to 6·5 mm and exceptionally eggs are laid soon after it reaches 7·0 mm carapace length (Fig. 6). The majority of the females do not develop so fast and first lay their eggs when the carapace measures between 8·5 and 9·5 mm. As the breeding season extends over 7 months and there appear to be two, or possibly three, peaks of egg laying, it was necessary to find whether the shrimps lay more than one brood during the season. Ovum length was plotted against stages in egg development (Fig. 7). Not all the ova are released at the time of the first egg laying. There remains a core of small ova

each approximately 50 μ long that increases rapidly in size during the period of egg carriage so that when the larvae are released a second brood is almost ready to be laid, the ova being approximately 370 μ long. In *Pandalus borealis* (Allen, 1959) the growth rate of the ovum in the latter half of its development in the ovary was shown to be a straight line. This also appears to be the

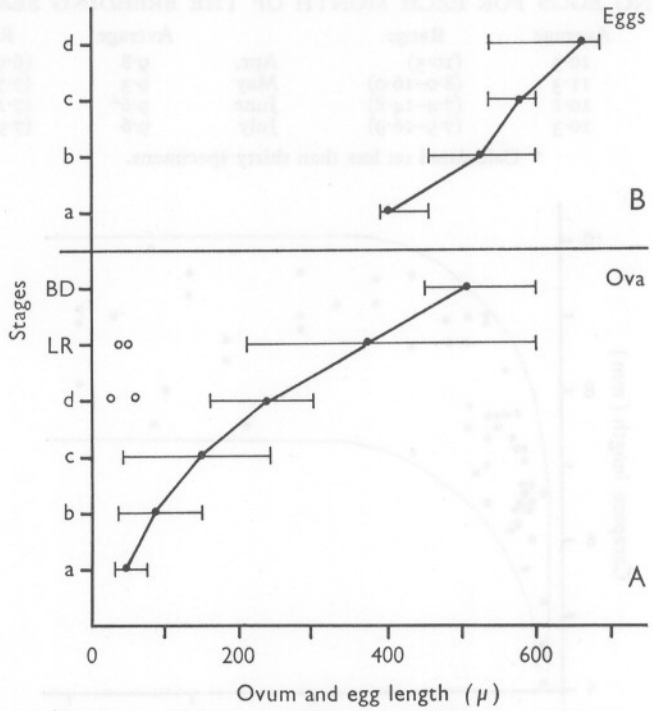

Fig. 7. To show, A, growth of the ovum during the development of the egg and, B, the increase in length of the egg during its development. o, indicates the length of the ova in females with eggs ready to hatch during June and July. BD, breeding dress; LR, egg remains following the release of the larvae; see p. 483 for explanation of stages *a*, *b*, *c* and *d*.

case in *C. allmani* and extrapolation of the graph indicates that the interval between release of the larvae and the re-assumption of breeding dress and the second egg laying is of the order of 2 or 3 weeks. The growth rate of the ova of egg-bearing females in the June and July samples is not rapid. The reduction in the growth rate is maintained during the late summer and autumn and the ova take 6 or 7 months to reach maturity as compared with 3 months for the second brood of the season (Fig. 8).

The ovary of the immature shrimp extends from the posterior end of the stomach to the dorsal posterior limit of the carapace, while that of the female with mature ova extends from the anterior limit of the carapace to the centre

of the third abdominal segment. Egg laying usually occurs shortly after the assumption of breeding dress. Most of the females caught in breeding dress were soft and so were many with newly laid eggs. The newly laid eggs are a transluscent gold colour and are remarkably constant in size irrespective of differences in the time taken for the ova to mature. They are spherical when first laid with a diameter of 390 μ. The eggs soon elongate and continue to do so throughout their development. Immediately before hatching the egg case

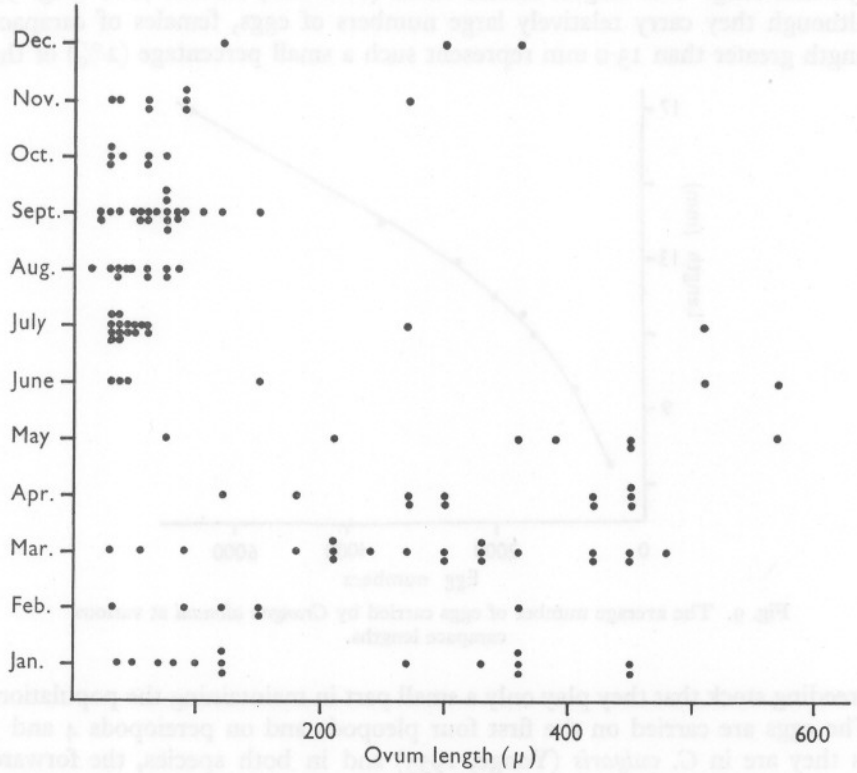

Fig. 8. Maximum ovum lengths in ovigerous females, or non-ovigerous females that have had at least one brood of eggs, plotted against month of capture.

is approximately 650 μ long (Fig. 7). It will be noticed (Figs. 7, 8) that the length of the mature ovum is greater than the diameter of the newly laid egg. This is due to the compression of the ovum within the ovary producing an elongate, angular shape.

Høglund (1943) shows that owing to the weakly developed epimera, short basipodites and endopodites, with the latter lacking stylamblys, the eggs of *Crangon* are more exposed and unprotected than those of any other caridean. This makes heavy demands on the fixing system and in *Crangon* the ovigerous

setae and the cement are particularly strong. Nevertheless, the eggs of *C. allmani* are easily detached and the possibility of loss increases with age as the developing eggs enlarge with the resulting increase in volume of the egg mass. Many shrimps with advanced eggs appeared to have considerably reduced numbers and for this reason egg counts were taken only in the case of females with stage *a* eggs. The average egg count for females with a carapace length of 7·5 mm is 400 and this increases to approximately 2500 on a shrimp 13·0 mm long. The largest female taken (17·0 mm) carried 7060 (Fig. 9). Although they carry relatively large numbers of eggs, females of carapace length greater than 13·0 mm represent such a small percentage (2%) of the

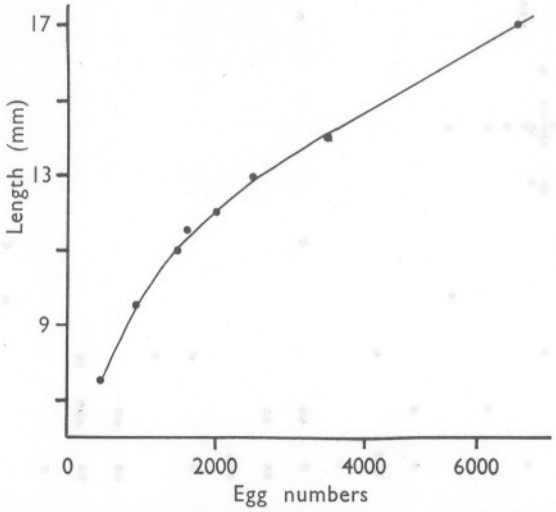

Fig. 9. The average number of eggs carried by *Crangon allmani* at various carapace lengths.

breeding stock that they play only a small part in maintaining the population. The eggs are carried on the first four pleopods and on pereiopods 4 and 5 as they are in *C. vulgaris* (Yonge, 1955) and in both species, the forward extension of the egg mass under the thorax is probably a modification related to the bottom feeding.

GROWTH

A prolonged breeding season with three breeding maxima makes it very difficult to decipher the monthly population histograms for the purpose of abstracting information on rate of growth (Figs. 3, 4). Furthermore, owing to the size of net used, few *C. allmani* smaller than 6·0 mm carapace length were caught. Dredge samples secured a few young *C. allmani* mainly during the months July to September. These had an average carapace length of 3·5 mm. As the carapace length of the newly metamorphosed *C. allmani*

must be of the order of 2·0 mm (the last larval stage is 6·5 mm long—Lebour, 1931), there can be little doubt that these are recently hatched 0-group. This group appeared in the trawl hauls inshore in November when a few females between 4·0 and 6·0 mm carapace length were caught. By January the average carapace length of the 0-group is 6·0 mm (Fig. 10). Although the youngest *C. allmani* are too small to be retained in the net in any numbers, a few specimens below 6·5 mm carapace length are caught throughout the year and it is probable that recruitment is continuous from April to October with the main peak from July to September. The only samples showing two clearly defined population peaks are those offshore in September (Fig. 4). One peak has an

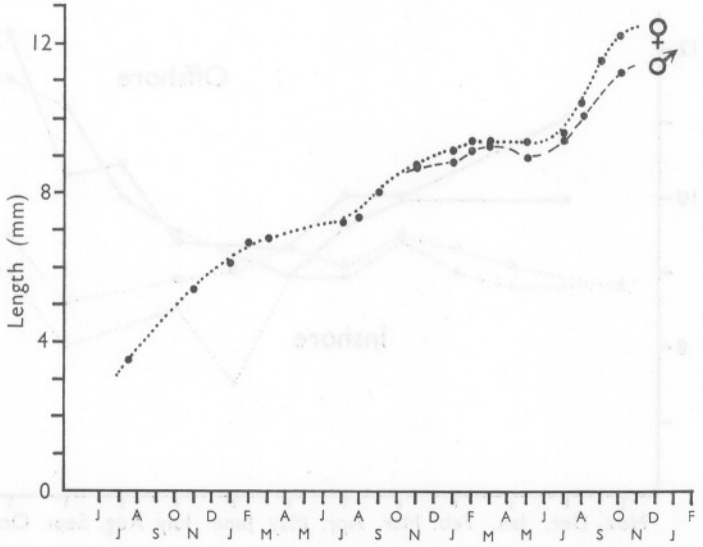

Fig. 10. The probable growth-rate curve of male and female *Crangon allmani* during their normal life span: mean carapace length plotted over a period of 2½ years.

average carapace length of 8·0 mm (1-group) and the other 11·5 mm (2-group). Peaks corresponding to the 8 mm 1-group are not seen in histograms of offshore samples in the following months and it is probable that this group migrates inshore during October and forms the greater part of the inshore population in the November samples (Fig. 3). This population has an average carapace length of 8·7 mm. November is the first month following the seasonal disappearance when *C. allmani* is taken in large numbers inshore. Some of the larger 2-group *C. allmani* also move inshore, mainly during December and January. Owing to the small numbers involved, differences between the rates of growth of males and females, are not apparent in shrimps less than 7·5 mm. The females of the inshore samples (mainly 1-group) from January to May show little increase in size, the average carapace length being 9·3 mm. This

lack of growth is no doubt due to the cessation of moults while egg bearing. The effect of the growth of shrimps maturing for the first time and also the continued entry of 0-group into the catches is offset by the interbrood growth. There is a gradual but slow increase in the average size of the males during January to March (8·8–9·3 mm) followed by a drop in April and May (8·9 mm). This drop is probably due to the effect of the offshore migration. During April and May the inshore population almost completely disappears, and it is probably significant that May is the only month in which the average length of the inshore and offshore populations is the same (Fig. 11). During the rest of the year the average length of the offshore population is greater

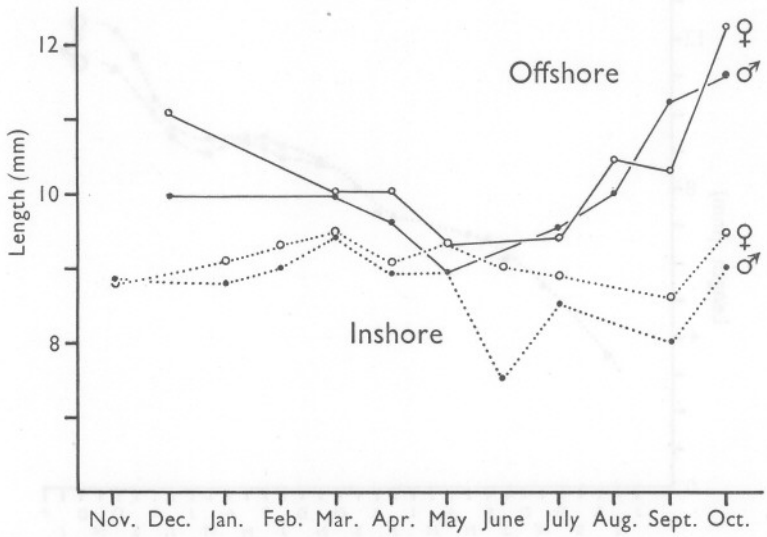

Fig. 11. Comparison of the average carapace length of the *Crangon allmani* caught inshore and offshore throughout the year.

than the inshore. In the period May to October a few *C. allmani* remain inshore. These are mostly small females about 8·5–9·0 mm carapace length (Table 7). During the same period offshore there is a steady increase in the average length of the population (Figs. 4 & 11), and by the end of the period the original 1-group and 0-group have become the new 2-group and 1-group, respectively. The new 2-group reaches a maximum average size of 12·5 mm in November, after which there is a drop probably due to the death of the largest shrimps following early spring breeding (see below).

Throughout life the male *C. allmani* is slightly smaller than the female. The females of the new brood are the first to appear in the catches, but the difference in the average carapace lengths is never greater than 1·0 mm in the oldest shrimps. Comparison of the mean lengths of the males and females of

each haul does not necessarily give a true figure for this difference in size. The two sexes appear to migrate at different times with the result that in some samples (e.g. offshore, September) the average length of the male is greater than the female (Fig. 11). Although most of the *C. allmani* die in their third year a few live at least one more year. The largest female caught was 17·0 mm carapace length and the largest male 14·0 mm. The male probably dies before the female, soon after copulation. Further examination of the data suggests that many 2-group shrimps which form a large part of the breeding stock during December to March die and do not breed a second time. It is interesting to note that Wollebaek (1908) reports that the average size of *C. allmani* in Norwegian waters is larger than that of *C. vulgaris* (100 mm as to 60–70 mm). The reverse is true in British waters.

MOULTS

The records of recently moulted shrimps show no significant difference between males and females from inshore or from offshore grounds. On the average, 4% of all *C. allmani* have recently moulted. There is some difference between the samples taken between January and June (3·1%) and July to December (6·6%). Such a difference might be expected as the former period covers the breeding season when egg bearing restricts moulting while the latter is the period of maximum growth when the new year group is entering the stock. Most of the specimens in breeding dress are soft as are many of the females bearing newly laid eggs. The data give no indication how frequently *C. allmani* moults, except that 9·0% of those less than 8·0 mm carapace length, 4·8% of those between 8·1 and 10·0 mm and 3·4% of those greater than 10·1 mm had recently moulted.

In the interval between successive broods there is a moult to dispose of the old breeding dress and egg remains followed by re-assumption of breeding dress within a maximum of 3 weeks. It is known that the moult frequency of other Caridea of similar size is about 20–35 days (Nouvel & Nouvel, 1937; Høglund, 1943) so that it seems unlikely that there are intermediate moults between the losing of the old and the gaining of the new breeding dress.

FOOD

The analysis of the stomach contents of more than 350 *C. allmani* is shown in Tables 4 & 5. Approximately 54% had food in the stomach. It will be seen from Table 4 that there is little difference in the percentages of shrimps with and without food in respect of sex and of maturity of the gonads. Females, with mature gonads taking all the available space in the thorax, had food present. Only in newly moulted shrimps was food invariably absent. Identification of the food proved far from easy as the mandibles (Fig. 12), which are both large and efficient, break the food into small fragments.

TABLE 4. THE PERCENTAGE OF *CRANGON ALLMANI* WITH FOOD PRESENT IN THE STOMACH WITH RESPECT TO SEX AND MATURITY

	Number examined	Percentage with food	Percentage without food
Male	150	52·7	47·3
Female	200	55·0	45·0
Immature testis	82	57·7	43·3
Mature testis	68	50·0	50·0
Females without eggs	147		
With ova length $< 150\mu$	101	52·5	47·5
With ova length $> 150\mu$	46	56·5	53·5
Females with eggs	52	55·8	44·2

The sample is representative of the size range.

C. allmani feeds predominantly on living Crustacea and Annelida. Mollusca, Foraminifera and Ophiuroidea are present in smaller quantities, while Whiting scales were present in a few stomachs. Sand and mud particles are always present with the food. In the laboratory the shrimp behaves in much the same way as *C. vulgaris* (Lloyd & Yonge, 1947), burrowing and searching in the top few millimetres of the substratum. Occasional specimens were taken with a small *Nephthys* held by the mouth parts. The chelae, maxillae and maxillipeds appear to be used for grasping and guiding the food into the mouth, the mandibles alone are used in mastication, although Havinga (1929) refers to 'chewing teeth' on the first maxilla in *C. vulgaris*. Identifiable annelidan remains consist of *Nephthys* (*ca.* 90%) and *Glycera* (*ca.* 10%). The crustacean remains are more varied and consist of small Cumacea, Amphipoda, Copepoda and young *C. allmani*. Of the identifiable Mollusca the most common were *Dosinia lupinus*, *Venus striatula* and *Cylichna cylindracea*.

TABLE 5. PERCENTAGES OF DIFFERENT TYPES OF FOOD ORGANISMS PRESENT IN STOMACHS OF *CRANGON ALLMANI* FROM INSHORE AND OFFSHORE STATIONS

	Inshore		Offshore	
	♂	♀	♂	♀
Crustacea	65·6	68·1	55·6	63·9
Annelida	43·1	43·1	59·3	61·1
Mollusca	12·1	16·7	7·4	5·6
Foraminifera	3·9	4·2	11·1	—
Ophiurida	1·7	1·4	—	—
Whiting scales	6·9	4·2	—	—
Without food	43·6	43·7	44·9	49·4
With food	56·4	56·3	55·1	50·6

Comparison of the stomach contents of the inshore and offshore populations shows a few differences. About 65% of the shrimps with food in the stomach have crustacean remains, with little difference between the two populations. Significantly more worms are eaten offshore (60%) than inshore

(43%), while more molluscs are eaten inshore than offshore (Table 5). Other food organisms are in too small quantity to make any comparison except that it should be noted that Whiting scales were only present in the stomachs of *C. allmani* from the inshore stations. There is no significant difference between the diet of the male and the female.

Analysis of food with respect to size and month of capture shows little variation in either case except that the smaller size groups have a high proportion of copepods in their crustacean food.

EXTERNAL MORPHOLOGY

The woodcuts of *C. allmani* illustrating the original descriptions by Kinahan (1857, 1861) are not accurate. They were improved upon by the photographs and drawings of Wollebaek (1908); but unfortunately these are poorly reproduced and, in addition to a hazy dorsal view of the shrimp, include only the first antenna, chela and sixth abdominal segment. A series of drawings of the external features of *C. allmani* has been included to fill this gap (Figs. 12–14). Little need be said in the way of description except that contrary to the account given by Kinahan (1857) there is a well-developed spine on the meropodite of the chela, as in *C. vulgaris*. The differences between *C. vulgaris* and *C. allmani* have been discussed by Wollebaek (1908) and the present study supported his findings.

Although the male pleopods are generally more setose than those of the female, except when the latter is in breeding dress, the only reliable method of sexing *C. allmani* short of dissection is by microscopic examination of the first and second pleopods. In practice the second pleopod was examined. The endopodite of the second pleopod of the male bears an appendix masculina above the base of its inner edge. In the smallest specimens (Fig. 14) the appendix masculina is small and easily overlooked. It is in the form of a small projection from the inner edge of the second segment and bears a single seta at its tip. The appendix increases in size and at maturity has 6 or 7 setae along its inner edge. In the oldest males an additional 6 or 7 setae are attached to the base of the organ. The second pleopod of the female is without an appendix. The endopodite of the first pleopod of the male differs in shape to that of the female (Fig. 14). In the smallest males it is blade shaped with three setae at the tip. As it increases in size the setae become more numerous, 6 or 7 at maturity and many more prior to copulation. It becomes more pointed with age. The endopodite of the female (Fig. 14) is similar in many respects to that of the male, but it is always more elongated and becomes progressively more so with increasing age. Except when the female is in breeding dress there are never more than three short setae present along the inner edge. On assumption of breeding dress the endopodite of the first pleopod, and those of pleopods 2–4, are much modified with numerous

ovigerous setae and long pinnate setae. The pattern of ovigerous setae is similar to that described by Yonge (1955) for *C. vulgaris* (Table 6) and the number of these setae varies with the size of the shrimp. The specimen of *C. vulgaris* chosen for comparison in Table 6 is 55 mm long, mature females ranging in size from 45 to 70 mm while *C. allmani* is 37 mm with a range of 26–54 mm.

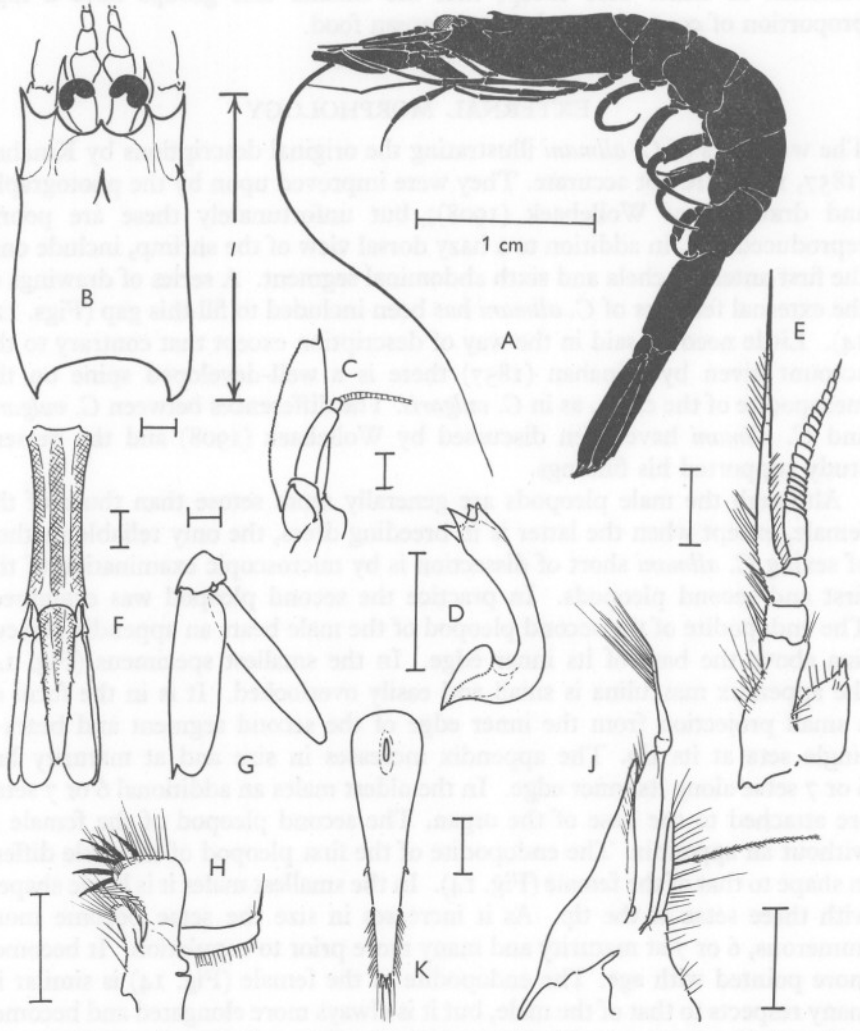

Fig. 12. External morphology of a male *Crangon allmani*. A, lateral view of the animal; B, dorsal view of the carapace with the measurement of length (l) indicated; C, peduncle of the 2nd antenna and its scale, setae not shown; D, mandible; E, 1st antenna; F, dorsal view of the 6th abdominal segment, telson and uropods; G, uropod, setae not shown; H, 1st maxilla; J, 1st maxilliped; K, ventral view of the telson. Except for A, all scales represent 1 mm.

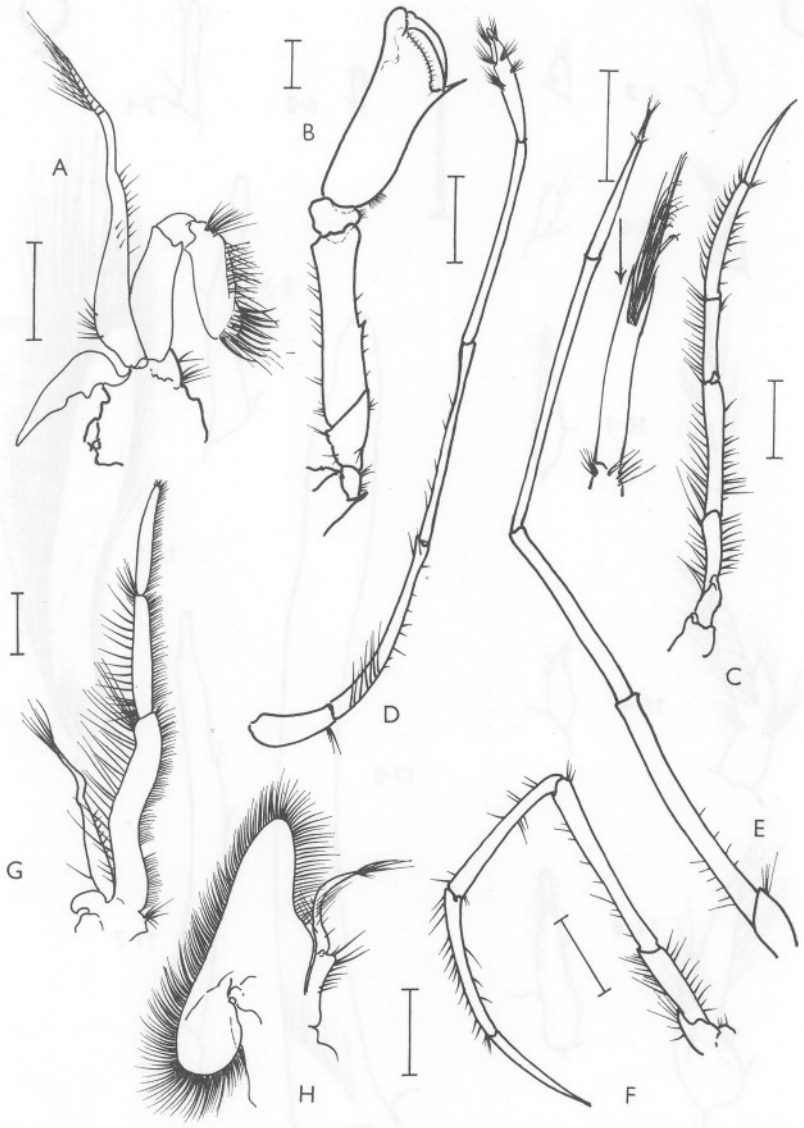

Fig. 13. External morphology of a male *Crangon allmani* continued. A, 2nd maxilliped; B, 1st pereiopod; C, 4th pereiopod; D, 2nd pereiopod; E, 3rd pereiopod; F, 5th pereiopod; G, 3rd maxilliped; H, 2nd maxilla. All scales represent 1 mm.

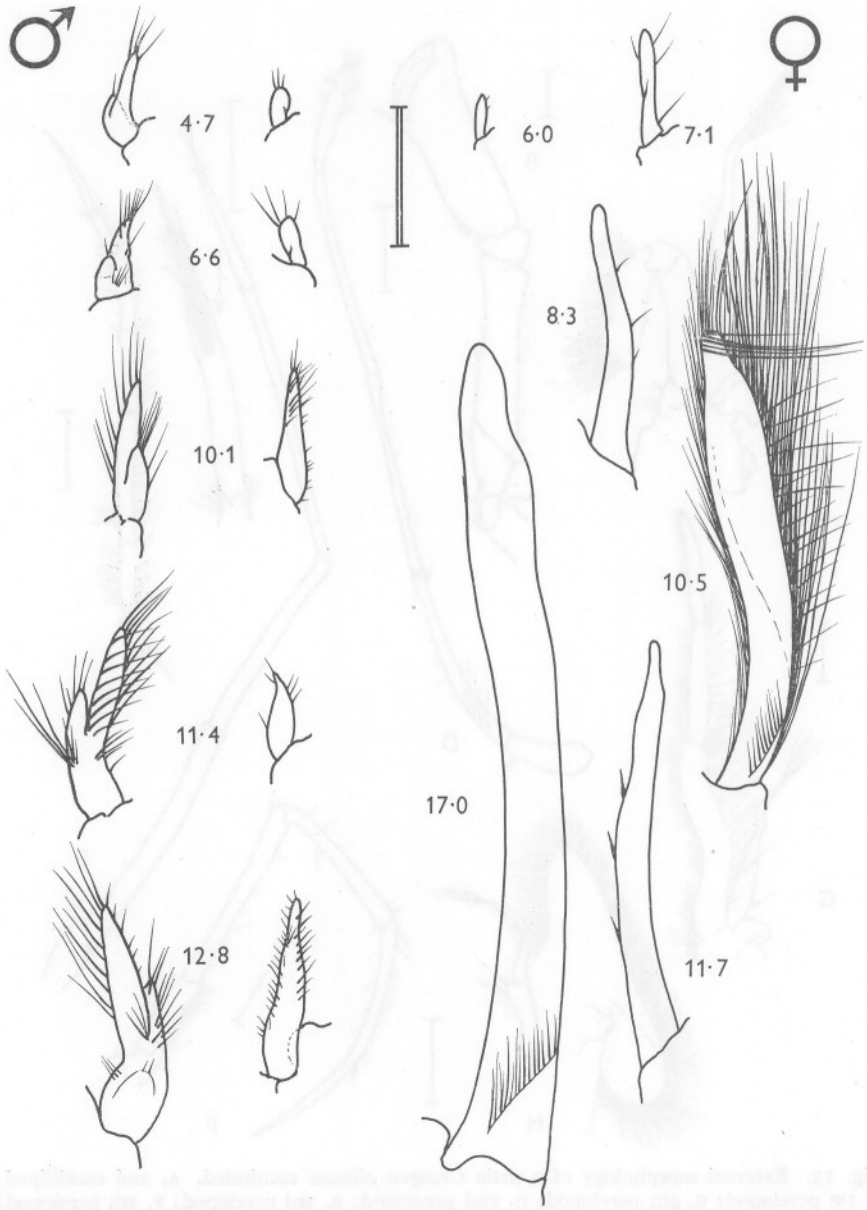

Fig. 14. The development of the endopodite of the 1st and 2nd pleopods of the male and the 1st pleopod of the female *Crangon allmani*. The carapace length of the specimens from which they were taken is indicated at the side of each appendage. The males measuring 10·1 and 12·8 mm have ripe gonads. The females measuring 10·5 and 17·0 mm are in breeding dress, the setae in the latter being omitted. The scale represents 1 mm.

TABLE 6. COMPARISON OF THE NUMBERS OF OVIGEROUS SETAE ON THE PLEOPODS OF *CRANGON VULGARIS* AND *C. ALLMANI* OF COMPARABLE SIZE (SEE TEXT p. 500)

Groups of setae	*C. vulgaris* Pleopods 1	2	3	4	*C. allmani* Pleopods 1	2	3	4
C	—	—	—	—	—	—	—	—
Bp	6	5	5	5	5	5	5	2
Bpa	10	3–4	4	2	8–9	5	4	3
Bm	8	8	8	—	6	6	6	—
Bd	5	4	4	—	4	4	4	—
Bda	3	—	—	—	—	—	—	—
E	19–22	—	—	—	21	—	—	—

Data on *C. vulgaris* abstracted from Yonge (1955). The lettering of the groups of ovigerous setae is the same as that used by Yonge (1955). The groups are on the coxopodites (C); the proximal (Bp), middle (Bm) and distal (Bd) regions of the inner margin of the basipodite and also on the anterior face in the proximal (Bpa) and distal (Bda) regions; on the endopodite (E).

DISCUSSION

It would seem that the disappearance of the inshore population during April and May until the following October can be explained by one or more of the following: deep burrowing, mortality, migration.

There is no evidence that the inshore population of *C. allmani* burrows deeper into the substratum during this period. They have not been found by extensive dredging with a variety of methods that sample the substratum to a depth of 10 in. Animals caught in April and kept in the aquarium show no change in burrowing habits. Similarly, there is no evidence for large-scale mortality. It seems possible that early breeding *C. allmani* of carapace length greater than 12·0 mm may die about May but these prawns represent less than 2% of the total population. Furthermore, the disappearance takes place at the height of the breeding season. Many females bear eggs at stages *a* and *b* at this time and it seems unlikely that these will die before releasing their larvae. By elimination of the other possibilities it seems likely that a migration is the explanation of the disappearance. The North Sea populations of the closely related *C. vulgaris* migrate inshore during May and migration is a feature of the life histories of *Crago francicorum* and *C. nigricauda* (Israel, 1936). Sampling shows that the *Crangon allmani* do not accompany *C. vulgaris* into shallow water nor are they present on the vast areas of rock that are close to the inshore stations. The only area in which *C. allmani* is found in large numbers from May to October is in depths of 40 fm. and over. Further indirect evidence of an offshore migration is that May is the only month in which the inshore and offshore populations have the same average length (see p. 496). Havinga (1929, 1930) and Broekema (1941) show that the largest specimens of *C. vulgaris* tend to remain in deeper water, the smallest specimens migrate first and those furthest inshore are predominantly females. *C. allmani* parallels its relative. Females predominate the inshore population

(Table 7), the average length of the first large inshore samples in November is smaller than those taken later in the inshore period and average length of the offshore samples is higher than those from inshore. It seems a reasonable assumption that the variations in the distribution of *C. allmani* are best explained by an inshore migration in October and an offshore migration in April and May.

TABLE 7. AVERAGE MONTHLY RATIO MALES/FEMALES AT INSHORE STATIONS

Jan.	0·48	July	0·33
Feb.	0·55	Aug.	0·25
Mar.	0·89	Sept.	0·62
Apr.	0·94	Oct.	1·38
May	0·75	Nov.	0·98
June	0·15	Dec.	?

Broekema (1941) finds that the seasonal movements of *C. vulgaris* are related to temperature and salinity. In the case of *C. allmani* the relationship of migration to these two factors is not so clear (see p. 489). Temperature and salinity data of deep water inshore and offshore off the Northumberland coast are given in Fig. 5. From this it is seen that offshore migration coincides with *inshore* minimum temperature. Little can be said of the salinity data except that offshore migration is into water of higher salinity.

Summary of the yearly cycle. In August the *C. allmani* population off Northumberland coast is in deep water (40–50 fm.) 10–15 miles off the coast. This population consists of three main age groups: 0-group, newly metamorphosed shrimps, 1-group, shrimps between 1 and 1½ years most, if not all, have yet to breed and, 2-group, shrimps 2–2½ years that have laid at least two batches of eggs (Fig. 15). In addition there may be a few older female shrimps. During late September and October an inshore migration commences that coincides with the upper temperature limit of the offshore deep water. The smallest 0-group and 1-group shrimps tend to migrate first and although 2-group take part in the migration many remain in deep water. Similarly, some 0-group and 1-group shrimps remain in deep water throughout the year, but the average length of the offshore population is higher than that of the inshore population. The predominance of young shrimps inshore during October to January shown by trawl sampling is confirmed by Goonewardene who in his analysis of the stomach contents of the Whiting (see p. 487) found that he could divide the *C. allmani* into two size-groups, the smaller predominating in the catches from September to January.

During September to December the gonads of 1-group and 2-group mature. The larger shrimps of each group mature first and egg laying commences in the second half of December and continues until the beginning of July. Although a quarter of the mature females lay their eggs in December and January the majority first lay their eggs between March and May. As a second batch of eggs is laid soon after the first hatch, many of the females

that bred early in the season will be included in the May breeding population. A third smaller breeding peak in June is probably composed of late spawners with their second brood and, possibly, the largest 0-group females that are a little over a year old. The larvae hatch in 10–12 weeks at the beginning of the breeding season and in 5–6 weeks at the end. Most of the 2-group shrimps

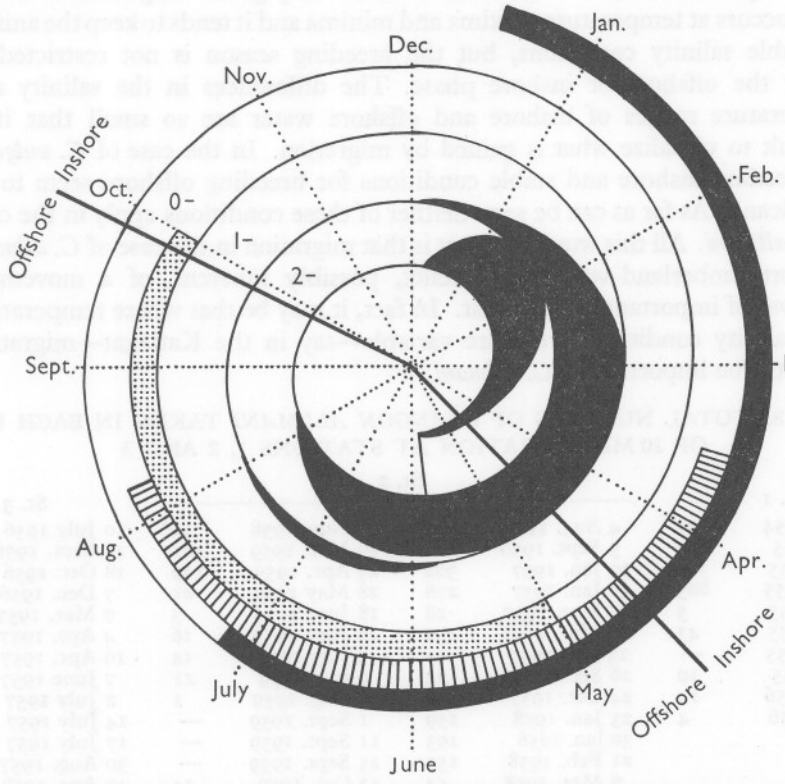

Fig. 15. Diagram representing the life cycle of a year-group. The outer black area is the period when the eggs forming the group were laid. The cross-hatched area is the period when the larvae were released and the dotted area when metamorphosis occurs. The inner black areas represent the period of egg-laying following maturity. The width of these areas gives some indication of the proportion of females with broods.

have died by the end of the breeding season (August) while newly metamorphosed larvae have joined the population. During April most of the *C. allmani* return to the deeper water, the movement coinciding with the minimum inshore temperature. A few smaller females remain inshore.

The life histories of *C. allmani* and *C. vulgaris* are very similar. The most striking difference between the two species is that when *C. vulgaris* migrates*

* Meredith (1952) reports that migration does not take place in the population in Liverpool Bay.

inshore *C. allmani* migrates offshore and vice versa. In the case of *C. vulgaris*, Havinga (1929, 1930), Broekema (1941) and others have shown that salinity, temperature and breeding are significant factors in this migration. While there are differences in temperature and salinity between the deep water at 20 fm. and that at 50 fm. off the Northumberland coast, in comparison with those experienced by *C. vulgaris* these are not very great. Migration of *C. allmani* occurs at temperature maxima and minima and it tends to keep the animal in stable salinity conditions, but the breeding season is not restricted to either the offshore or inshore phase. The differences in the salinity and temperature ranges of inshore and offshore water are so small that it is difficult to visualize what is gained by migration. In the case of *C. vulgaris* rich feeding inshore and stable conditions for breeding offshore seem to be significant. As far as can be seen neither of these conditions apply in the case of *C. allmani*. All this would suggest is that migration in the case of *C. allmani* in Northumberland waters is a relict, possibly inherent, of a movement that was of importance in the past. In fact, it may be that where temperature and salinity conditions are more variable—say in the Kattegat—migration may still be important to *C. allmani*.

TABLE 8. TOTAL NUMBERS OF *CRANGON ALLMANI* TAKEN IN EACH HAUL OF 20 MIN DURATION AT STATIONS 1, 2 AND 3

St. 1		St. 2				St. 3	
18 Nov. 1954	329	4 Aug. 1956	—	6 Nov. 1958	30*	10 July 1956	—
25 Jan. 1955	852	5 Sept. 1956	—	19 Mar. 1959	321	12 Sept. 1956	41
15 Feb. 1955	314	30 Jan. 1957	302	23 Apr. 1959	129	18 Oct. 1956	77
31 Mar. 1955	803	31 Jan. 1957	276	28 May 1959	81	7 Dec. 1956	138
29 Apr. 1955	5	1 Mar. 1957	28	18 June 1959	5	7 Mar. 1957	182
16 May 1955	43	28 Mar. 1957	172	29 June 1959	16	4 Apr. 1957	23
30 Aug. 1955	—	23 July 1957	—	3 July 1959	14	16 Apr. 1957	53
5 Oct. 1955	10	26 Sept. 1942	42	9 July 1959	11	7 June 1957	—
28 Mar. 1956	14	24 Oct. 1957	36	4 Aug. 1959	1	2 July 1957	9
19 Apr. 1956	4	23 Jan. 1958	159	1 Sept. 1959	—	14 July 1957	199
		30 Jan. 1958	193	11 Sept. 1959	—	17 July 1957	3
		21 Feb. 1958	153	25 Sept. 1959	—	30 Aug. 1957	11
		6 Mar. 1958	54	13 Oct. 1959	14	10 Apr. 1958	1
		25 Aug. 1958	4*	10 Nov. 1959	94	22 Sept. 1958	37
						26 May 1959	182
						1 July 1959	224
						11 Aug. 1959	322
						8 Sept. 1959	487
						24 Sept. 1959	118

* Two hauls.

SUMMARY

Since November 1954 the population of *C. allmani* off the Northumberland coast has been sampled at a number of stations.

The collections show that there is a prolonged breeding season from late December to early July. Most females produce at least two broods during each season. The time of development of the eggs of the second brood is half that of the first. Egg numbers vary from 400 to 7000 according to the size of the female and have a diameter of 390 μ throughout the season.

Growth rates and age are difficult to determine, but it is probable that *C. allmani* lives for 3–3½ years with a few females living at least one further year. Males are slightly smaller than the females.

Evidence for migration is discussed. There is an inshore movement in October and an offshore movement in April which appears to be related to temperature.

Examination of the stomach contents shows that *C. allmani* feeds predominantly on *Nephthys* and a variety of small crustacea. There is little difference in diet between inshore and offshore populations.

Details of the external morphology and development of secondary sexual characters are given.

Comparison is made with the life history of the closely related *C. vulgaris*.

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THE IDENTITY OF THE ASCIDIANS *STYELA MAMMICULATA* CARLISLE AND *S. CLAVA* HERDMAN

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(Text-fig. 1)

Carlisle (1954) described *Styela mammiculata*, a new species of stalked ascidian from the Plymouth area, and suggested that it had been brought into British waters, probably with oysters. Its recent discovery on other parts of the south coast of England (Houghton & Millar, 1960) supports the idea that it is an introduced species which is now spreading through a favourable environ-

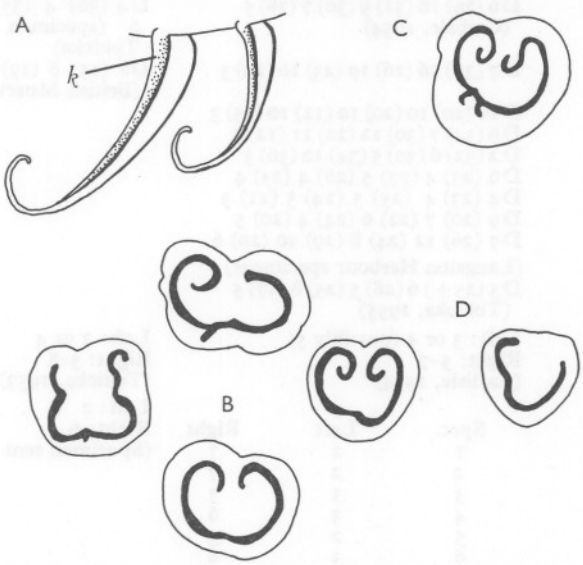

Fig. 1. A, oral tentacles of a specimen from Langston Harbour, to show keel (*k*). B, dorsal tubercles of specimens from Langston Harbour. C, dorsal tubercle of specimen of *S. clava* sent by Dr Tokioka. D, dorsal tubercle of specimen of *S. clava* from the British Museum.

ment. It is well, therefore, to consider whether this may not be a species known from another part of the world. Tokioka (1955) examined one of Carlisle's specimens and suggested that it fell within the range of variation of *S. clava* Herdman. As many specimens of *S. mammiculata* are now available, a more extensive comparison has been made and is reported in this paper.

I wish to thank Mr D. R. Houghton for specimens of *S. mammiculata* from Langston Harbour, Hants., Dr T. Tokioka for specimens of *S. clava* and for a translation of his Japanese paper (1955), and the British Museum (Natural History) for the loan of a specimen of *S. clava*.

Herdman's (1882) account of *S. clava* is not very detailed, but has been confirmed and amplified from the only one of Herdman's named specimens in the British Museum which was available for dissection.

TABLE 1. COMPARISON OF *STYELA MAMMICULATA* AND *S. CLAVA*

	S. mammiculata	*S. clava*
No. of oral tentacles	'About 40' (Carlisle, 1954) 40, 45, 47, 48, 48, 50, 65, 68 (Langston Harbour specimens) 33 (Tokioka, 1955)	'About 30' (Herdman, 1882) 'More than 45' (Tokioka, 1953) About 70 (specimen sent by Dr Tokioka) About 35 (British Museum specimen)
Branchial bars on right side	D 7 (30) 12 (36) 9 (32) 8 (30) 6 D 6 (29) 10 (31) 9 (30) 7 (28) 5 (Carlisle, 1954) D 7 (30) 16 (26) 19 (23) 10 (20) 5 D 10 (20) 10 (20) 10 (12) 10 (15) 3 D 6 (34) 7 (30) 12 (22) 11 (12) 5 D 2 (32) 6 (30) 5 (34) 12 (36) 3 D 6 (25) 4 (27) 5 (28) 4 (23) 4 D 4 (23) 4 (25) 5 (24) 5 (21) 3 D 9 (20) 7 (22) 6 (24) 4 (20) 5 D 7 (26) 12 (24) 8 (29) 10 (20) 6 (Langston Harbour specimens) D 5 (25+) 6 (28) 5 (25) 8 (17) 5 (Tokioka, 1955)	D1 (39) 4 (37) 5 (40) 5 (34) 3 (Tokioka, 1953) D 4 (36) 4 (35) 5 (42) 5 (20) 6 (specimen sent by Dr Tokioka) D8 (15) 6 (19) 7 (22) 7 (10) 3 (British Museum specimen)
No. of gonads	Left: 3 or 4 (possibly 5) Right: 5–7 (Carlisle, 1954)	Left: 3 or 4 Right: 5–8 (Tokioka, 1953)
	Spec. Left Right 1 2 7 2 2 7 3 3 5 4 3 6 5 2 5 6 3 6 7 2 6 (Langston Harbour specimens)	Left: 2 Right: 6 (Specimen sent by Dr Tokioka) Gonads not developed in British Museum specimen

S. mammiculata and *S. clava* cannot be distinguished by external form (Carlisle, 1954, fig. 1; Herdman, 1882, pl. XIX, fig. 9; Tokioka, 1953, pl. LXIV, fig. 6). I find that the oral tentacles of *S. mammiculata*, described by Carlisle as winged, not distinctly keeled, and all of one order of size, are in fact essentially similar in structure, number and arrangement to those of *S. clava* (Fig. 1, A, Table 1). The dorsal tubercle (Fig. 1, B, C, D; Carlisle,

1954, fig. 2E; Tokioka, 1953, pl. LXIV, fig. 9), the arrangement of branchial bars (Table 1), the number, structure and arrangement of the gonads (Table 1) and the form of the gut also fail to separate the species. In the absence of any other distinguishing features I conclude that *S. mammiculata* is a synonym of *S. clava*.

Hitherto *S. clava* has been known only from Japanese waters, the Sea of Okhotsk, and the coasts of Korea and Siberia. Within that area there are places with an annual fluctuation of sea temperature similar to that on the south coast of England. A species surviving accidental transport from the north-west Pacific to the English Channel might spread rapidly under favourable local conditions. This seems to have happened to *S. clava*, the first Japanese ascidian species known to have become established in British waters.

SUMMARY

A comparison of *Styela mammiculata* Carlisle with *S. clava* Herdman shows that they are synonymous. The name *S. clava* has priority.

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ON THE ORGANIC BINDING OF IODINE IN THE TUNIC OF *CIONA INTESTINALIS* L.

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(Text-figs. 1–3)

It is now known that organic binding of iodine takes place in the endostyle of *Ciona* (Barrington, 1957) and *Amphioxus* (Thomas, 1956; Barrington, 1958), and there is evidence that at least di-iodotyrosine and thyroxine are formed as a result of this process in *Ciona* (Barrington, 1959; Robertson, personal communication. Since this biosynthesis appears to be a specialized property of a restricted group of cells, it has been suggested (Barrington, 1959) that it is not a chance by-product of endostylar secretion but that the thyroidal products are a biochemical necessity for the animals concerned. Attention has been drawn also to the occurrence of iodine binding at the surface of the tunic (or test) of *Ciona* (Barrington, 1957), and it is the purpose of the present paper to present some analysis of this latter situation and to enquire as to its possible relationship with the endostylar activity.

The whole of this work has been carried out at Nottingham on animals sent from the Plymouth Laboratory of the Marine Biological Association, and we are indebted to the Supply Department of that Laboratory for the trouble taken in despatching them.

In addition to routine fixation in Bouin's fluid in sea water, followed by staining with the Azan technique, a variety of histochemical procedures have been used. These include chiefly the periodic acid/Schiff (PAS) technique, the Millon reaction (Lison, 1953), the coupled tetrazonium technique of Barnard & Danielli (1956 and personal communication), the alcian blue technique (Steedman, 1950; Lison, 1954) the ferric-ferricyanide technique of Chèvremont and Frédéricq (Lison, 1953), and the DDD method for sulphydryl and disulphide groups (Barrnet, 1953; Barrnet & Seligman, 1954).

HISTOLOGICAL AND HISTOCHEMICAL OBSERVATIONS

The ascidian tunic is bounded on the outside by a thin surface layer which it is convenient to term the 'cuticle' (Saint-Hilaire, 1931). Pérès (1948*a*, *b*), whose studies have been of the greatest value to us in formulating our own interpretation, has concluded that this is composed of pure protein, in contrast with the remainder of the tunic which he describes as formed of cellulose (tunicin) with some glycoprotein.

The cuticle (Fig. 1), when well developed, is conspicuous in Azan preparations as a layer which stains sometimes red, sometimes blue, and which shows no obvious structure apart from a thin membrane-like boundary at its upper and lower surfaces. Saint-Hilaire (1931) referred to the fact that many cells with large granules lie near the cuticle and, in his words, appear to adhere to it. In fact, the cuticle (Fig. 1A) is continued inwards into numerous flask-shaped extensions, each of which encloses one of these cells with its characteristic granule, the latter always staining brilliantly with azocarmine. In this region it is often difficult to decide whether or not the granule is actually

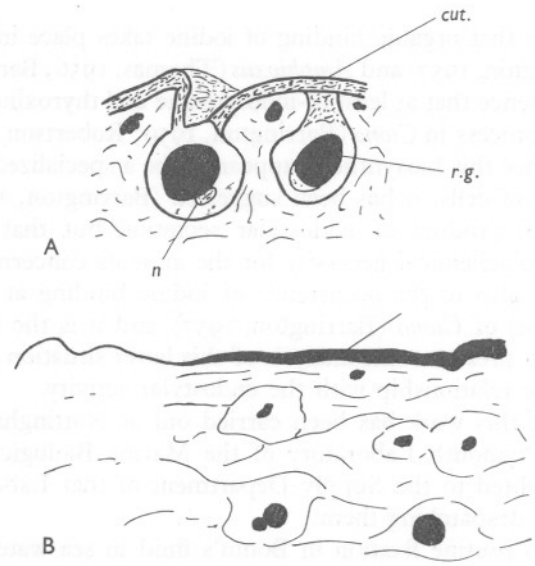

Fig. 1. A. Transverse section of the surface of the tunic of *Ciona*. B. Ditto, showing an early stage in the formation of the cuticle. *cut.*, cuticle; *n.*, nucleus of refringent granule; *r.g.*, refringent granule.

still enclosed in a cell, but similar granules are found in wandering cells throughout the tunic; in these the nucleus is clearly defined with the cytoplasm just distinguishable as a very thin bounding layer, and such features are also sometimes visible in the cuticular region (Fig. 1A). These are clearly the cells which Pérès describes as characterized by possessing a single large 'refringent granule', and we shall therefore use the latter term. According to him they are particularly concerned with the secretion of the cuticle, and our own observations support this view.

For example, the cuticle varies greatly in development from specimen to specimen. It may appear as no more than a very thin membrane, but in sections of such material (Fig. 1B) areas can be found where it is becoming much thicker, and at such points there is an accumulation of refringent

granules which look as though they are undergoing reduction or fragmentation. It seems evident that these are the source of the increased cuticular deposit, which they resemble in their staining reactions, and that this is why the granules and their cells become enclosed in extensions of the cuticle.

Pérès found that the cuticle and the refringent granules reacted positively to the Millon test, and in confirmation of this we have obtained a definite pink colour in the granules and a fainter one in the surface layer. The reaction has, however, proved rather weak, and we have found the coupled tetrazonium technique of Barnard & Danielli (1956) to give a more precise response, with the added advantage of permanence. With this method, we find that a positive red coloration is given by the refringent granules (more especially at their surface), as also by the cuticle. The remainder of the tunic is predominantly unstained, but the fibres are positive, as are also numerous fine particles, which may perhaps be fibre material. Blocking by benzoylation for 9 h almost completely eliminates this reaction, apart from an occasional weak response at restricted points of the cuticle. We therefore infer that the cuticle and refringent granules include protein, containing tyrosine and perhaps also histidine and tryptophan, and that this is also true of the fibres. Saint-Hilaire (1931) noted the presence of protein in the ascidian tunic, but, using the Millon test, found a good deal of variation between different genera, with a positive reaction from the whole of the tunic of *Halocynthia papillosa*, but none from the tunic of *Tethyum gyrosum*. The significance of such variations is not at present clear, and it will be desirable to investigate them further, particularly in relation to their possible influence upon the degree of iodine binding in different genera.

The results of the alcian blue test are in sharp contrast with the above, for the cuticle and the refringent granules are negative, while the remainder of the tunic, together with the fibres, are positive. This implies that acid mucopolysaccharides are present in the main body of the tunic but are absent from the cuticle and refringent granules, a result which is in agreement with Pérès's description of the former as differing from the latter in staining metachromatically with toluidine blue (presumably gamma metachromasia). He also uses the term 'glycoprotein' in this context, but in current terminology a positive alcian blue response and gamma metachromasia are held to be an indication specifically of acid mucopolysaccharides (Lison, 1953; Pearse, 1954).

With the PAS test, which was not used by Pérès, a positive reaction is given by the cuticle and by the refringent granules; in the rest of the tunic the fibres are positive, and there is a good deal of fine granulation which reacts in the same way, while the general matrix gives a very faint coloration. It seems clear from this response of the cuticle that it cannot be composed of pure protein, as Pérès supposed. Both it and the granules are negative to Sudan black, so that there is no evidence for the presence of lipoidal compounds

which might account for the response, and in view of this, and of the absence of acid mucopolysaccharides, it seems likely that the cuticle and granules must consist of protein associated with carbohydrate in some form of glycoprotein complex.

Because of this, and of the recent demonstration by Brunet & Carlisle (1958) of the presence of chitin in the tubes of the Pogonophora, it seemed necessary to re-examine the possibility of chitin being also responsible for the PAS-positive reaction in the cuticle of *Ciona*. For this purpose we have used the standard colour and solubility tests for chitosan as defined by Campbell (1929), using as test material the cuticle of *Ciona*, after removal of as much as possible of the underlying jelly, and comparing the reactions of this with those of *Flustra* (Hyman, 1958) and the cuticle of the locust, and also with samples of bacterial cellulose and of filter-paper.

After treatment for 20 min at 160° C in saturated potassium hydroxide the reactions of *Flustra* and of the locust cuticle were as expected; the material was coloured dark brown on the addition of the iodine solution, on adding 1% sulphuric acid it became dark blue by reflected light and violet by transmitted light, while on adding 75% sulphuric acid it became reddish-brown and dissolved. The material also dissolved rapidly in 3% acetic acid and the solution gave a conspicuous white precipitate on the addition of 1% sulphuric acid. The *Ciona* cuticle was coloured light brown by the iodine solution, on adding 1% sulphuric acid it became dark blue by reflected light but blue with a greenish tinge (and definitely not violet) by transmitted light, and on adding 75% sulphuric acid it became blue and dissolved. It would appear that these reactions must be largely due to the presence of cellulose (tunicin), the presence of this in the tunic being very well-established and readily demonstrable by the Schulze and cuprammonia tests. It is said (Campbell, 1929) that cellulose gives no colour either with the iodine solution or with 1% sulphuric acid, but we find that while filter-paper and bacterial cellulose, after alkali treatment, certainly give no colour with iodine they can develop a variable degree of blue-black colour on the addition of the acid. Thus the only positive indication of the presence of a substance other than cellulose in the *Ciona* cuticle after alkali treatment is the brown colour reaction which it gives in the presence of the iodine solution; it may be that this indicates the presence of some stable glycoprotein complex, but there is no evidence that it is chitin. This negative conclusion is reinforced by two additional observations. First, the cuticle gives no obvious response to treatment with 3% acetic acid and no white precipitate can be obtained from the latter by the addition of sulphuric acid. Secondly, Dr S. Wallwork of the Department of Chemistry of this University has been kind enough to carry out an X-ray diffraction study of the cuticle and finds no evidence for the presence of chitin in it. It may be added that earlier workers have obtained negative results from tests for chitin applied to the tunics of *Halocynthia papillosa*

(Saint-Hilaire, 1931) and *Phallusia mammillata* (Saint-Hilaire, 1931; Wester, 1910), and Rudall (1955) found no evidence for its presence in *Rhabdopleura* and the Enteropneusta.

Pérès obtained a positive response from the refringent granules with the Chèvremont and Frédéricq (ferric-ferricyanide) test, and concluded that they perhaps contained sulphydryl groups. We have ourselves obtained with this test a positive response both from the cuticle and the granules, but we have been unable to secure satisfactory blocking in the control preparations. In consequence of this we have preferred to rely upon the more recently developed DDD methods (Barrnett, 1953; Barrnet & Seligman, 1954), and have obtained positive results with them. The procedure for disulphide groups evoked a very faint but definite positive reaction in the cuticle and granules, although the cuticular ingrowths around the latter seem mostly negative. With the procedure for sulphydryl groups a positive response is given by the cuticle, granules and cuticular ingrowths. This reaction, which can be satisfactorily blocked by the method recommended by Barrnet & Seligman (1954), is slightly stronger than that obtained with the disulphide procedure, but the difference is too slight to justify much emphasis. Using the procedure for demonstrating simultaneously both sulphydryl and disulphide groups, with sodium thioglycollate as the reducing agent, a well-defined purple colour is obtained from the cuticle granules and ingrowths, this reaction being decidedly stronger than either of the previous ones. The fibres in the rest of the tunic are very faintly coloured, but it is doubtful whether this could be regarded as a positive response. Slides of sections of the skin of the mouse were processed simultaneously with the tunic sections, and it was apparent that the reactions in the cuticle and granules of the latter, although quite definitely positive, were substantially weaker than those given by regions of relatively high sulphur content such as are found in the stratum corneum and hair follicles of the mouse.

CHROMATOGRAPHY

For the identification of the products of iodination we have made use of radioactive iodine. Animals were immersed for 48 h in sea-water containing 200 μC of ^{131}I per litre, and paper chromatography of the tunics was then carried out according to the procedure of Bowden, Maclagen & Wilkinson (1955), with *tert.*-amyl alcohol/2N ammonia as solvent (Gleason, 1955). Potassium iodide, di-iodotyrosine, tri-iodothyronine and thyroxine were usually added as carriers to the tissue extracts either before distillation or when the drops were placed on the paper, but in some cases a mixture of these was run side by side with the extracts and none was added to the latter. When the run had proceeded sufficiently far the chromatogram was dried and the distribution of the radioactive iodinated compounds recorded by leaving the paper in contact with X-ray film; the latter was developed and fixed and then

superimposed on the chromatogram after the distribution on this of the carrier spots had been visualized with the ceric sulphate-arsenious acid reaction (Bowden *et al.*, 1955). Permanent records of these spots were made either by tracing or by ultra-violet exposure.

The material consisted either of the whole tunic, or of the surface layer remaining after as much as possible of the gelatinous tunicin had been removed, and the method of preparing extracts of this for chromatography was varied in the following ways:

(*a*) Material, cut into small pieces, was treated at 37° C for 48 h with buffered trypsin solution. After centrifuging and ether extraction, the supernatant was extracted with butanol/HCl. Chromatography of this extract would reveal iodinated amino acids released by the tryptic hydrolysis of protein present in the tunic, together with any free amino acids.

(*b*) Material, cut into small pieces, was extracted at 4° C for 24 h in saline, a few drops of toluene being added. After centrifuging and ether extraction, the supernatant was extracted with butanol/HCl for chromatography; this would reveal any free iodinated amino acids present in the tunic, together, of course, with any which might have been liberated by autolytic action.

(*c*) The fluid residue left after the butanol/HCl extraction in procedure '*b*' was hydrolysed at 37° C for 48 h by the addition of trypsin solution buffered to pH 8·5, and was then extracted with butanol/HCl. Chromatography of the extract would reveal iodinated amino acids released by hydrolysis of any saline-soluble proteins or polypeptides which were present in the original saline extract.

(*d*) The solid centrifugate from procedure '*b*' was treated with N-NaOH for 5 h at 50° C; after centrifuging and ether extraction, the supernatant was extracted with butanol/HCl. Chromatography of the extract would reveal iodinated amino acids arising from the alkaline hydrolysis of any saline-insoluble protein present in the tunic.

Results

A number of preliminary runs were made with procedure '*a*' in order to standardize the technique, and the resultant chromatograms gave from the beginning clear evidence for the presence of di-iodotyrosine and thyroxine, in addition to iodide. In a series of four definitive runs, each from a different batch of animals, di-iodotyrosine was clearly present in all, while thyroxine was detectible in three (Fig. 2). There was a suggestion also of the presence of tri-iodothyronine, but the separation in this terminal region of the chromatogram was unsatisfactory and the matter needs further study before any conclusion can be drawn. It has been common in our chromatograms for an additional substance to be closely associated with the iodide, and this, too, needs further study.

As regards the saline extracts (procedure '*b*'), a definitive set of three runs (from three separate batches of animals) showed that iodide was clearly demonstrable, as would be expected (Fig. 3). Iodinated amino acids were, however, absent from two, and there was no more than a doubtful trace of di-iodotyrosine in the third. After tryptic hydrolysis of these extracts

(procedure '*c*'), iodinated amino acids were still absent from the two mentioned (Fig. 3), while the third showed some di-iodotyrosine and a doubtful trace of thyroxine.

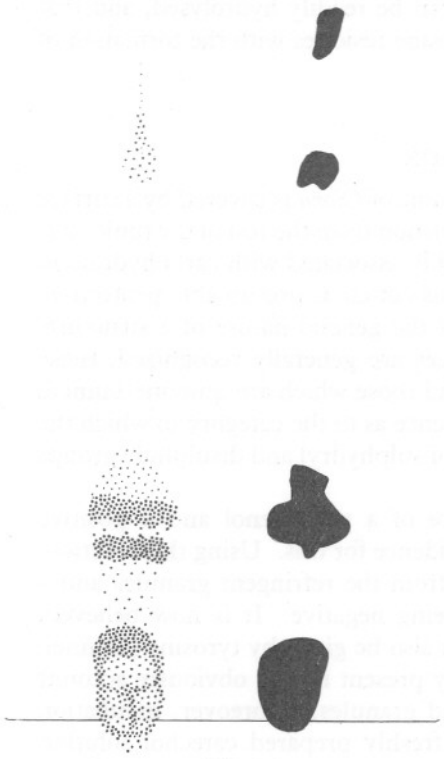

Fig. 2

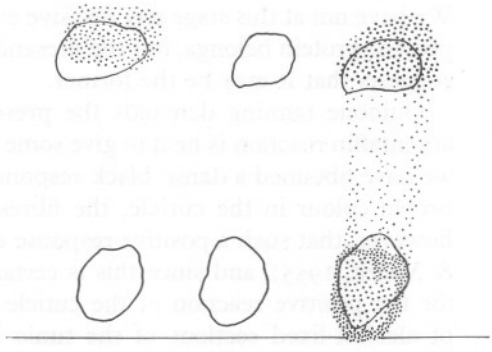

Fig. 3

Fig. 2. Tracings of chromatograms of (to the right) a carrier mixture, showing (reading from the bottom upwards), di-iodotyrosine, iodide, thyroxine and tri-iodothyronine, and (to the left) an extract of the tunic of *Ciona* (procedure '*a*'). Both drops were run in parallel on the same paper. The chromatogram of the carrier mixture was recorded by ultra-violet exposure and that of the tunic by exposure on X-ray film of the sites of radioactive iodine. For further explanation, see text.

Fig. 3. Tracings of chromatograms of extracts of the tunic of *Ciona*, procedure '*b*' to the left, procedure '*c*' in the centre and procedure '*d*' to the right. A drop of carrier mixture was added to each drop on the paper. The sites of radioactive iodine are shown by stippling and of the carrier substances by simple outline (di-iodotyrosine, iodide and thyroxine, reading from the bottom upwards). For further explanation, see text.

By contrast with this, NaOH hydrolysis of the saline-insoluble residue left after these extractions (procedure '*d*') gave clear evidence of the presence of iodide, di-iodotyrosine and thyroxine (Fig. 3), and the last of these seemed a little more readily detectible after this procedure than after tryptic hydrolysis (procedure '*a*'). The tracings shown in Fig. 3 illustrate the results obtained

with parallel runs of each of the procedures '*b*', '*c*' and '*d*', using extracts derived from the same batch of material as a starting point. We conclude from the results as a whole that iodine is bound in the surface layer of the tunic mainly to saline-insoluble protein which can be readily hydrolysed, and that the binding involves the iodination of tyrosine residues with the formation of at least di-iodotyrosine and thyroxine.

DISCUSSION

Our observations clearly confirm that the tunic of *Ciona* is covered by a surface layer, or cuticle, which is distinct in composition from the rest of the tunic; it is certainly rich in protein, but this is probably associated with carbohydrate in a glycoprotein complex. The function of this cuticle is presumably protective, and one would expect its protein to be of the general nature of a structural protein. Two categories of such substances are generally recognized, those which are bonded by disulphide groups and those which are quinone-tanned. We have not at this stage any decisive evidence as to the category to which the present protein belongs, but the presence of sulphydryl and disulphide groups suggests that it may be the former.

Quinone tanning demands the presence of a polyphenol and a positive argentaffin reaction is held to give some evidence for this. Using this reaction, we have obtained a dense black response from the refringent granules and a brown colour in the cuticle, the fibres being negative. It is now believed, however, that such a positive response can also be given by tyrosine (Dennell & Malek, 1955), and since this is certainly present it may obviously account for the positive reaction of the cuticle and granules. Moreover, incubation of alcohol-fixed sections of the tunic in freshly prepared catechol solution (Smyth, 1954) has given no evidence for the presence of polyphenol oxidase, while the pale colour of the surface does not in itself suggest that quinone tanning is involved in its formation. While, therefore, a final decision on this point must await the study of a wider range of ascidians, the present evidence certainly favours the view that the surface protein is a keratin-like substance.

Since it appears to follow from the chromatography results that the iodine binding at the surface is associated with this protein, it becomes possible to relate the situation with that which has been noted in many invertebrates. The binding of iodine by scleroproteins has been recorded in a number of groups (Gorbman, 1955; Roche & Michel, 1951). It is certainly true of some of these, and probably of all, that the iodine is bound by the tyrosine residues, for the formation of mono-iodotyrosine and di-iodotyrosine has been clearly demonstrated. Thyroxine can also be formed, and it has been suggested that the yield of this is peculiar to each protein, being determined by the position of its tyrosine residues and the consequent facility for polymerization. In the gorgonids and sponges, for example, where the proteins concerned are

pseudo-keratins (Roche & Michel, 1951), only traces of thyroxine have been demonstrated; presumably, therefore, the architecture of the protein molecules of the cuticle of *Ciona* is somewhat more favourable for the formation of this product than is that of the scleroproteins of those groups.

Such considerations bring us to the question as to what relationship, if any, exists between the iodine binding in the cuticle of *Ciona* and that which has been shown (Barrington, 1957) to be associated in the endostyle with a particular group of acid mucopolysaccharide-secreting cells. It may well be, of course, that the co-existence of these two types of iodine binding is entirely fortuitous, but there is another line of thought which bears on this problem. Hecht (1918) has given some reason for supposing that the surface of the tunic is being continuously worn away and replaced. Our observations provide a basis for such a process, for the accumulation of the refringent granules at the surface, and their enclosure by cuticular material, show that continuous deposition of the protein could readily occur. It is worth noting here, incidentally, that according to Roche & Michel (1951) iodination in invertebrate pseudo-keratins occurs most abundantly in the young and rapidly growing parts, so that continued deposition of new protein at the surface of the tunic might well favour the occurrence of iodination there. Now it has been suggested (Barrington, 1959) that the wearing away of the cuticle would result in the release into the water of an iodinated protein which could easily enter the alimentary canal with the food particles carried in by the ciliary currents, particularly since the animals concerned are sedentary and gregarious (while, of course, other ascidian genera are colonial), and that in this way the tunicates might have come to utilize the products of iodination and to have become dependent upon them. Theoretically, this could have been a starting point for the subsequent evolution in the endostyle of a group of cells specialized for the more efficient production of these iodinated products and so, ultimately, for the origin of the thyroid gland as a derivative of that organ.

This argument requires that the animals should be able to digest the protein and so release the iodinated amino acids, and our present results show that this would, in fact, be possible. Scleroproteins are in general thought of as being proteins which are especially resistant to enzymic digestion, but the softer pseudo-keratins are much less resistant than are the hard eukeratins, as much as 25–60% being dissolved by treatment with pepsin and trypsin (Block & Bolling, 1939). Our chromatographic results show that di-iodotyrosine and thyroxine are readily released from the cuticle by tryptic digestion as well as by treatment with N-NaOH. This suggests that we may here be dealing with a soft pseudo-keratin, although it must be emphasized that information as to the amino-acid composition of the cuticle is necessary before this can be established with any assurance. What is clear, however, is that the protein could be digested under physiological conditions, and that its iodinated

residues could be taken up by the animal. Here, then, is a possibility, and at present it is no more than that, of visualizing how the iodination of tyrosine, beginning as a chance by-product of the organization of the surface of the tunic, might have become incorporated into the normal biochemical processes of the tunicates. Even if this possibility is accepted, however, the extension of it to provide an explanation of the origin of the thyroid gland could only be justified if the tunicates are regarded as a basal group from which the vertebrates were derived. Such a view has been widely favoured, but it is not the only one (Bone, 1960), and the matter is raised here primarily because it is at least certain that the facts relating to the distribution of iodine-binding capacity in the Protochordata must be incorporated into any general theory of the origin of vertebrates.

We are greatly indebted to Dr Hamish Robertson, of the Department of Agricultural Chemistry, University of Aberdeen, for guidance in the application of paper chromatography to the identification of thyroidal compounds, and to Dr S. Wallwork, of the Department of Chemistry, University of Nottingham, for carrying out an X-ray diffraction study of the cuticle.

SUMMARY

Organic binding of iodine occurs at the surface of the tunic of *Ciona* with the formation of at least di-iodotyrosine and thyroxine. This process is associated with the presence of a cuticle which is rich in protein, and which contains —SH and S—S groups and probably also some carbohydrate. The protein is largely insoluble in saline, but is readily hydrolysed by trypsin or by N-NaOH with the consequent release of the iodinated amino acids. Attention is drawn to the possible bearing of this situation on the evolution of thyroidal biosynthesis in the Chordata.

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CHEMICAL CHANGES IN SEA WATER OFF PLYMOUTH DURING 1959

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(Text-figs. 1–3)

Analyses of sea water collected during 1959 at the International Hydrographic Station E 1 (lat. 50° 02′ N., long. 4° 22′ W.) are given here in the same form as earlier reports (Armstrong, 1954, 1955, 1957, 1958; Armstrong & Butler, 1959, 1960). The methods of collection and analysis remain the same. Salinities were determined by the Government Chemist, Department of Scientific and Industrial Research. We wish once more to thank Lt.-Cdr. C. A. Hoodless, D.S.C. and the crew of R.V. 'Sarsia', and Capt. W. J. Creese and the crew of R.V. 'Sula' for help at sea.

RESULTS

Temperature and salinity

The vertical distribution of temperature during the year is shown in Fig. 1. The lowest surface temperature was 9·37° C on 10 February; the highest was 18·13° C on 11 August. The surface was appreciably warmer than the bottom in April, and by 12 May a well-marked thermocline at 14 m had developed. It varied between 15 and 23 m in depth during the summer, and vertical mixing was not complete even in October.

Some changes in salinity, suggestive of changes in water mass, occurred in September and October. In August the mean salinity in the water column was 35·07‰ with no significant variation with depth. This changed to 35·11 on 8 September, the increase being accountable to values of 35·19, 35·18 and 35·15 at 0, 5 and 10 m. The mean further increased to 35·19 on 13 October, with values of 35·21 and 35·23 at 50 and 70 m. At the same time mean temperature increased from 14·71 to 15·67° C and silicate decreased from 3·39 to 3·00 μg atom Si/l.

Phosphate

The vertical distribution is shown in Fig. 2, and integral mean concentrations in Table 1. The winter maximum found in January and February was 0·50 μg atom P/l, which is somewhat lower than in the last 3 or 4 years. Consistently low values of 0·08–0·10 μg atom P/l. were found in the upper

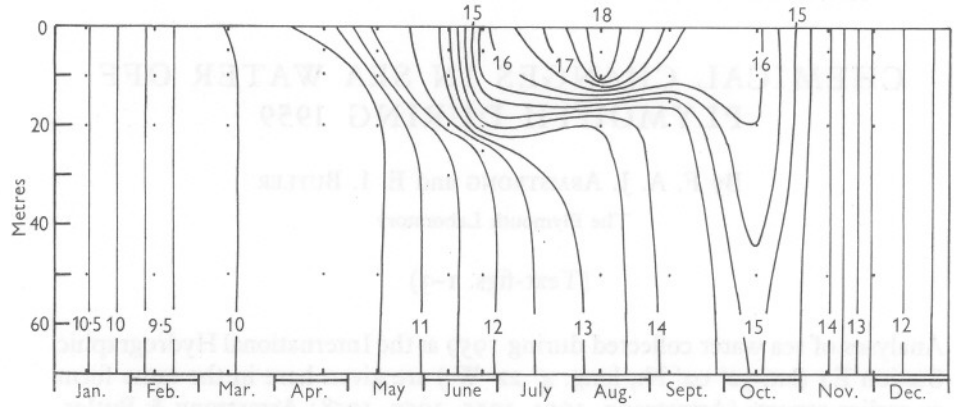

Fig. 1. Vertical temperature distribution at International Hydrographic Station E 1, 1959. Contour lines at 0·5° C intervals.

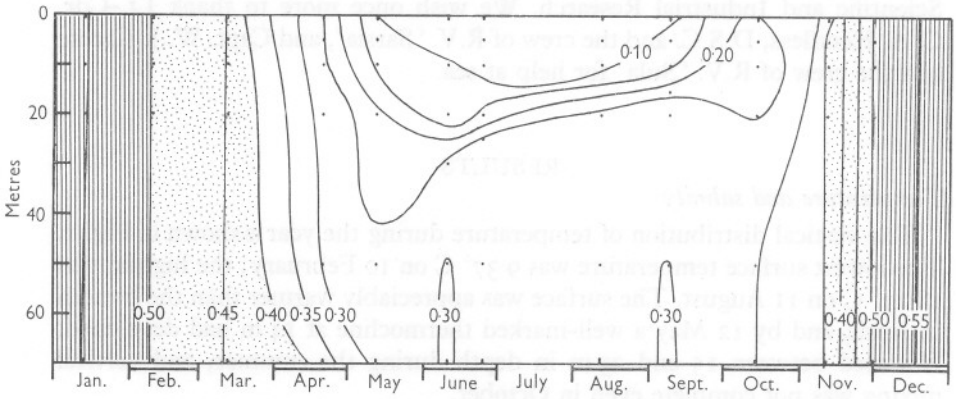

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E 1, 1959. Contour lines at 0·05 μg atom P/l. intervals.

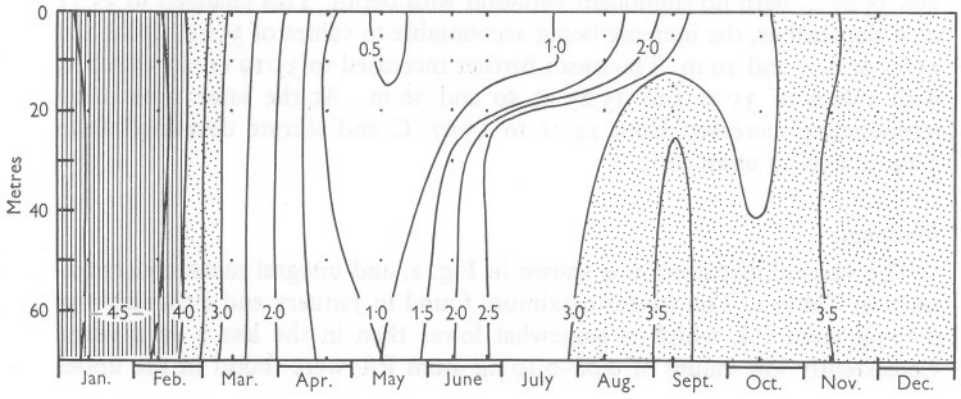

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E 1, 1959. Contour lines at 0·5 μg atom Si/l. intervals.

10 m from May to September. The vertical distribution did not become uniform until 11 November.

Total phosphorus

Determinations made in January, February and March showed the highest values in January. The value 1·36 for the ratio of 'total' to 'inorganic' phosphorus was again unusually high, being the same as in 1958 (Armstrong & Butler, 1959).

Silicate

Vertical distribution is shown in Fig. 3, and integral mean concentrations in Table 1. The winter maximum found was 4·83 μg atom Si/l. in January, and is the highest value recorded since 1950 when the present series of observations started. Silicate had decreased very considerably throughout the water column by 12 May but summer values were not as low as might have been expected, since the summer was unusually sunny. In fact, silicate increased each month during June to September.

TABLE 1. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1, 1959

Date	Phosphate (μg/atom P/l.)	Total P (μg atom P/l.)	Silicate (μg atom Si/l.)
13 Jan.	0·50	0·68	4·83
10 Feb.	0·50	0·63	4·62
12 Mar.	0·45	0·61	2·83
20 Apr.	0·29	—	1·06
12 May	0·22	—	0·68
10 June	0·23	—	1·54
24 June	0·22	—	1·99
11 Aug.	0·23	—	2·67
8 Sept.	0·28	—	3·39
13 Oct.	0·27	—	3·00
11 Nov.	0·36	—	3·59
1 Dec.	0·50	—	3·74

Integral mean concentrations

Some of the values have been discussed. The spring decreases were: phosphate 0·28 μg atom P/l., silicate 4·15 μg/atom Si/l.

SUMMARY

The results of analysis of sea water samples from the International Hydrographic Station E1 during 1959 are given in graphical form and as integral mean values for the water column of 70 m. The winter maximum values were found in January. The spring decreases of nutrients were: phosphate 0·28 μg atom P/l., silicate 4·15 μg atom Si/l.

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STUDIES ON LUMINESCENCE. ON THE SUBOCULAR LIGHT-ORGANS OF STOMIATOID FISHES

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(Text-figs. 1–10)

Many stomiatoid fishes possess a peculiar light-organ below and behind the eye, as well as other kinds of photophores. This light-organ, of diagnostic importance, is termed the subocular, postocular or cheek-organ. Stomiatoid fishes, suborder Stomiatoidei, form a suborder of the Isospondyli. Subocular organs are found in the following groups:

Superfamily Stomiatoidae
Stomiatidae and Chauliodontidae
Superfamily Astronesthoidae (= Gymnophotodermi)
Astronesthidae, Melanostomiatidae and Idiacanthidae.

Over the course of the past 8 years I have collected specimens of species belonging to each of the above families, and this material has made possible a comparative study of the subocular organs of the Stomiatoidei.

MATERIALS AND METHODS

Specimens of stomiatoid fishes were obtained from deep-sea catches of the R.R.S. 'Discovery II' and R.V. 'Sarsia'. I am indebted to the Director of the National Institute of Oceanography for the former material. The following species were examined.

Stomiatidae
Stomias brevibarbatus Ege, 1918. One specimen, 'Discovery' station No. 3354.
S. ferox Reinhardt (Zugmayer, 1911; Ege, 1918). Four specimens, 'Sarsia' stations No. 7/1957, No. 11 (Kon & Fisher)/1959, No. 15/1959.
Chauliodontidae
Chauliodus sloani Schneider (Regan & Trewavas, 1929). One specimen, 'Discovery' station No. 3051.
Astronesthidae
Astronesthes elucens Brauer (Parr, 1927). Two specimens, 'Sarsia' stations Nos. 23/1957, 14/1959.

Astronesthes richardsoni Poey (Parr, 1927). One specimen, 'Sarsia' station No. 12/1959.

Melanostomiatidae

Photostomias guernei Collett (Parr, 1927). One specimen, 'Discovery' station No. 3254.

Idiacanthidae

Idiacanthus fasciola Peters (Parr, 1927). One specimen, 'Discovery' station No. 3354.

Station details

'Discovery' station No. 3051. 26 August 1952. 39° 29′ N., 9° 50′ W. TYF oblique. Estimated depth 700 m.

'Discovery' station No. 3354. See Nicol (1958).

'Sarsia' station No. 23/1957. See Nicol (1958).

'Sarsia' station No. 7/1957. 20 June 1957. 47° 07′ N., 6° 06′ W. Isaacs Kidd trawl oblique. 1800 m of wire out.

'Sarsia' station No. 11 (Kon & Fisher)/1959. 11 October, 1959. 44° 19′ N, 3° 56′ W. Isaacs Kidd trawl oblique. 1800 m. of wire out.

'Sarsia' station No. 12/1959. 9 June 1959. 46° 59′ N., 6° 03′ W. to 47° 01′ N., 6° 00′ W. Isaacs Kidd trawl oblique. 915 m of wire out.

'Sarsia' station No. 14/1959. 10 June 1959. 46° 59′ N., 6° 02′ W. to 46° 57′ N., 6° 03′ W. Isaacs Kidd trawl oblique. 1830 m of wire out.

'Sarsia' station No. 15/1959. 10 June 1959. 46° 47′ N., 6° 03′ W. Isaacs Kidd trawl oblique. 1829 m of wire out.

Treatment

All the stomiatoid fishes listed above were dead when taken from the bucket, or were obtained from preserved collections. They were preserved in formalin and the majority were post-fixed—in Heidenhain's Susa, Bouin's or Zenker's fluids. When necessary, decalcification was carried out with weak formic acid. Embedding media were paraffin wax, polyester wax and celloidin.

Stains used were Ehrlich's haematoxylin and eosin plus Biebrich scarlet; Ehrlich's haematoxylin and eosin plus azure II; a modification of Masson's trichrome consisting of iron haematoxylin, aniline blue and Biebrich scarlet (M 1); a modification of Masson's trichrome consisting of iron haematoxylin, fast green FCF and Biebrich scarlet (M2), iron haematoxylin and orange G; Heidenhain's azan; Holmes's silver.

DESCRIPTIVE HISTOLOGY

In all the stomiatoid fishes examined the suborbital light-organs have the following fundamental plan. A dense mass of photogenic tissue lies underneath the skin. The skin over the light-organ forms a clear window and is separated from the light-organ proper by a narrow space. Investing the back (i.e. the internal surface) of the photogenic mass is an inner tunic or reflector, then a layer of dark pigment. A muscle inserted on the light-organ runs behind and underneath the organ.

The dimensions of the light-organs, and of their component parts, given in the following sections, refer to the specimens which I have examined and

are presented merely to give some idea of the degree of magnitude of the structures under consideration. Since deep-sea fish, in illustrations, often seem much larger than they actually are, I have shown the size range of each species, as given in the pertinent literature.

The light-organs of most of the species examined are very similar to each other, the chief exception being *Idiacanthus*. To obviate repetition, the subocular organ of *Astronesthes elucens*, selected as a representative type, is described in detail. Peculiarities and differences encountered in the light-organs of the other species are then presented.

A. elucens Brauer. 146–197 mm. The subocular organ is a small, oval, white structure lying below and behind the eye. On one side of the head of one fish there is a small accessory organ in front of the main subocular organ. External dimensions are 1·5 mm long and 0·8 mm high. The white surfaces of the organs are exposed, i.e. the organs are open in both specimens examined.

The subocular organ proper, i.e. the photogenic mass plus reflector, is beaker-shaped in transverse section (Fig. 1). The outer surface is convex. Dimensions are 0·7 mm high and 0·65 mm deep.

The skin over the light-organ is 10–20μ thick. It consists of a thin epidermis made of stratified squamous epithelial cells, and an underlying dense dermis staining with aniline blue. A space between the dermis and the light-organ ranges from 12 to 100 μ across.

A thin sheath of connective tissue over the outer face of the photogenic mass is 5–10 μ thick. It consists of a dense layer of fibres staining with aniline blue. A little loose connective tissue, also staining faintly with aniline blue, lies over this outer sheath. The outer sheath and loose connective tissue are continuous with loose connective tissue on either side of the light-organ.

The centre of the light-organ is occupied by a mass of glandular photogenic tissue. This is a compact accumulation of cells arranged in cords or circlets. The photocytes are polygonal in section, about 10 μ in diameter, and each contains a central oval nucleus. Around the circumference of the photogenic mass the photocytes appear elongate, with the nucleus in the peripheral half of the cell (i.e. the half of the cell towards the circumference of the photogenic mass). The cytoplasm is granular and stains as follows: M 1, purple (same colour as muscle); eosin and Biebrich scarlet, red; eosin-azure, centre of cell pink, periphery blue; orange G, orange. In photocytes stained with Ehrlich's haematoxylin and eosin, cytoplasmic differentiation appears as follows. Peripheral photocytes have a homogeneous basic cytoplasm, staining blue with haematoxylin below the nucleus. Above the nucleus the cytoplasm is packed with eosinophilic granules. More central cells have a blue peripheral band, tenuous to very broad, about the cell periphery. Within this is red eosinophilic granular material. These apparent differences may result from photocytes being cut at different levels. In this event all photocytes have a homogeneous basiphilic ground cytoplasm, conspicuous at the cell periphery

and below the nucleus; the centre of the cell above the nucleus is loaded with acidophilic granules.

The reflector layer, backing the photogenic mass, is 30–60 μ thick. It contains very dense tissue which shines blue by reflected light, and contains some kind of reflecting pigment. By transmitted light the unstained tissue appears light yellow-brown. The reflecting pigment is missing in many

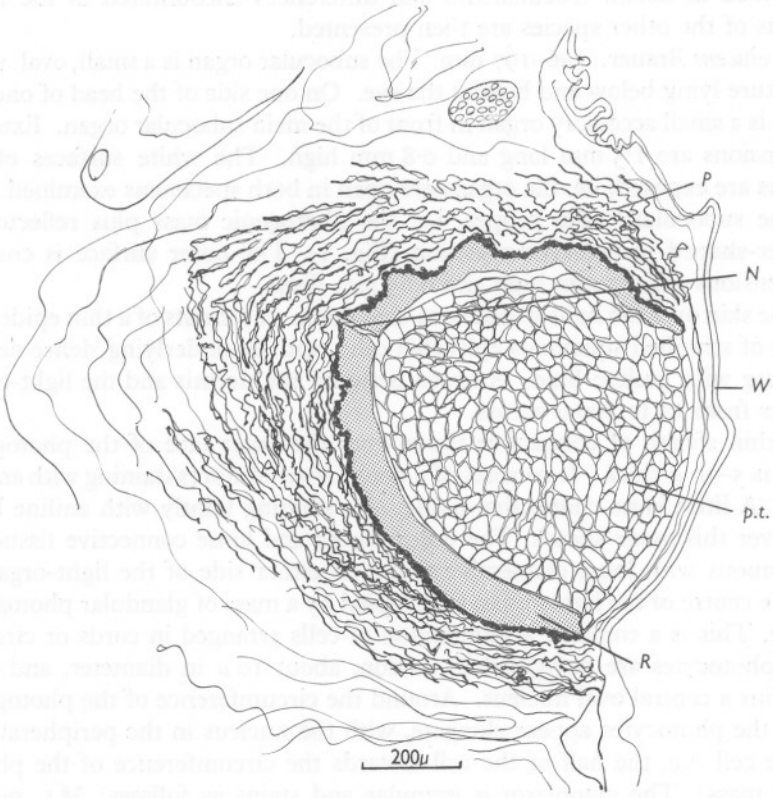

Fig. 1. Transverse vertical section through a subocular light-organ of *Astronesthes elucens*. (*N*, nerve. *P*, pigment. *p.t.*, photogenic tissue. *R*, reflector. *W*, clear window.

sections, dissolved out, perhaps, by some of the staining reagents. The reflecting layer appears to consist of long thin cells. Nuclei are elongate, thin and fusiform. Staining affinities of the tissue are poor: light blue with aniline blue; faint pink with eosin. Blood vessels and at least one nerve penetrate the reflector to supply the photogenic tissue within.

Behind (i.e. internal to) the reflector is a wide area of very loose connective tissue containing numerous pigmented cells. These possess dark yellow-brown

granules. Some pigmented cells are conspicuously oriented as a unicellular dark sheet immediately behind (internal to) the reflector.

Below the reflector there is a cleft in the pigmented connective tissue, this cleft being continuous with the space in front of the light-organ. There are pigmented cells in the loose connective tissue below the cleft. A long strap-like muscle runs down through the pigmented tissue at the back of the organ, and is inserted in the loose connective tissue underneath the organ, towards the external surface, as described by Brauer (1904, 1908). This muscle passes dorsally, behind the eye, between two sheets of the m. adductor mandibulae, to its origin on the hyomandibula. It is a striated muscle having more slender fibres than the m. adductor mandibulae, from which it is possibly derived.

Astronesthes richardsoni Poey. 150–234 mm. The subocular organs of this fish are rather large, 3·2 mm long and 1·5 mm high. Each organ is oblong in shape and shows as a conspicuous white object against the surrounding skin. In this specimen both organs are exposed, i.e. they are in the 'open' position.

The light-organ proper is lenticular in section, the outer surface being particularly convex (Fig. 2). Dimensions are 1·8 mm high and 1 mm thick. A thin connective tissue sheath covers the outer surface of the photogenic mass.

The photogenic tissue is a dense mass of closely packed glandular cells. These are aggregated into groups, appearing as bands or rosettes in section. They are polyhedral in shape, about 12 μ in size, except at the outer margin of the photogenic mass, described below. The cytoplasm is granular, and generally stains with eosin and orange G. An outer margin or marginal crescent-shaped area of some cells is darker than the centre, and has taken up some haematoxylin.

On the front of the photogenic mass, beginning at the outer margin of the reflector, the photogenic tissue shows another pattern. Externally there is a regular unicellular layer of glandular cells, forming a simple columnar or cuboidal epithelium. The nuclei lie at the outer ends of the cells, against the external surfaces. There is a granular eosinophilic cytoplasm, which stains less intensely in the external region of the cell, and more intensely internally. Inside this layer is a region, one or two cells deep, in which the photocytes appear highly vacuolated, each cell containing a huge vacuole or a poorly staining globular area. With Heidenhain-azan, the outermost cells of the photogenic mass stain blue.

The inner tunic contains reflecting pigment. Nerves and blood vessels penetrate the pigment and reflector layers to invade the photogenic tissue. The muscle to the light-organ is inserted in the connective tissue sheath over the external surface of the photogenic mass.

Stomias brevibarbatus Ege. 39–100 mm (excluding caudal fin). In the specimen available, both subocular organs are rotated equally so that most of the light-emitting surface faces downwards and is concealed; the exposed surface is dark (Fig. 3).

In a transverse section (vertically across the head) the photogenic mass plus tunic is almost circular, 372 μ high and 348 μ deep (Fig. 4). The clear skin over the organ consists of thin stratified squamous epithelium and a little loose connective tissue.

The photocytes are 6–8 μ in size, polygonal, and aggregated into cords or bands. The cytoplasm is dense, granular and acidophilic. No reflecting pigment was observed in the inner tunic. Below the photogenic mass is a cleft or pocket in the connective tissue and underneath the cleft are several layers of pigmented cells.

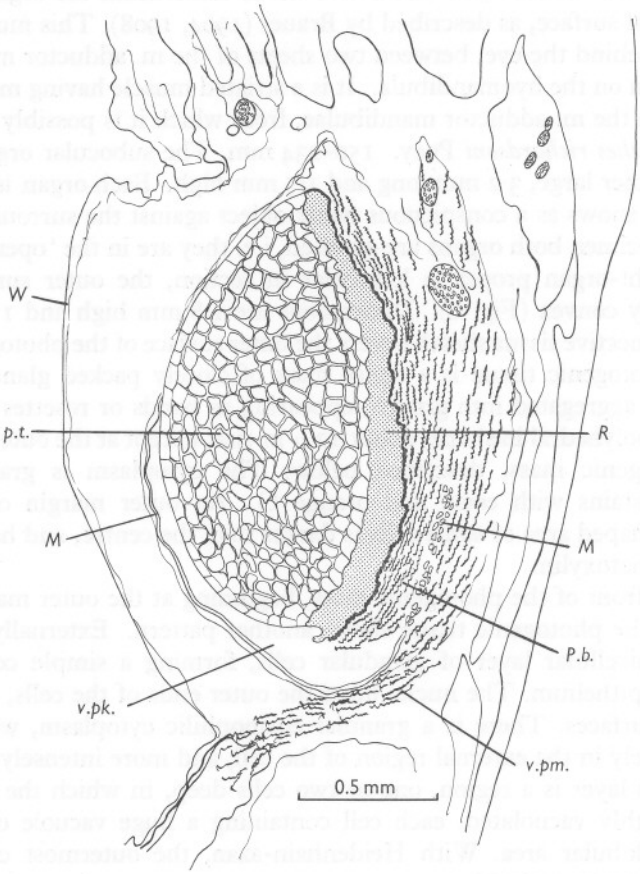

Fig. 2. Transverse vertical section through a subocular light-organ of *Astronesthes richardsoni*. *M*, muscle. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *R*, reflector. *v.pm.* ventral pigment. *v.pk.*, ventral pocket. *W*, clear window.

Stomias ferox Reinhardt. 50–170 mm (exclusive of caudal fin). Four specimens were available, two large and two small. In the two larger specimens

the subocular light organs were in the exposed position, i.e. the light-emitting surfaces faced outwards. The organ appeared as a white ovate or pyriform area in a densely pigmented surround. Dimensions were 0·68 mm across and 0·96 mm high, and 0·60 mm across and 0·85 mm high. In the two smaller specimens the subocular light-organs were not visible externally.

In vertical section the photogenic mass is bowl-shaped, with a strongly convex inner, and a slightly convex outer, surface (Fig. 5). Dimensions of the photogenic mass plus pigmented backing are 0·87 mm tall and 0·48 mm thick. Investing the photogenic mass is a thin sheath of connective tissue. The photocytes have a clear ground cytoplasm and contain many small granules, about 1 μ in size, staining with orange G and azocarmine.

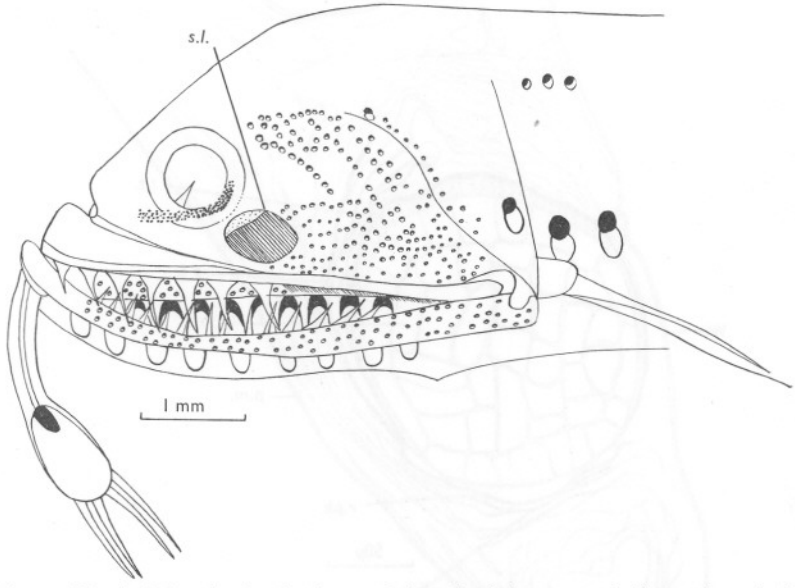

Fig. 3. Head of *Stomias brevibarbatus*. Subocular light-organs (*s.l.*) mostly occluded (rolled downwards.)

Chauliodus sloani Schneider. 20–270 mm (excluding caudal fin). Both subocular organs have the light-emitting surface exposed. Dimensions are 0·38 mm long and 0·29 mm high, including the narrow pigmented surround.

In transverse section, the photogenic organ proper (photogenic mass plus inner tunic and pigmented sheath) is beaker shaped, with a convex outer surface (Fig. 6). It is 384 μ high and 325 μ thick. The photogenic cells are elongate, radiating inwards towards the centre from the margin. They are about 6 μ in diameter, the length is uncertain, perhaps 130–140 μ. The cytoplasm is packed with granular inclusions staining red with Biebrich scarlet.

The internal tunic consists of loosely disposed thin cells, having their longitudinal axes lying parallel to the inner (internal) surface of the photogenic mass. According to Brauer (1904, 1908), this is a reflector layer. Pigment cells form a dense mantle immediately against the light-organ. Beyond this region the pigment cells are arranged more loosely. A ventral screen of pigment cells serves to occlude the emitting surface when the photogenic organ is rotated downwards.

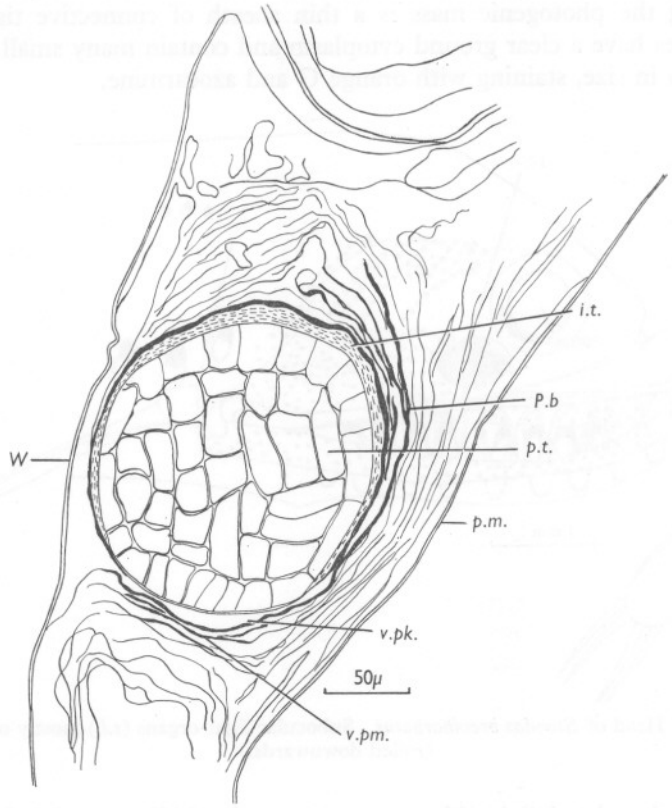

Fig. 4. Transverse vertical section through a subocular light-organ of *Stomias brevibarbatus*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.m.*, pharyngeal mucosa. *p.t.*, photogenic tissue. *v.pm.*, ventral pigment. *v.pk.*, ventral pocket. *W*, clear window.

A band-like muscle, connected to the light-organ, arises dorsally on a long aponeurosis from the hyomandibular bone. The muscle extends ventrally between two sheets of the muscularis adductor mandibulae, then runs through connective tissue obliquely outwards below the light-organ. It is inserted, behind the light-organ, on a long tendon, staining with Light Green (Fig. 7). The tendon runs between pigment cells behind (i.e. internal to) and below

the light-organ, and is inserted on the ventro-lateral face of the latter. This muscle-band, serving the light-organ, retains its identity throughout its course; its fibres are striated and smaller than those of the m. adductor mandibulae. It is muscle mm 6 of Tchernavin (1953), who traced it to the dorsal side of the maxillary division of m. add. mandibulae. Tchernavin considered that the photophore-muscle exposed the light-organ, i.e. it rotated it so that the light-emitting surface came to face outwards. This statement

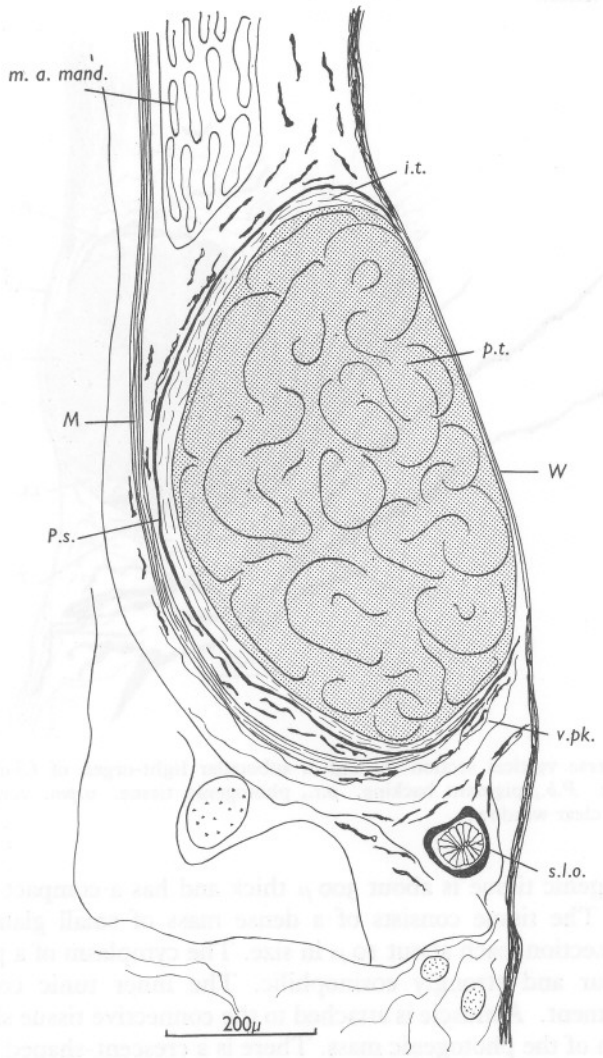

Fig. 5. Transverse vertical section through a subocular light-organ of *Stomias ferox*. *i.t.*, inner tunic. *M*, muscle. *m. a. mand.*, muscularis adductor mandibulae. *P.s.*, pigment sheath. *p.t.*, photogenic tissue. *s.l.o.*, small light-organ. *v.pk.*, ventral pocket. *W*, clear window.

suggests that Tchernavin believed that the muscle was inserted on the dorsal side of the organ. In fact, since the tendon connecting the muscle to the light-organ is inserted on the ventral side of the organ, contraction of the muscle should pull the outer face of the organ downwards, thus occluding the light-emitting surface.

Photostomias guernei Collett. 38–106 mm (excluding caudal fin). The subocular organ is oval-shaped; its dimensions are 0·4 mm high, 0·8 mm long and 0·4 mm thick.

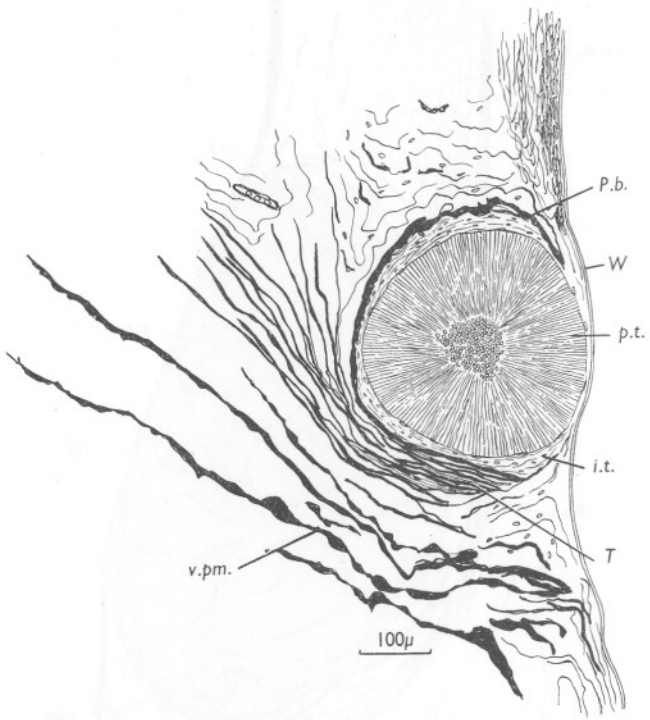

Fig. 6. Transverse vertical section through a subocular light-organ of *Chauliodus sloani*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *v.pm.* ventral pigment. *T*, tendon. *W*, clear window.

The photogenic tissue is about 300 μ thick and has a compact appearance (Figs. 8, 9). The tissue consists of a dense mass of small glandular cells, polygonal in section, each about 10 μ in size. The cytoplasm of a photocyte is finely granular and strongly eosinophilic. The inner tunic contained no reflecting pigment. A muscle is attached to the connective tissue sheath in the ventral region of the photogenic mass. There is a crescent-shaped cleft or gap in the loose connective tissue beneath the light-organ. The depth of this cleft is about equal to the height of the external face of the light-organ. The

connective tissue beneath the cleft (and above the mandible) contains black pigment cells.

Idiacanthus fasciola Peters. 80–225 mm (excluding caudal fin). The subocular light-organs are exposed. Each organ is oblong in shape, 0·25 mm long and 0·13 mm high. These dimensions include the pigmented surround.

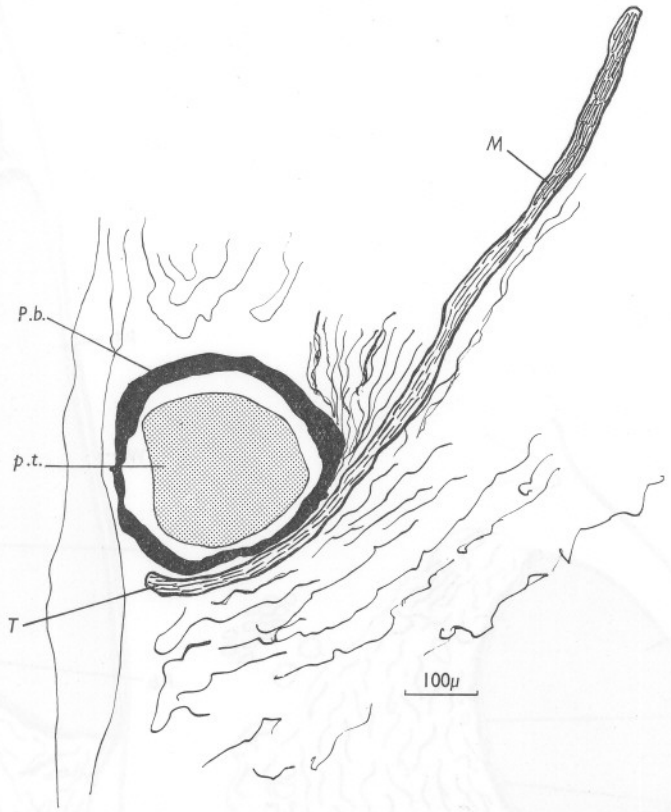

Fig. 7. Transverse vertical section through the head of *Chauliodus sloani*, showing the disposition of tissues in the vicinity of the subocular light-organ. *M*, muscle. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *T*, tendon.

In section the photogenic mass is subspherical, oblate on the outer surface. Dimensions (including pigment tunic) are 96 μ high by 99 μ thick Fig. 10).

The photogenic mass is packed with photocytes. The photocytes are polygonal in shape, 5–9 μ in size. The cytoplasm is granular; the granules are acidophilic, staining with orange G. The internal tunic contains elongate cells having little staining affinity; according to Brauer (1908), this is a reflector layer.

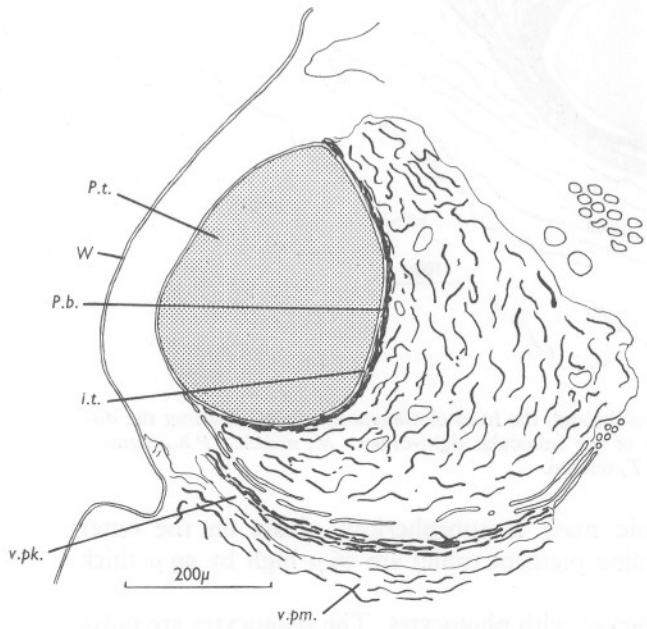

Fig. 8

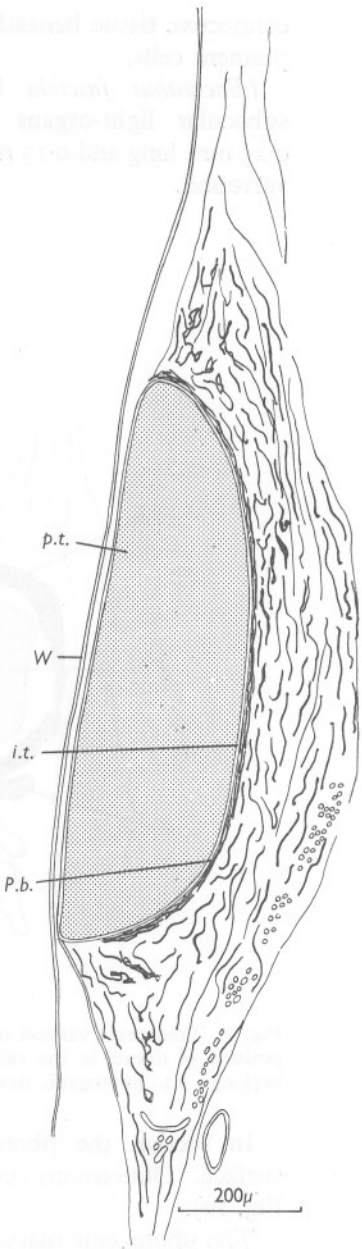

Fig. 9

Fig. 8. Transverse vertical section through a subocular light-organ of *Photostomias guernei*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *v.pk.*, ventral pocket. *W*, clear window.

Fig. 9. Transverse longitudinal section through a subocular light-organ of *Photostomias guernei*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *W*, clear window.

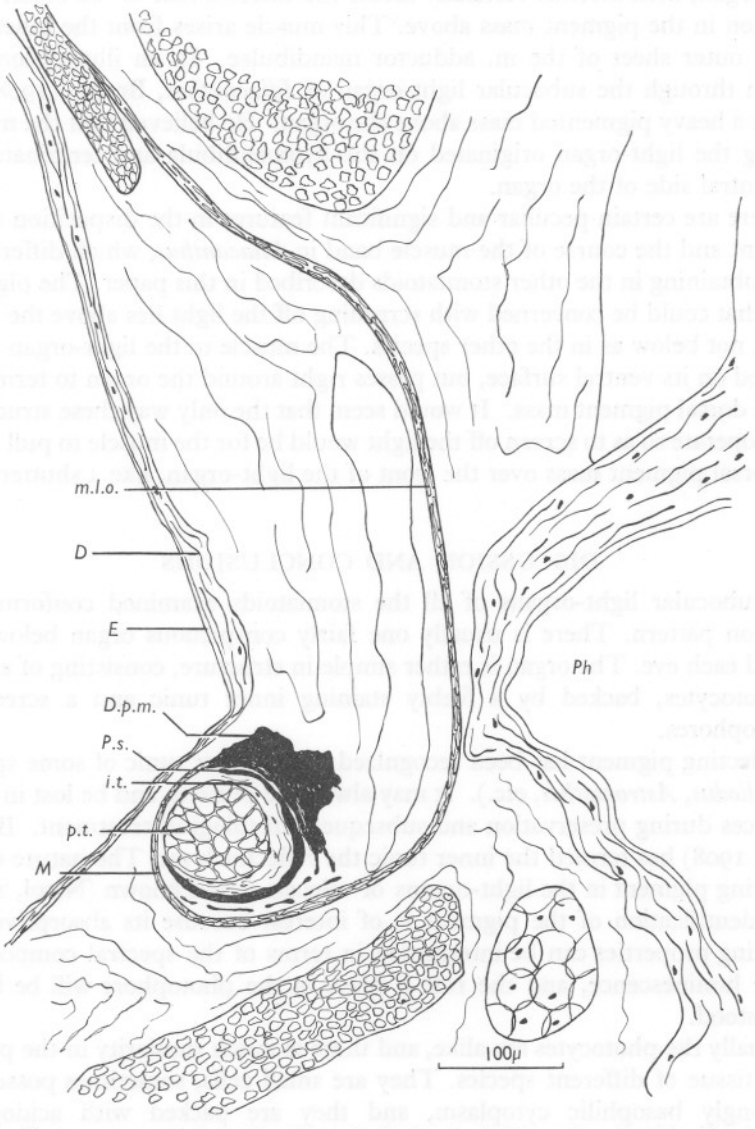

Fig. 10. Transverse vertical section through the head of *Idiacanthus fasciola*, showing the disposition of tissues in the vicinity of the subocular light-organ. *D*, dermis. *D.p.m.* dorsal pigmented mass. *E.*, epidermis. *i.t.*, inner tunic. *M*, muscle. *m.l.o.*, muscle to light-organ. *Ph.*, pharynx. *P.s.*, pigment sheath. *p.t.*, photogenic tissue.

Above the light-organ there is a dense and thick mass of pigmented tissue. A narrow strap-like muscle runs down along the inner surface and below the light-organ, then ascends vertically across the external face of the organ to an insertion in the pigment mass above. This muscle arises from the inner face of the outer sheet of the m. adductor mandibulae. In an illustration of a section through the subocular light-organ of *Idiacanthus*, Brauer (1908) has shown a heavy pigmented mass above the organ. He believed that the muscle serving the light-organ originated on the hyomandibula and terminated on the ventral side of the organ.

There are certain peculiar and significant features in the disposition of the pigment and the course of the muscle band in *Idiacanthus*, which differ from those obtaining in the other stomiatoids described in this paper. The pigment mass that could be concerned with screening off the light lies above the light-organ, not below as in the other species. The muscle to the light-organ is not inserted on its ventral surface, but passes right around the organ to terminate on the dorsal pigment mass. It would seem that the only way these structures could operate so as to screen off the light would be for the muscle to pull down the dorsal pigment mass over the front of the light-organ, like a shutter.

DISCUSSION AND CONCLUSIONS

The subocular light-organs of all the stomiatoids examined conform to a common pattern. There is usually one fairly conspicuous organ below and behind each eye. The organ is rather simple in structure, consisting of a mass of photocytes, backed by a feebly staining inner tunic and a screen of melanophores.

Reflecting pigment has been recognized in the inner tunic of some species (*Chauliodus*, *Astronesthes*, etc.). It may always be present, and be lost in some instances during preservation and subsequent histological treatment. Brauer (1904, 1908) has termed the inner tunic the reflector layer. The nature of the reflecting pigment in the light-organs of teleosts is not known (Nicol, 1957). The identification of the pigment is of interest because its absorptive and reflecting properties can be interpreted in terms of the spectral composition of the luminescence, and the role it plays in the photophore will be better understood.

Usually the photocytes are alike, and there is much similarity in the photogenic tissue of different species. They are small cells, sometimes possessing a strongly basophilic cytoplasm, and they are packed with acidophilic granules. In one species, viz. *Astronesthes richardsoni*, cytological differentiation within the photogenic tissue is recognizable.

There is no lens system for focusing the light, nor for enlarging the apparent size of the source. When a reflector is present, it is possible that it acts to some extent as a parabolic mirror.

A muscle goes to each light-organ. It arises from the hyomandibula, or from the muscularis adductor mandibulae, and runs down behind the eye inside and below the light-organ. It is usually inserted in the connective tissue sheath on the outer surface or ventro-lateral surface of the photogenic mass. In *Chauliodus* the muscle arises from an aponeurosis attached to the hyomandibula, and is inserted on a tendon which goes to the ventral surface of the light-organ. Its action appears to be the same as in the other species in which the muscle extends over the entire path from hyomandibula to light-organ. From the manner in which this muscle is arranged it is probable that it pulls the outer face of the light-organ downwards. Brauer (1904, 1908) recognized this muscle in a number of different stomiatoids (*Chauliodus*, *Astronesthes*, etc.), and he also believed that it rotated the light organ ventrally. Since there is a black pigmented layer in the connective tissue below the light-organ, this action serves to screen the light-emitting surface.

Idiacanthus is peculiar in that a pigment layer lies above the light-organ, and the muscle passes upwards, in front of (i.e. external to) the light-organ, to be inserted in this pigment layer. It seems that the muscle pulls the pigment down in front of the light-organ of *Idiacanthus* and does not move the photogenic mass.

Confirming Tchernavin (1953), I have found no antagonist to the muscle mentioned above. It is not apparent how the light-organ (or shutter in the case of *Idiacanthus*) is rotated to a position so that the light-emitting surface is exposed. Suggestions awaiting confirmation are that the muscle works against elasticity of connective tissue, or that some displacement of fluid is involved, and raised hydrostatic pressure moves the light-organ back into the exposed position when muscle traction is released.

The light-organ muscle appears to originate anatomically in some instances from the maxillary division of the m. adductor mandibulae, and it may be derived ontogenetically from the latter (cf. Tchernavin, 1953). In this event, its innervation may be ascribed to the trigeminal nerve which supplies the m. add. mandibulae (cf. Allis, 1897). Apart from this muscle-innervation, the light organ is supplied directly by nerves which penetrate the enveloping tunics and sheaths to reach the photogenic tissue. I have identified these nerves in *Astronesthes* and Brauer (1904, 1908) observed nerves in the sub-ocular light-organs of other stomiatoids. The origin of these nerves has still to be traced.

Examining young stomiatoids, Brauer (1904, 1908) observed a lumen in the photogenic mass. In adults the photogenic tissue appears to be made up of convoluted cords of photocytes. Brauer suggested that this tissue is formed by invagination of surface epithelium, which then proliferates. Support is given to this hypothesis by the observations of Greene (1899), who actually found a process of this kind taking place in the development of skin photophores in the midshipman *Porichthys*.

Living stomiatoids have been seen luminescing by a few observers. Haneda (1955) stated that the subocular light-organ of *Astronesthes ijimai* luminesces continuously, and that the luminous surface appears and disappears by rotating the organ. He suggests that luminous bacteria may be present, but in conversation recently he has discounted this idea. There is no doubt, from histological examination, that luminescence is autogenous, not bacterial.

Specimens of living *Echiostoma* have been observed to luminesce. Harvey (1931) found that the cheek organ, partially pink in life, flashed with a blue luminescence when the fish was handled. Following the injection of adrenaline, yellowish luminescence appeared in the photophores near the point of injection and soon spread to most of the other photophores. No luminescence appeared in the barbel. The cheek (subocular) organ continued to flash at intervals after the injection of adrenaline, but its rhythm and brightness were unaltered. Harvey asserted that the light appeared and disappeared in the subocular organ itself; the flashing was not due to unscreening of a continuously luminous surface. Beebe & Crane (1939) have written that 'The postorbital is definitely under control of the fish, can be rolled down out of sight, and made to glow steadily or emit sharp flashes', and 'In the new *Tactostoma*..., it apparently rotates forward and downward, instead of the usual downward'. Melanostomiatoids were observed from the 'Bathysphere' by Beebe (1935). The lateral serial organs usually glowed steadily; cheek organs, occasionally blinked and were rolled 'down' into sight.

In *Chauliodus sloani*, a weak continuous blue light has been observed on the ventral surface; the intensity of this light was not increased by mechanical stimulation. Following mechanical stimulation the serially arranged photophores luminesced, the response beginning near the point stimulated and spreading along the length of the fish; after a few seconds the light faded (Grassi, n.d.; Skowron, 1928).

Beebe (1935) has also observed luminescence in the barbel of various stomiatoids, and I found that the barbel of *Leptostomias* lighted momentarily after mechanical stimulation (Nicol, 1958).

The behaviour of a living stomiatoid (species unknown) under natural conditions has been reported by Clarke (1950). The fish was observed near the surface from the deck of a ship near the South Sandwich Islands. The stomiatoid fish, about 25 cm long, emitted a beam of varying intensity which shone directly forwards for a distance of about 0·6 m. The fish was lurking 0·6–1·8 m below the surface, poised at an angle of 35–40° from the horizontal, in which position the beam had an upward tilt. Occasionally, the fish swam around and with a quick action snapped at a cloud of krill above it.

Some miscellaneous references to luminescence in stomiatoids are given by Brauer (1908). These accounts do not clearly distinguish between the several kinds of light-organs.

From the view point of functional anatomy some tentative conclusions may be induced from the miscellaneous observations now available dealing with the subocular light-organs of stomiatoids. Light-production is intracellular and autogenous; this follows from the histological evidence, and from Harvey's observation (1931). Luminescence is subject to direct nervous control; evidence includes periodic flashing and innervation of photocytes. The organ also can be rotated so that the light-emitting surface is hidden. Haneda (1955) states that this is a way of extinguishing the light. Mechanical screening, then, forms a second method of regulating emission. It may be that direct nervous action is concerned with protracted emission; rotation, with brief periodicity. An analogous situation is encountered in squids which have photophores provided with screens of chromatophores. The photophores are innervated directly and the chromatophores, by expansion and contraction, occlude and expose the luminous surface of the photophore. The surface of the subocular light-organ is white or coloured, reflecting and conspicuous against the black background of the head, and rotation provides a means of hiding this salient feature.

In all specimens in which the subocular light-organs were partly or wholly occluded, both organs in the fish were rotated to the same extent. It seems fairly certain that both members of the pair are operated in unison.

Luminescence appeared in the submental barbel of *Leptostomias* and in the subocular organ of *Echiostoma* after mechanical stimulation; in neither animal were the other photophores affected. Continuous light has been observed in the multitudinous small (simple) photophores of the outer corium of *Chauliodus*; the serial photophores lit up when the fish was stimulated mechanically. Beebe found that the injection of adrenaline induced luminescence in the serial photophores of *Echiostoma* without affecting other light organs.

Elsewhere, I have suggested (Nicol, 1957) that the serial photophores of teleosts are controlled by adrenergic nerve fibres of the sympathetic nervous system. When excited, the photophores of this system appear to respond as a unit. Since the other photophores of the head (viz. subocular, barbel) are not necessarily called into action at the same times, it is likely that their respective innervations are from a different source; indeed, the innervations of barbel and subocular light-organs may themselves be dissimilar from each other.

I would suggest that the dissimilar kinds of light-organs plus their different innervations signify that they are employed in several different ways. Stomiatoids are carnivores living below the level of effective light-penetration; some species are reported to come to the surface at night to feed (Beebe, 1926; Clarke, 1950). To judge from the frequency with which they are captured in nets, they are solitary hunters. In the dark depths where they live, much of the light needed for vision they must generate themselves. In shallow waters, in the neritic zone and in upper pelagic reaches, some fishes possess attractively shaped, coloured or actuated lures. In these regions, fishes make use of

concealing coloration and warning coloration; males and females sometimes have dissimilar colour patterns concerned with occupation of territory and mating; some fishes advertise by suddenly exhibiting conspicuous fin-patches, etc. With these chromatic features are linked special behavioural characteristics. By analogy we might expect to find many of these roles, and perhaps others as well, performed by the light-organs of deep-sea fishes.

Bulbs on submental and dorsal tentacles may be fishing lures; this suggestion derives from analogy with the fishing tentacles of surface or neritic antennariids and lophiids, and the escal bulbs of deep-water Pediculati. The large subocular organs may be used as torches, for illuminating the surrounding water. The serially arranged photophores may permit the animals to recognize each other. The result may be mutual repulsion, thus keeping the fish spread out in hunting territories delimited by the intensity of the light and the distance at which it can be seen; or mutual attraction when the animals differ in sex. Possibly the same light-organs are used for different purposes; there may be patterns of signals and response, just as there are among inshore fishes, that allow the sexes to be distinguished. Although these problems seem rather intangible, there is a fair possibility that answers to them can be secured by various lines of attack, as the opportunities arise.

I would thank Mr A. C. G. Best for help with histological preparations.

SUMMARY

A histological study of the subocular light-organs of the following stomiatoid fishes has been carried out, viz. *Stomias brevibarbatus*, *S. ferox*, *Chauliodus sloani*, *Astronesthes elucens*, *A. richardsoni*, *Photostomias guernei* and *Idiacanthus fasciola*.

The subocular light-organ is a fairly large photophore lying just behind and below the eye. In all the species examined, except the last, it consists of a subspherical or elongate mass of photocytes, backed by an inner tunic and black pigment sheath. This assemblage, the light-organ proper, lies in the corium. The inner tunic sometimes contains reflecting material.

The photocytes are small polygonal cells, sometimes elongate and radiating outwards from the centre of the photogenic mass. They contain abundant acidophilic granules. In some species the ground cytoplasm is strongly basophilic.

The skin forms a clear window over the light-organ. There is a space between the dermis and the external face of the light-organ proper. Beneath the light-organ there is another layer of pigmented cells. A nerve penetrates the back of the light-organ to reach the photogenic tissue.

A long strap-like muscle, arising from the hyomandibula, runs down inside and beneath the light-organ to an insertion on the ventro-lateral or external

face of the light-organ (except *Idiacanthus*). The function of this muscle is to pull the outer face of the light-organ downwards, in which position the light-emitting surface faces the ventral pigmented layer and is occluded.

In *Idiacanthus* the light-organ proper is similar. A pigmented layer lies above the light-organ, and the muscle passes underneath and across the external surface of the photogenic mass, to be inserted in the dorsal pigmented layer. The muscle pulls the dorsal pigmented layer down in front of the light-organ, like a screen.

From observations on the histology of the light-organs, and on living fish, some conclusions are drawn. Luminescence is autogenous and is subject to direct nervous control. In addition luminescence can be cut off by rotating the light-organ (or by pulling down the shutter in *Idiacanthus*). This action also conceals a conspicuous reflecting surface, apart from affecting luminescence. Control of the several kinds of light-organs of stomiatoids appears to be independent of each other, viz. regulation of tentacle bulb, subocular organs, and serial photophores, seemingly by different parts of the nervous system.

Suggested roles of luminescence are discussed.

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A CONTRIBUTION TO THE BIOLOGY OF *ASTRORHIZA LIMICOLA* (FORAMINIFERA)

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British Museum (Natural History), London S.W. 7

(Text-figs. 1–5)

In the last few years the exceptionally large monothalamous arenaceous rhizopod, *Astrorhiza limicola* Sandahl, 1858, has been collected in appreciable numbers from the Blyth and Plymouth areas of British coastal waters. These collections of the living animals have enabled the authors, both independently and jointly, to make certain observations of the behaviour of the animal, and of the structure of the test, which have not been appreciated hitherto. With the exception of two early accounts of *A. limicola*, one by Bessels (1875) under the name *Haeckelina gigantea* and the other by Schultz (1915), very little appears to be known of the biology of any member of the family Astrorhizidae.

DISTRIBUTION

Astrorhiza limicola, the type species of the genus *Astrorhiza*, was first described from specimens collected off the Bolus coast, Skagerak (Sandahl, 1858) and recent faunistic accounts by Högland (1947) and Christiansen (1958) indicate that it is well established in the sandy-mud sediments in shallow water (12–58 m) of the Kattegat, Skagerak, the Gullmar and Oslo Fjords (Dröbak Sound). The numerous records of the animal in British coastal areas are all from sand, sandy-mud, or miry sediments at depths ranging from 20 to 130 m (Brady, 1884, 1887; Robertson, 1901; Heron-Allen and Earland, 1909; Stephen, 1923; Plymouth Marine Fauna, 1957). This apparently consistent occurrence in shallow waters, also noted by Cushman (1918) who lists early records from the North Atlantic coast of America, is upset by two old yet often neglected records, one by Carpenter & Wyville Thomson (1868) from a station due north of the Hebrides at 59° 36′ N. 7° 20′ W. and the other by Norman (*teste* Jeffreys, 1876) in the Davis Strait at 59° 10′ N. 50° 25′ W., where the depths are 970 and 3200 m, respectively. Although the specimens do not appear to be available for examination, the short descriptive accounts indicate that the records are justified, so that

the depth range of the species has to be extended beyond that which it is customary to acknowledge.

Apart from the North Atlantic, records from the Arctic north of the New Siberian Islands (Stschedrina, 1946) of *A. limicola* var. *arenifera* and *A. limicola* var. *sabulifera* are of interest, although in a recent private communication Mrs Stschedrina has informed one of us that she is revising her opinion about the systematic position of these forms. The only reports of *A. limicola* from the southern hemisphere are those from the east coast of Africa (Heron-Allen & Earland, 1915), the Antarctic (Heron-Allen & Earland, 1922) and South Georgia (Earland, 1934) all of which are based on either fragments or odd specimens. Re-examination of this material from the southern hemisphere has led to the conclusion that these records should be provisionally considered as doubtful.

QUANTITATIVE DATA AND THE NATURE OF THE ENVIRONMENT

The distribution of *A. limicola* has been most fully studied on the offshore grounds of the southern half of the Northumberland coast. All along this coast there is a strip of muddy sand from 8 to 10 miles wide at depths from 30 to 70 m running parallel to the coastline. Farther offshore the bottom falls off to depths of 80–100 m where the sediments are predominantly sandy silt. At a distance of 20–25 miles offshore the bottom rises once again to depths of 60–70 m and muddy sand sediments are again encountered. Broadly speaking the sediments can be regarded as being a broad area of muddy sand divided down the middle by a strip of sandy silt which corresponds to a tongue of deep water (80–100 m) running approximately north to south at a distance of about 15 miles offshore all along the southern half of the Northumberland coast. The inshore strip of muddy sand is itself divided approximately down the middle by a long tongue of almost clean sand over 20 miles in length and varying from 1 to 7 miles in width at depths of 40–60 m. The offshore area of muddy sand also has areas, like the inshore, which as a result of tidal scour are swept almost clean of fine sedimentary material. It is on these sandy areas both inshore and offshore that *A. limicola* is a constant and conspicuous constituent of the benthic fauna. The bottom in these areas is fine to medium sand (250–500 μ) with generally less than 10% silt (particles less than 62 μ) and less than 2% clay (particles less than 4 μ). It should be emphasized that these sandy areas are isolated patches or strips surrounded by muddy sand and that their fauna does not represent a discrete community of species, but rather a modification of the fauna found on the muddy sand surrounding them, which can be broadly described as belonging to the classical 'Echinocardium-filiformis' community of Petersen.

Fifty-six stations were sampled with a Van Veen grab throughout the extent of the sandy area with *A. limicola* occurring in 82% of the hauls at an

average density of 53 specimens per square metre, the greatest density being 240 individuals per square metre. The animals found commonly in this association are listed in Table 1.

TABLE 1. OTHER ANIMALS FOUND ASSOCIATED WITH *A. LIMICOLA* WITH THEIR AVERAGE NUMBERS PER SQUARE METRE FOR FIFTY-SIX HAULS

	No. per m²		No. per m²
Astrorhiza limicola	53	*Dentalium entalis*	4
Amphiura filiformis	47	*Echinocyamus pusillus*	4
Nephthys spp.	13	*Venus striatula*	3
		Ampelisca brevicornis	2
Owenia fusiformis	5	*A. macrocephala*	1
Echinocardium flavescens	4	*Phaxas pellucidus*	2
E. cordatum	1	*Sthenelais limicola*	2
Goniada maculata	4	*Astropecten irregularis*	2
Dosinia lupinus	4	*Abra prismatica*	1

Quantitative data are sparse for other areas but two records are worth noting. Stephen (1923) reports the rhizopod from a grab haul taken at a depth of 101 m off the Butt of Lewis where ten specimens were obtained in 0·1 m², together with *Echinocardium flavescens*, *Dentalium entalis*, *Ophiura affinis*, *Abra prismatica* and *Mactra elliptica*. Secondly, an association similar to that found off Northumberland has been described by Caspers (1950) from off the Heligoland coast. Here *Astrorhiza limicola* reached a maximum density, in one haul, of sixty-seven individuals in 0·1 m² but this high density appears to be confined to a very small area. Figures given by Caspers (1950) for the particle size analysis of the bottom sediment also appear to be very similar to the Northumberland sediments and consist mainly of sand fractions from 125 to 500 μ at a depth of 22–25 m. The associated animals off Heligoland are *Amphiura filiformis*, *Owenia fusiformis*, *Nephthys* spp., *Venus striatula*, *Spisula solida*, *Cochlodesma praetenue*, *Echinocyamus pusillus* and *Phoronis mulleri*. In both the Northumberland and Heligoland areas the ecological conditions appear to be very similar and both are isolated sandy areas more or less surrounded by a typical 'Amphiura' community. Thorson (1957) suggested that the Heligoland association, in which *Astrorhiza limicola* is dominant, may be regarded as a 'Foraminifera' community, whereas we are of the opinion that this association should be regarded as a variation or faciation of the 'Amphiura' community (Thorson, 1957) where it is in a state of transition to a 'Venus' community. This transition is never completed off the Northumberland coast, since the sediments rapidly become more muddy again as deeper water is approached and the characteristic associations of a true 'Venus' community are never found to be sufficiently significant to dominate the population.

Dense populations of *A. limicola* always appear to be associated with stable areas of fine to medium sand, with only small amounts of silt and clay, containing a relatively rich interstitial fauna. Such areas seem to lie intermediate,

in bottom conditions, between the muddy sand areas, with slow bottom currents allowing quantities of silt and clay to accumulate, and clean sand areas with relatively strong bottom currents and probably less interstitial stability. In the few areas which have been quantitatively studied the intermediate bottom conditions are confirmed by a fauna, occurring with *A. limicola*, which is generally in the nature of a mixed community.

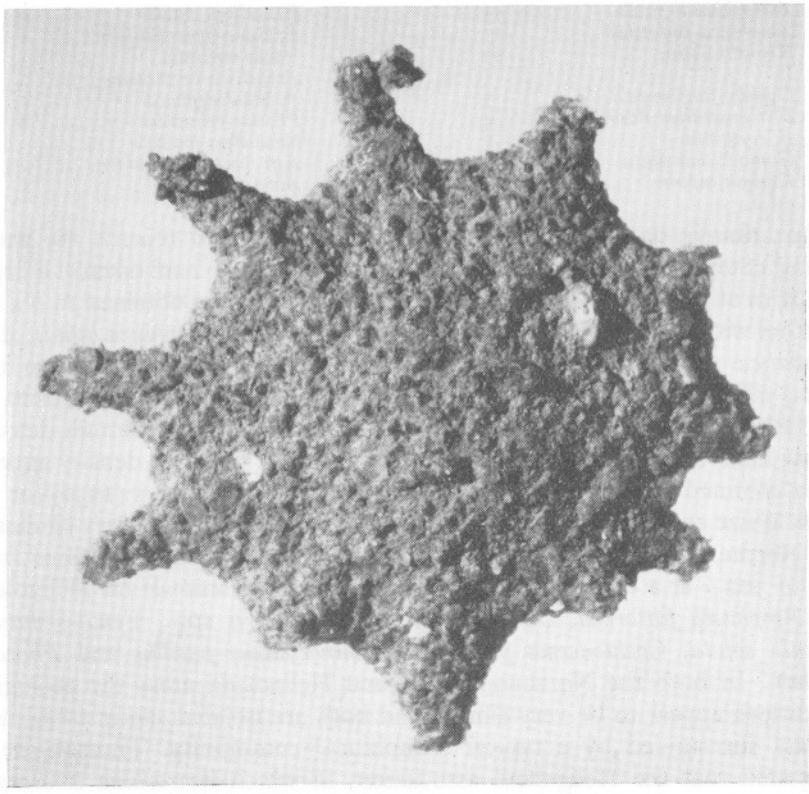

Fig. 1. A typical *Astrorhiza limicola* collected from the Northumberland coast.

STRUCTURE OF THE TEST

Individuals of *A. limicola* are surrounded by a well-defined stellate test built up of extraneous material from the bottom sediments on which they lie (Figs. 1, 2). In addition to this foreign material there is an organic cement, secreted by the animal, causing the sand grains to cohere and ensuring the stability and form of the arenaceous test.

The extraneous constituents

In the Northumberland specimens the tests are constructed for the most part from inorganic material in which quartz grains predominate, although other materials, such as shell fragments and small echinoderm spines, are often incorporated. Although quantitative sampling has shown that the rhizopods occur in the largest numbers on the clean, comparatively silt free, sands, they can be collected in small numbers over a wide range of bottom conditions from fine silty sand to clean coarse sand. Individuals collected from these different areas show obvious superficial differences in external appearance suggesting that the material utilized in test building is obtained in a non-selective manner. Furthermore, in laboratory experiments *A. limicola* will readily utilize such materials as powdered glass and 'Perspex ' shavings to effect a repair of a damaged test.

A large sample of individuals collected from several different types of sea bottom was treated with sodium hypochlorite solution resulting in the destruction of the organic matter and leaving a dispersed sample of the inorganic constituents of the test. Particle size analysis of this material showed that a complete range of particles was present from somewhat over 1000 μ down to slightly under 30 μ. Several other samples of *Astrorhiza* were similarly analysed along with analyses of the bottom sediment from which they were collected. It was found that for any particular locality the material in the test and the material from the bottom sediment produced an almost exact correspondence in analysis figures, indicating, that with the exception of the coarsest material and fine gravels, the animal incorporates the bottom sediment material into its test in almost exactly the same proportions as it is found in the sediment samples.

Specimens obtained from Plymouth had tests constructed of rather coarse sand and shell particles indicating that the bottom on which they lie is probably of shelly-gravel and coarse sand. The superficial difference between these specimens and those from the muddier areas of Northumberland is very marked, again suggesting that the nature of the material incorporated into the test appears to have little significance.

The organic cement

Microscopic examination and manipulation of a portion of the test wall shows this interstitial substance to have the consistency of a rigid gel, whereas after fixation in alcohol and in dried specimens, it is very contracted, giving the impression that little organic cement is present.

The cement has an affinity for basic dyes; it stains when immersed in a 0·01 % aqueous solution of toluidine blue, exhibiting γ-metachromasia when examined in water (Pearse, 1953) and reacts positively with Schiff's reagent

after prior oxidation with periodic acid (Hotchkiss, 1948). Attempts to demonstrate the presence of certain amino acids, and thereby protein, by the Millon and Sakaguchi reactions, have not been successful, although a positive result was obtained after the coupled tetrazonium reaction procedure for tyrosine, tryptophane or histidine (Pearse, 1953). From these results it appears that the cement is a protein-carbohydrate material with part at least being an acid mucopolysaccharide. Little more of any significance can be said about the chemical composition of the cement in the absence of a full analysis. It can, however, be referred to as 'tectin' (Hyman, 1940), although it must be emphasized that this term implies no precise chemical composition beyond the fact that the substance is composed of protein and carbohydrate in combination, that is, a type of glycoprotein. As there are many different forms of glycoproteins so there will be many different tectins.

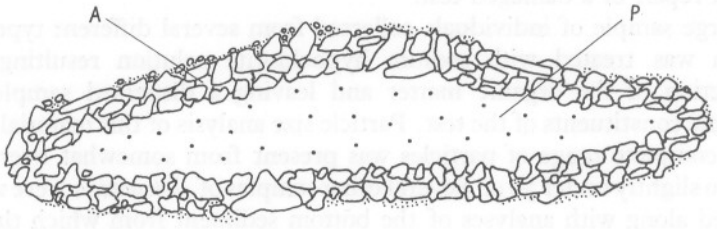

Fig. 2. A diagrammatic transverse section of *Astrorhiza limicola*. *A*, arenaceous wall; *P*, protoplasm.

The 'inner chitinous lining' of the test

The term 'chitinous' has often been used in foraminiferal work as an adjective of convenience to describe any of a variety of organic structures, including a thin lining to the interior of the test wall in *A. limicola* (Cushman, 1948). No worker, to the authors' knowledge, has demonstrated chitin in any part of the test of *A. limicola*, or indeed in any arenaceous foraminifer, and as no organic residue has been found after boiling in caustic potash there is no reason to suppose that chitin is present.

The inner organic layer of the test, just referred to, has some taxonomic significance, for Stschedrina (1946) notes that *A. limicola* var. *arenifera* differs from the typical *A. limicola* in having a more fragile and thin test and in the absence of an 'inner chitinous lining'. It must be pointed out that to the authors' knowledge the inner lining to the test of *A. limicola* has never been described or figured, and the question arises, does one exist at all? The following observations are relevant to this problem.

None of the living specimens from Blyth and Plymouth which have been examined possessed a recognizable inner organic lining to the test, nor was there an excessively large amount of organic cement on the internal surface

which could have been mistaken for a distinct inner layer. In alcohol-preserved and particularly dried specimens, however, the protoplasm has invariably changed colour from the normal cream to a dark red-brown and with the resultant dehydration the shrivelled protoplasm has assumed positions, especially in the radiating arms, which give the impression of a brown organic lining. It is quite likely that this abnormal state may account for some of the categorical statements of the presence of an inner lining, especially when it is noted that many faunistic accounts of Foraminifera have been based on dry collections.

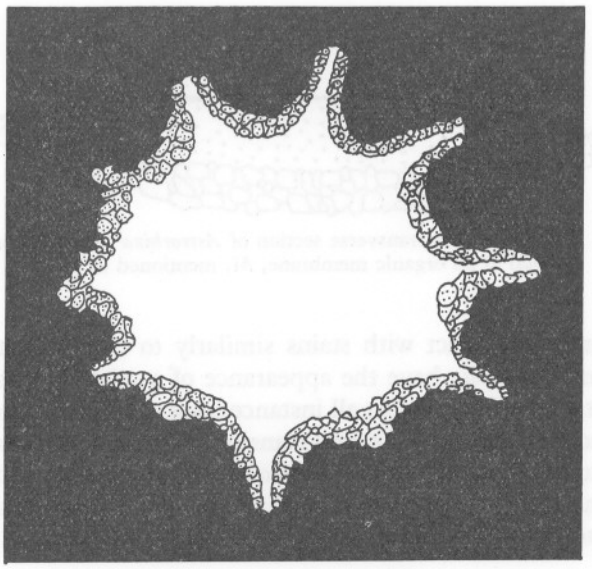

Fig. 3. A diagrammatic top view of *Astrorhiza limicola* after the roof has been removed to reveal the internal creamy protoplasm.

Another way in which the 'inner lining' character may have become established in the literature is through the examination of specimens which have at some time been damaged and have subsequently undergone repair. Although no examples of this sort have been collected by us, certain laboratory experiments of a damage and repair nature have been carried out, and the results may have some bearing on the problem. If, for example, the roof of a test is removed leaving the creamy protoplasm exposed (Fig. 3) and this damaged animal is left in a container without sand grains it will always secrete a membrane (Fig. 4), usually within 12 h. This organic membrane is approximately 10 μ thick, separate from and independent of the protoplasm which has secreted it, and completely covers that part of the test which has been damaged. If a

damaged animal such as this is now placed in a container with sand grains these are manoeuvred by the pseudopodia on to the membrane and cemented to it until the wall appears normal. In this case *A. limicola* does have an inner organic lining to the test, but only to that part which has been repaired. When animals are placed among sand grains immediately after being damaged they usually repair their tests by incorporating the sand grains on the exposed surface without the secretion of a definite foundation membrane. There is, however, no precise procedure which can be said to take place in every case. If the animal is squeezed out of the test and left naked in a container free of sand grains it soon secretes a membranous test, completely surrounding the protoplasm.

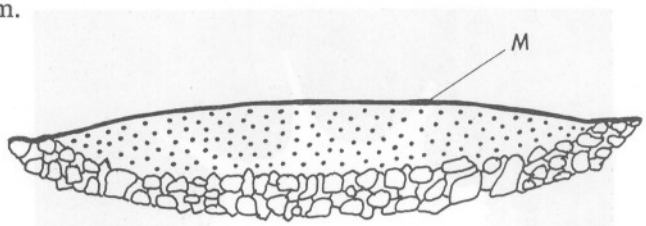

Fig. 4. A diagrammatic transverse section of *Astrorhiza limicola* to show the position of an organic membrane, *M*, mentioned in the text.

These membranes react with stains similarly to the cement of the test wall. They are isotropic, have the appearance of a relatively strong proteinaceous structure, and, in almost all instances, are clear and transparent when newly formed, becoming brown and translucent after a few days.

It is concluded that normally *A. limicola* does not possess a distinct lining of organic material on the interior wall of the test, although under certain rather unusual conditions an organic membrane is secreted.

The presence of iron in the test

The ferruginous nature of *A. limicola* is demonstrated when the sand grains and organic cement are coloured blue after immersion in acidified potassium ferrocyanide (equal parts 2% hydrochloric acid and 2% potassium ferrocyanide). This production of the Prussian blue compound is the end product of a specific reaction and chemical test for ferric iron. The presence of iron in the tests of a number of other arenaceous forms has been commented upon by Vinogradov (1953) and a question of some interest is whether the source of the iron is directly from the immediate environment or whether it is being secreted by the animal. The same problem is discussed by Hedley (1960) in relation to *Gromia oviformis*, a rhizopod with an organic test, where it does appear that the animal is secreting iron in some form which, in part at least, is deposited in the test wall. As far as the arenaceous foraminifera are concerned Vinogradov (1953) summarizes the available data and infers that there is an

active physiological process whereby iron is 'precipitated' by the animals. One of us is currently investigating a number of arenaceous forms with this problem in mind, so that at this stage only those observations on *A. limicola* will be discussed: (*a*) Tests for iron in the protoplasm, using 6 μ paraffin sections, have failed to reveal any structures which are iron positive. (*b*) Freshly secreted membranes of damaged animals are iron negative. (*c*) If *A. limicola* is placed in a dish containing sand grains from the sediment in which it was living at the time of collection, but which have been treated with concentrated hydrochloric acid to remove the iron and then thoroughly washed, any subsequent addition to the test, either sand grains or organic cement, is iron negative.

The foregoing observations suggest that the ferruginous nature of the test wall is the result of the iron already present on the sand grains of the sediment which are incorporated into the test by the animal. Consequently at this stage there is no evidence of the animal secreting iron.

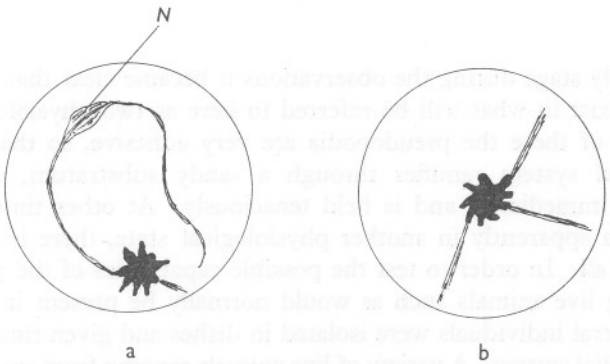

Fig. 5. Drawings showing the extent of two pseudopodial systems as they were seen when individuals were isolated in plastic dishes in the laboratory. The black circles represent the edges of the dishes and the nodule, N, is noted in the text (natural size).

BEHAVIOUR

The presence of epizoic growths of hydroids, ascidians and other arenaceous foraminifera on the upper surface of many tests of *Astrorhiza* shows that the animal normally lives on the sand surface and does not burrow. This was confirmed by observation of living material in the laboratory. When freshly collected animals are isolated in dishes with a sand substratum, they move in a more or less elliptical path for considerable distances. Schultz (1915) noted a distance of 25 cm covered in 24 h and speeds of this order have been confirmed on several occasions. The distance and route covered by isolated animals can be easily observed, since a furrow is left in the sand as a result of the leading edge of the test being preceded by a raised mound or

'bow-wave' of sand. When movement ceases this mound of sand may cause the test to appear buried to a very small extent. After a period of roaming about the dish, often lasting 24 hr, the animal settles and proceeds to develop an extensive pseudopodial system.

The pseudopodia ramify both over the sand surface and through the interstitial spaces to a depth of about 2–3 mm below the surface. Naturally they are more readily observed in dishes without a sand substratum and in such cases it is apparent that the pseudopodia occasionally have relatively large masses of protoplasm, forming nodules, along their length. Two typical pseudopodial arrangements are presented in Fig. 5a, b. Bessels (1875) drew a group of *Astrorhiza* showing seven specimens connected together to form a network, but we have not observed any actual union of different pseudopodial systems or of tests belonging to two or more individuals. Nevertheless a sediment inhabited by a number of *A. limicola* must be regarded as being very extensively ramified by their pseudopodia which may extend to distances of more than 6–7 cm from the central protoplasmic mass of each individual.

Feeding

At an early stage during the observations it became clear that the pseudopodia can exist in what will be referred to here as two physiological states. In the first of these the pseudopodia are very adhesive, so that, when the pseudopodial system ramifies through a sandy substratum, any particle sticks to it immediately and is held tenaciously. At other times, with the pseudopodia apparently in another physiological state, there is no adhesive property at all. In order to test the possible capabilities of the pseudopodia for catching live animals such as would normally be present in the natural habitat, several individuals were isolated in dishes and given time to develop a pseudopodial system. A variety of live animals ranging from small copepods and amphipods to nematodes and small echinoderms were then introduced. Although these animals were in a healthy state and moving briskly, they were firmly held whenever they came in contact with the adhesive pseudopodia. *A. limicola* proved itself quite capable of holding and eventually immobilizing such animals as fully grown cumaceans (*Diastylis laevis*), caprellids up to 2–3 cm in length and small recently metamorphosed *Echinocardium flavescens* as well as a variety of small crustacea. Similar experiments were carried out in dishes with a sandy substratum into which actively swimming *Artemia* were introduced. Whenever an *Artemia* landed on the bottom at a point where the pseudopodia were exposed it was firmly held. In all these experiments the captured animals struggled for long periods, invariably in vain, gradually becoming weaker and eventually dying. On examination after a period of 1–2 days nothing remained of a caught animal other than a clean cuticle.

There is no evidence that a toxin is secreted by *Astrorhiza* to kill the animals after they have been caught by the pseudopodia. Observations of the

process tend rather to support the opinion that the prey gradually dies through exhaustion and perhaps suffocation as a result of being firmly held by the pseudopodia. As no process of ingestion has been observed it is implicit that there is some process of extracellular digestion such as is said to occur in the case of *Elphidium crispum* (Jepps, 1942).

From the information obtained from laboratory feeding experiments there would seem to be strong evidence that *Astrorhiza limicola* is an active, mobile predator of the interstitial sand fauna and of the smaller faunal elements associated with the sediment surface. Schultz (1915) suggested that it feeds on small protozoans and flagellates, and from sections we have seen that diatoms are ingested. It seems likely that just as the animal is non-selective in test building it is also not very selective in feeding. If, as seems probable, interstitial organisms constitute the main food supply, the interstitial microfauna of those areas where *A. limicola* occur in large numbers must be profoundly affected.

SUMMARY

A general account, based on literature records, is given of the distribution of *Astrorhiza limicola* in addition to a more detailed account of its distribution and ecology off the Northumberland coast. The animal is seen to be non-selective of the materials used for test construction and an account of the test structure considers the significance of its ferruginous nature, the organic cement component secreted by the animal, and an 'inner chitinous lining' often reported in the literature.

Laboratory observations of living animals indicate that *A. limicola* may be regarded as a mobile predator of interstitial sand metazoans.

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AMPHIBDELLID (MONOGENEAN) PARASITES OF ELECTRIC RAYS (TORPEDINIDAE)

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(Plates I–III and Text-figs. 1–28)

Electric rays (Torpedinidae) are known to harbour on their gills certain monogenean parasites (*Amphibdella* spp. and *Amphibdelloides* spp.) whose taxonomy is in a very confused state. Much of this confusion has centred around a single morphological feature: a 'transverse bar' has been variously held to be present or absent from the adhesive apparatus, or sometimes two such bars have been stated to be present. Among those who have regarded the transverse bar as having taxonomic importance, Price (1937) recognized two genera of amphibdellids distinguishable by the presence or absence of the bar, but Palombi (1949) and Bychowsky (1957) believe that the bar may be present in young specimens but absent or inconspicuous in older specimens. No-one has investigated the function of this transverse bar, or, indeed, any functional aspect of the adhesive apparatus. Again little attention has been paid in taxonomy to the genitalia or host specificity, or, in spite of a record of an amphibdellid from the heart of its host, to micro-habitat.

As part of an attempt to repair these omissions, a general watch was kept for electric rays landed by the research vessels at Plymouth in July and August in the period 1953–59. During this time only three specimens of *Torpedo nobiliana* were brought in, but fortunately these yielded supplies of the parasites in question. In addition, as a result of the most helpful co-operation on the part of the Staff of the Plymouth Laboratory, especially Mr J. E. Green, fresh gills of a further two specimens of *T. nobiliana* were sent to Birmingham in October 1956 and September 1959, respectively, and were found to bear living parasites.

Amphibdellids were collected from three distinct micro-habitats on *T. nobiliana*, and for reasons to be given later (pp. 580–5) were identified as follows:

1. Secondary gill lamellae (see Pl. I, fig. 2)	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price, 1937
2. Parietal mucosa of gills (see Pl. I, fig. 1)	*Amphibdella flavolineata* MacCallum, 1916. Adult specimens
3. Cavity of heart	*A. flavolineata* MacCallum, 1916. Juvenile specimens

Amphibdelloides maccallumi was found to be very common, some 100 to over 2000 specimens being present on each of the five host specimens examined; adult specimens of *Amphibdella flavolineata* were found on the gill mucosa of four of the five host specimens, the maximum infestation being six parasites per host; and juvenile specimens of *A. flavolineata* were found in the heart of two host specimens, one of these hosts bearing two parasites, and the other a single parasite.

All these parasites were studied living and *in situ*, as living specimens under pressure of a cover-glass, as stained whole mounts, and by means of paraffin sections. In studying the adhesive apparatus, whole specimens relaxed in propylene phenoxetol (Owen, 1955), mounted freely in glycerol, and examined stereoscopically, were especially useful, as also was phase-contrast microscopy of flattened whole mounts in balsam.

These monogenean parasites of *Torpedo nobiliana* at Plymouth have been compared with various amphibdellid parasites from electric rays from other regions as indicated in Table 1, in which the hosts have been named as in Bigelow & Schroeder (1953). As a result of the comparison it became necessary to propose certain taxonomic revisions. For convenience these are listed in Table 1 but the taxonomic diagnoses will be given later (pp. 580–2) following descriptions of the kinds of characters used in the recognition of the different species.

MICRO-HABITAT

Amphibdelloides maccallumi lies between two adjacent secondary gill lamellae (Pl. I, fig. 2) with its posterior end in contact with the primary lamella (Pl. II, fig. 1). It maintains this position by the use of two pairs of hooks, one pair directed dorsally and the other ventrally. These hooks are inserted into the bases of the secondary lamellae, the points of the hooks often emerging on the other side of the lamella.

Adult specimens of *Amphibdella flavolineata* attach themselves to the proximal region of a primary gill lamella, i.e. a region adjacent to the interbranchial septum and lacking secondary lamellae (Pl. I, fig. 1), and referred to in *Torpedo torpedo* by Parona & Perugia (1890, p. 364) as 'mucosa parietale'. The whole of the relatively bulky haptor is accommodated subcutaneously within the host tissues, the remainder of the body of the parasite being connected to the haptor by a neck region which is constricted by the superficial tissues of the host (Pl. II, fig. 2).

Amphibdelloides vallei attaches itself to the gills of *Torpedo marmorata* (Pl. I, fig. 3) in exactly the same manner as does its counterpart *Amphibdelloides maccallumi* to *Torpedo nobiliana*, but there is less correspondence between the attachment of *Amphibdella torpedinis* to *Torpedo marmorata* and that of *Amphibdella flavolineata* to *Torpedo nobiliana*. Although *Amphibdella torpedinis* attaches itself to the parietal mucosa rather than to the secondary

TABLE 1. TAXONOMIC DESIGNATIONS, HOSTS, AND GEOGRAPHICAL SOURCES OF AMPHIBDELLID SPECIMENS STUDIED

Host	Locality	Author/ collector	Parasites	
			Genus *Amphibdelloides* Price, 1937	Genus *Amphibdella* Chatin, 1874
Torpedo nobiliana Bonaparte syn. *Tetronarce occidentalis* Storer syn. *Tetranarce occidentalis* Storer	Irish Sea Irish Atlantic Slope Sète, Mediterranean Wood's Hole, U.S.A. Plymouth	Rees & Llewellyn (1941) Dr H. H. Williams Dr L. Euzet MacCallum (1916) Llewellyn	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price, 1937 syn. *Amphibdella maccallumi* Johnston & Tiegs, 1922 syn. '*Amphibdella torpedinis* Chatin' of MacCallum (1916)	*Amphibdella flavolineata* MacCallum, 1916
Torpedo californica Ayres	California	Alexander (1954)	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922)	—
Torpedo marmorata Risso	Sète, Mediterranean	Dr L. Euzet	*Amphibdelloides vallei* sp.nov. syn. '*Amphibdelloides maccallumi*' of Euzet (1957) in part syn. '*Amphibdella torpedinis*' of Perugia & Parona (1889) = Valle's specimens from Trieste	*Amphibdella torpedinis* Chatin, 1874
Torpedo torpedo (L.) syn. *T. narke* Risso syn. *T. ocellata* Rudolphi syn. *Raja narce* Nardo	Genoa, Mediterranean	Parona & Perugia (1890)	—	*Amphibdella parona-perugiae* sp.nov. syn. '*Amphibdella torpedinis* Chatin' of Parona & Perugia (1890) and Ruszkowski (1931)
Narcine brasiliensis (Olfers)	Florida	Hargis (1955)	*Amphibdelloides narcine* Hargis, 1955	—

lamellae, it may be found not only on the proximal region of the primary lamella (Pl. I, fig. 4B), i.e. near to the interbranchial septum, as in *A. flavolineata*, but on the distal region as well (Pl. I, fig. 4A); like *A. flavolineata*, *A. torpedinis* buries the posterior end of its body subcutaneously in its host.

I have not seen attached specimens of *Amphibdelloides narcine* or *Amphibdella paronaperugiae*, but Parona & Perugia (1890, p. 364) stated that the latter species was attached to the 'mucosa parietale'.

The three juvenile specimens of *A. flavolineata* collected in the present study were all found among the loosely woven muscle strands in the ventricle of the heart, and did not appear to be attached to the host tissue. Other parts of the blood system of *Torpedo nobiliana* were not searched. Juvenile specimens of *Amphibdella torpedinis* were collected for me from the heart of *Torpedo marmorata* by Dr Louis Euzet.

The micro-habitat of juvenile specimens of *Amphibdella flavolineata* and *A. torpedinis* thus differs from that of any other known monogenean, excepting Ruszkowski's (1931) specimens of *A. paronaperugiae* (syn. *A. torpedinis*) from the blood system of *Torpedo torpedo*. By far the greater number of monogeneans are ectoparasitic, but a few are endoparasitic in the coelom, oviducts, ureters, or urinary bladders of their hosts (see Llewellyn, 1957). The invasion of the blood system of an elasmobranch by a monogenean is not likely to have incurred undue physiological problems: food and oxygen supplies would change but little, and the osmotic relations with the ambient medium would also be relatively unchanged, since elasmobranchs are known to be approximately isosmotic with sea water (Smith, 1936). Probably the greatest novelty was the assumption of a tolerance of the high urea concentrations known to be present in elasmobranchs (Smith, 1936). The egg capsules could be released when the anterior end of the parasite emerges through the gill tissues to take up the definitive adhesive attitude illustrated for *Amphibdella flavolineata* in Pl. II, fig. 2.

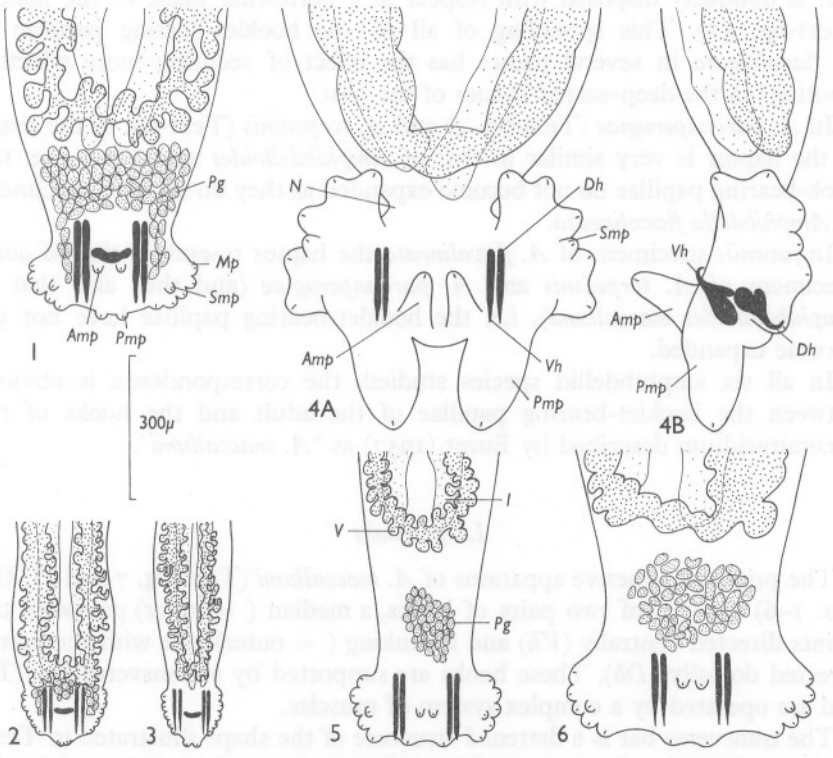
ATTACHMENT TO THE HOST

The haptor of amphibdellids may contain three kinds of adhesive apparatus: 'hooklets' (= persistent oncomiracidial hooks) borne on papillae; large hooks, with or without an accessory sclerite (= 'transverse bar'); and glands.

Hooklet-bearing papillae

Along the lateral margins of the haptor of *Amphibdelloides maccallumi* are borne, on each side, six very labile muscular papillae (Text-fig. 1); five of these are truly marginal, but the remaining one is submarginal on the ventral surface immediately medial to the interval between the 3rd and 4th marginal papillae from the anterior end. In addition to these six pairs of papillae, two other pairs are present: first, a median pair on the posterior margin of the haptor, separated by a relatively wide interval from the remaining marginal

(lateral) papillae, and secondly, a median pair on the ventral surface of the body immediately posterior to the transverse bar of the main hook-apparatus (see below). Each of the sixteen papillae bears an apical hooklet of about 6–8 μ long. These papillae are often obliterated if the usual practice is followed of flattening specimens before mounting them; the papillae are best seen in living specimens or in specimens relaxed in propylene phenexetol.



Text-figs. 1–6. The haptors of amphibdellids, all drawn to the same scale. Fig. 1. *Amphibdelloides maccallumi*. Fig. 2. *A. vallei*. Fig. 3. *A. narcine*. Figs. 4A, B. *Amphibdella flavolineata*, 4A ventral view, 4B side view. Fig. 5. *A. paronaperugiae*. Fig. 6. *A. torpedinis*. *Amp*, anterior median papilla; *Dh*, dorsal hook; *I*, intestine; *Mp*, marginal papilla; *N*, neck; *Pg*, posterior gland; *Pmp*, posterior median papilla; *Smp*, submarginal papilla; *V*, vitellarium; *Vh*, ventral hook.

In *A. vallei* (Text-fig. 2) and *A. narcine* (Text-fig. 3) the haptor is less expanded laterally than in *A. maccallumi*, and in dorsal or ventral view is approximately triangular with the apex directed posteriorly. Suitably treated material for a detailed study of the distribution of the papillae in these two species was not available.

In *Amphibdella flavolineata* (Text-figs. 4A, B) there is a very well-marked neck region separating the haptor from the body-proper, the narrowness of

the neck being emphasized by the great expansion of the haptor in the subcutaneous tissues of the host (Pl. II, fig. 2). The two median pairs of papillae are very much larger than the lateral marginal ones: the posterior median papillae are greatly extended in a posterior direction (Text-fig. 4A) and the anterior median papillae are greatly extended in a ventral direction (Text-fig. 4B). The lateral papillae are borne on a considerably expanded flange that is obliquely disposed with respect to a horizontal plane of the haptor (Text-fig. 4B). This spreading of all of the hooklet-bearing papillae of *A. flavolineata* in several planes has the effect of securing more effective 'rooting' in the deep-seated tissues of the host.

In *A. paronaperugiae* (Text-fig. 5) and *A. torpedinis* (Text-fig. 6) the shape of the haptor is very similar to that of *Amphibdelloides maccallumi*, i.e. the hook-bearing papillae do not become expanded as they do in adult specimens of *Amphibdella flavolineata*.

In *juvenile* specimens of *A. flavolineata* the haptor resembles that of *adult* specimens of *A. torpedinis* and *A. paronaperugiae* (and thus also that of *Amphibdelloides maccallumi*), i.e. the hooklet-bearing papillae have not yet become expanded.

In all six amphibdellid species studied, the correspondence is obvious between the hooklet-bearing papillae of the adult and the hooks of the oncomiracidium described by Euzet (1957) as '*A. maccallumi*'.

Large hooks

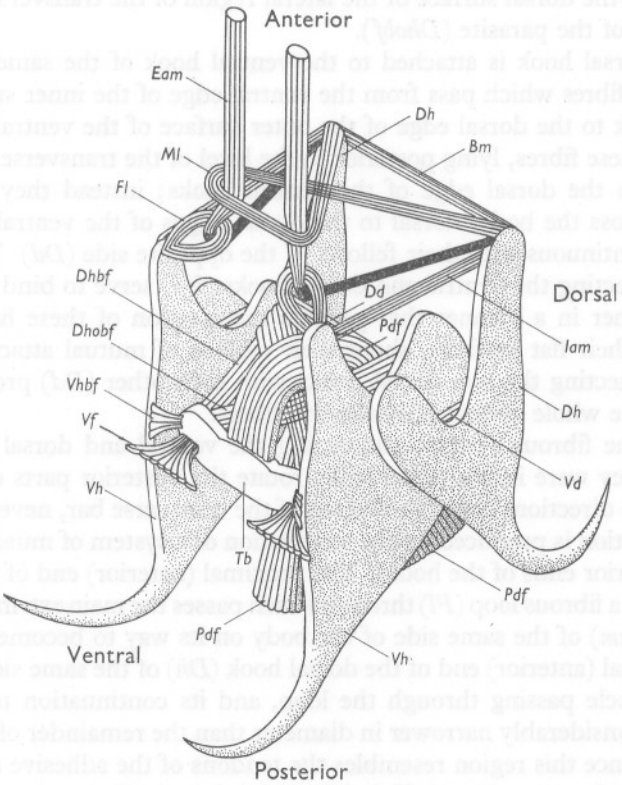
The principal adhesive apparatus of *A. maccallumi* (Text-fig. 7 and Pl. III, figs. 1–6) consists of two pairs of hooks, a median (= inner) pair with the points directed ventrally (*Vh*) and a flanking (= outer) pair with the points directed dorsally (*Dh*). These hooks are supported by a transverse bar (*Tb*) and are operated by a complex system of muscles.

The transverse bar is a flattened structure of the shape illustrated in Text-figs. 7 and 8C, i.e. it consists of a median region and two antero-laterally inclined lateral regions. This bar lies transversely in the ventral region of the body at a position approximately midway along the length of the hooks. It is suspended from the integument of the body by two antagonistic systems of fibres: one set (*Vf*) joins the lateral regions of the bar directly to the integument of the ventral surface of the body, and the other, more powerful set (*Pdf*) curves dorsally and then posteriorly from the anterior surface of the transverse bar to the integument of the dorsal and posterior regions of the haptor.

It is not known whether these fibres are contractile, but their function appears to be that of anchoring the transverse bar firmly to the integument. It will be shown later than when the main hook-operating muscles contract there would be a tendency for the hooks to be drawn forwards in the body were

they not attached to a bar which is itself tethered to resist a pull in this direction.

The hooks are of the form illustrated in Text-figs. 8A and B. There is a slight but characteristic dissimilarity between the ventral and dorsal hooks, the former being the larger, especially in the 'shoulder' region. The distal curved regions of all four hooks are strongly birefringent, but the proximal



Text-fig. 7. The principal adhesive apparatus of *Amphibdelloides maccallumi*. For explanation of lettering see text pp. 566–9.

blade-like regions much less so. All parts of the hooks may be differentially stained with malachite green, and, less readily so, with haematoxylin. Such is the affinity of the strongly birefringent regions for picric acid that, following fixation in Bouin's fluid, they remain yellow even after prolonged immersion in alcohol, and subsequent staining with haematoxylin is inhibited. At the place where the tip of each hook leaves the body it is surrounded by a muscular sheath (Pl. III, fig. 1, *Ms*) which, in living specimens forcibly detached from the host, has been seen to oscillate rhythmically along the length of the basal region of the curved portion.

Each ventral hook is attached to the transverse bar by three bundles of fibres: short fibres from the ventral edge of the hook to the adjacent lateral ends of the transverse bar (*Vhbf*); long fibres from the dorsal region of the inner (= medial) surface of the hook to the lateral end of the transverse bar on the same side of the parasite (*Dhbf*); and long fibres from the same region of the hook (i.e. the dorsal region of the inner surface) obliquely ventro-laterally to the dorsal surface of the lateral region of the transverse bar on the other side of the parasite (*Dhobf*).

Each dorsal hook is attached to the ventral hook of the same side of the animal by fibres which pass from the ventral edge of the inner surface of the dorsal hook to the dorsal edge of the outer surface of the ventral hook (*Vd*). Some of these fibres, lying posterior to the level of the transverse bar, are not attached to the dorsal edge of the ventral hooks; instead they pass transversely across the body, dorsal to the dorsal edges of the ventral hooks, and become continuous with their fellows of the opposite side (*Dd*). Those fibres inter-connecting the ventral and dorsal hooks (*Vd*) serve to bind these hooks to each other in a manner that permits the rotation of these hooks, in the planes of their flat surfaces, about their regions of mutual attachment. The fibres connecting the two dorsal hooks with each other (*Dd*) probably serve to brace the whole system of hooks and fibres.

While the fibrous systems connecting the ventral and dorsal hooks (*Vd*) *could*, if they were indeed contractile, rotate the posterior parts of the hooks in opposite directions about the region of the transverse bar, nevertheless, the main actuation is produced by the contraction of a system of muscles attached to the anterior ends of the hooks. The proximal (anterior) end of each ventral hook bears a fibrous loop (*Fl*) through which passes the main extrinsic adductor muscle (*Eam*) of the same side of the body on its way to become attached to the proximal (anterior) end of the dorsal hook (*Dh*) of the same side. The part of the muscle passing through the loop, and its continuation to the dorsal hook are considerably narrower in diameter than the remainder of the muscle. In appearance this region resembles the tendons of the adhesive apparatus of *Plectanocotyle gurnardi* and *Kuhnia scombri*, but, unlike such tendons, they take up haematoxylin and xylidine ponceau and not light green in Masson's trichrome stain.

Since the hooks are pivoted about the transverse bar, contraction of the extrinsic adductor muscles (*Eam*) would draw the proximal ends of the dorsal and ventral hooks towards each other, and so cause the distal tips of the ventral hooks to rotate ventrally, and the distal tips of the dorsal hooks to rotate dorsally. When the parasite is located between successive secondary gill lamellae, such movements would result in the hooks impaling these lamellae and so securing the parasite to its host (Pl. II, fig. 1).

The action of the main extrinsic adductor muscles is augmented by the contraction of smaller intrinsic adductor muscles (*Iam*) connecting directly

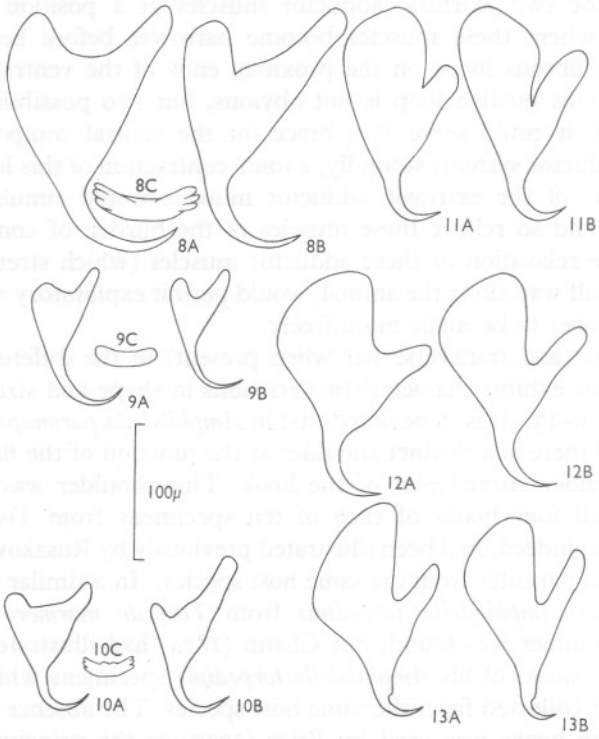
with one another the proximal ends of the dorsal and ventral hooks on the same side of the body. The proximal ends of the dorsal hooks are connected to each other by a bracing muscle (*Bm*).

From the proximal end of each of the dorsal hooks a muscle passes ventrolaterally towards the other side of the body, crosses its fellow from the other side, and then contributes to the formation of a single median loop (*Ml*) that surrounds the two extrinsic adductor muscles at a position immediately anterior to where these muscles become narrower before being threaded through the fibrous loops on the proximal ends of the ventral hooks. The function of this median loop is not obvious, but two possibilities are suggested: first, it could serve as a brace for the ventral components of the extrinsic adductor system; secondly, a tonic contraction of this loop about the narrow parts of the extrinsic adductor muscles would simulate a 'catch' mechanism and so relieve these muscles of the burden of continuous contraction; the relaxation of these adductor muscles (which stretch anteriorly more than half way along the animal) would permit exploratory movements of the body proper to be made more freely.

The hooks (and transverse bar when present) in the different species of amphibdellids exhibit characteristic variations in shape and size as indicated in Text-figs. 8–13. It is to be noted that in *Amphibdella paronaperugiae* (Text-figs. 13A, B) there is a distinct shoulder at the junction of the flattened blade with the slender curved part of the hook. This shoulder was found to be present in all four hooks of each of ten specimens from *Torpedo torpedo* examined, as, indeed, had been illustrated previously by Ruszkowski (1931) in amphibdellid parasites from the same host species. In a similar sample of ten specimens of *Amphibdella torpedinis* from *Torpedo marmorata* no corresponding shoulder was found, but Chatin (1874) had illustrated a shoulder region in the hooks of his *Amphibdella torpedinis* specimens which were said to have been collected from the same host species. The absence of a shoulder region in the hooks was used by Price (1937) as the principal distinction between *A. flavolineata* MacCallum, 1916 and Chatin's *A. torpedinis*. The evidence from the present study of amphibdellids suggests very strongly that either Chatin's drawing of the hooks, or his identification of the host, was inaccurate. Since the remainder of Chatin's description of *A. torpedinis* would be grossly inaccurate for any amphibdellid, it is proposed here to disregard his description of the shape of the hook, and to accept his identification of the host.

The muscles associated with the hooks and transverse bar in *Amphibdelloides vallei* and *A. narcine* are arranged exactly as those in *A. maccallumi* described above. In *Amphibdella flavolineata*, *A. torpedinis*, and *A. paronaperugiae* there is no transverse bar, and the fibres associated with such a bar in *Amphibdelloides* are absent. In *Amphibdella torpedinis* and *A. paronaperugiae* the adductor muscle system differs from that of *Amphibdelloides*

maccallumi in that no median loop (*Ml* in Text-fig. 7) is present, but the 'bracing muscle' (*Bm* in Text-fig. 7) is relatively much better developed. The hook muscles in *Amphibdella flavolineata* are arranged completely differently from those of the other five amphibdellid species studied: there are no fibrous loops on the proximal ends of the ventral hooks (*Fl* in Text-fig. 7), there is



Text-figs. 8–13. The hooks and supporting bars of amphibdellids, all drawn to the same scale. A, ventral hooks; B, dorsal hooks, C, supporting bars. Figs. 8A, B. C. *Amphibdelloides maccallumi*. Figs. 9A, B, C. *A. vallei*. Figs. 10A, B, C. *A narcine*. Figs. 11A, B. *Amphibdella flavolineata*. Figs. 12A, B. *A. torpedinis*. Figs. 13A, B. *A. paronaperugiae*. (Figs. 10A, B after Hargis, 1955.)

no 'median loop' (*Ml* in Text-fig. 7) and there are no muscles connecting the hooks of the left side of the parasite with those of the right. The muscles that are present consist of simple longitudinally running bundles, one relatively weak bundle from each hook going posteriorly to the integument between the posterior median hooklet-bearing lobes, and much better developed bundles on each side running anteriorly to beyond the neck region of the haptor.

Posterior glands

At the posterior end of the body of *Amphibdelloides maccallumi*, between the posterior regions of the vitellaria and the hooks of the adhesive apparatus, is a prominent mass of gland cells (Text-fig. 1). Posteriorly some extensions from the gland flank the large hooks of the adhesive apparatus and probably lead one to each of the two posterior median hooklet-bearing lobes.

There is no trace whatsoever, in whole specimens or in sections, of a corresponding gland in either juveniles or adults of *Amphibdella flavolineata*, but well-developed glands are present in *A. torpedinis* and *A. paronaperugiae*. A prominent posterior gland is also present in *Amphibdelloides vallei* but Hargis (1955) did not report a posterior gland in *A. narcine*, nor have I been able to find one in Hargis's specimens.

The gland cells have coarsely granular contents that readily take up carmine stains and acid dyes such as light green, aniline blue, and xylidine ponceau; they give a strongly positive result when treated with the periodic acid-Schiff test for polysaccharides. Because of its topographical situation, the gland appears likely to play a part in the attachment of the parasite to its host. If this be so, the secretion of the gland might either histolyse the host tissues or act as a cement. However, in sections of *A. maccallumi* attached to *Torpedo nobiliana* (Pl. II, fig. 1) the host epidermis, though stretched and compressed, showed no signs of erosion apart from the perforations made by the large hooks themselves; nor was any cement substance to be seen between the parasite and host tissues though such cement, if present in living parasites, could of course have been removed by histological processing.

ANTERIOR GLANDS

At the anterior end of *Amphibdelloides maccallumi*, and opening on to the three pairs of papillae on the anterio-lateral borders of the parasite, are some well defined anterior glands (Text-fig. 14). Their function is not known, but presumably it is either adhesive (to keep the mouth in a feeding position) or histolytic (to soften host tissues to permit ingestion).

Exactly similarly disposed glands are present in *A. vallei* and *A. narcine*, but in all three species of *Amphibdella*, namely, *A. flavolineata*, *A. torpedinis*, and *A. paronaperugiae*, there are no papillae and the openings of the ducts of the glands nearly always converge to form a single mass on each side of the body (Text-fig. 15). In a sample of ten balsam-mounted preparations of *A. flavolineata* a subdivision into three tracts of ducts could be recognized on one side only of each of two specimens, and in one living specimen examined especially for this character, there was no trace of subdivision within the paired masses of anterior glands. The same situation occurs in *A. torpedinis*, but I have found no evidence of any subdivision at all in the paired anterior

glands of *A. paronaperugiae*. Ruszkowski (1931, fig. 1) illustrated a single mass of 'cephalic glands' in parasites from *Torpedo torpedo* which he called *Amphibdella torpedinis* but which the present study shows to belong to the new species *A. paronaperugiae*.

GENITALIA

Male (Text-figs. 14–22)

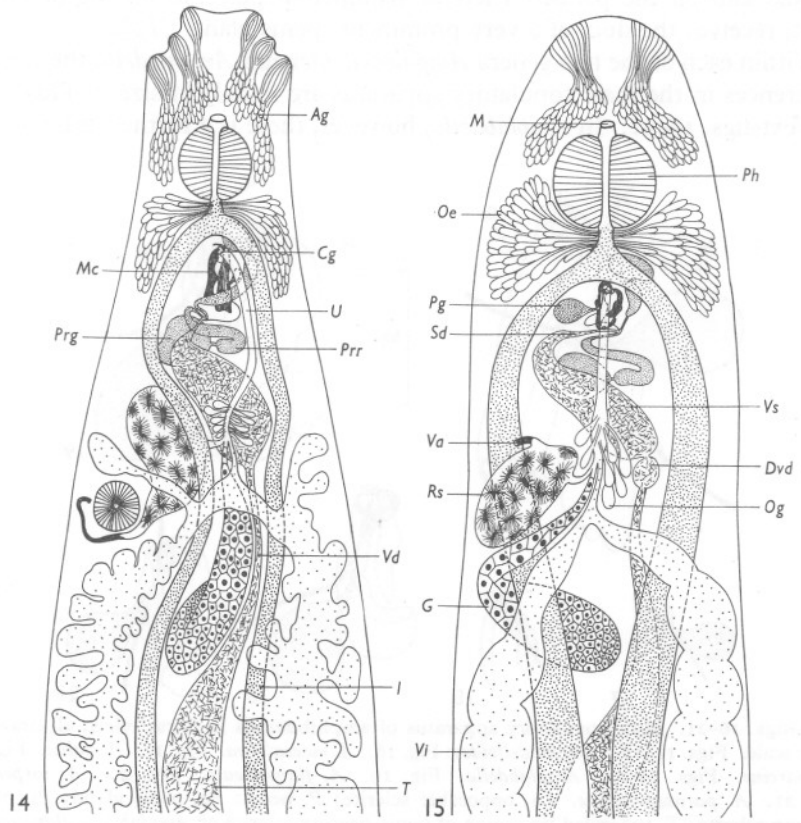
In all of the six species of amphibdellid studied there is a single testis (*T*) lying between the two intestinal limbs in the mid-dorsal region of the body, and extending posteriorly almost to the posterior ends of these intestinal limbs. Anteriorly the testis gives rise to the vas deferens (*Vd*) which passes obliquely forwards, towards the animal's left, to the posterior end of the vesicula seminalis (*Vs*). In *Amphibdelloides* the undifferentiated vas deferens enters the vesicula seminalis directly, but in *Amphibdella* a well developed and characteristic dilatation of the vas deferens (*Dvd*) is present immediately posterior to the vesicula seminalis.

The vesicula seminalis is a prominent organ with walls provided with well developed longitudinal and transverse muscle fibres that may be seen especially easily in living specimens examined in polarized light. The vesicula seminalis passes obliquely forwards from the animal's left towards the right, and at its anterior end gives off a sperm duct (*Sd*) which passes towards the left. This sperm duct then receives two ducts, one from each of the two prominent 'prostate' reservoirs (*Prr*) and the union of all three ducts has common and direct access to the slightly expanded base of the sclerotized penis which curves away anteriorly. Each prostate reservoir is connected by a short and very narrow duct (2–3 μ in diameter) with a relatively large 'prostate' gland (*Prg*). The disposition of the two prostate reservoirs (which, in whole specimens, are much more prominent than their associated glands), one anterior and the other posterior to the junction of the sperm duct with the penis, is characteristic of the family.

The copulatory apparatus consists of a very long slender sclerotized penis accompanied by a pair of relatively very large robust accessory sclerites which resemble somewhat a pair of pincers. This apparatus lies in the sagittal plane of the parasite with its proximal, posterior end lying dorsally in the body and with its long axis sloping anteriorly and ventrally so that the penis emerges on the ventral surface of the body. Its detailed structure may be seen only in well-flattened and consequently distorted specimens, and is best studied when dissected from fresh or partly decomposed specimens.

In both *Amphibdella* and *Amphibdelloides* (Text-figs. 16–21) there is a single-pointed strongly curved hook-like accessory sclerite on the parasite's left, and a differently shaped accessory sclerite on the right. In *Amphibdella* this right sclerite is a tube with an open trumpet-shaped distal end, but in

Amphibdelloides it is a hook. In *A. maccallumi* this hook bears five prongs lying in different planes so that it is only rarely that all five may be seen in one specimen. While the function of the combined pair of accessory sclerites is probably identical in *Amphibdella* and *Amphibdelloides*, namely, to act as a



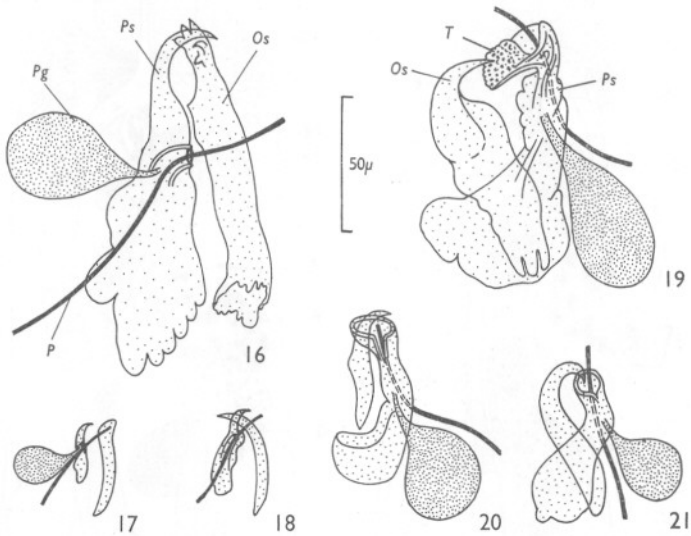
Text-figs. 14, 15. Genitalia and anterior glands of amphibdellids. Fig. 14. *Amphibdelloides maccallumi*. Fig. 15. *Amphibdella flavolineata*. *Ag*, anterior gland; *Cg*, common genital opening; *Dvd*, dilatation of vas deferens; *I*, intestine; *G*, germarium; *M*, mouth; *Mc*, male copulatory apparatus; *Oe*, oesophageal glands; *Og*, ootype glands; *Pg*, penis gland; *Ph*, pharynx; *Prg*, 'prostate' gland; *Prr*, 'prostate' reservoir; *Rs*, receptaculum seminis; *Sd*, sperm duct; *U*, uterus; *Va*, vagina; *Vd*, vas deferens; *Vi*, vitellarium; *Vs*, vesicula seminalis; *T*, testis.

pair of pincers to grasp the vaginal region of the co-copulant and so to facilitate the insertion of the slender penis, nevertheless, there is a great difference in the division of labour between the two members of the pair of accessory sclerites in the two genera. In *Amphibdelloides* the single-hooked sclerite of the left (*Ps*) is perforated to carry the penis, with the hook of the right serving as the opposable pincer (*Os*), whereas in *Amphibdella* it is the trumpet-like

sclerite of the right side which acts as the penis-bearer (*Ps*) and the single-hooked sclerite of the left as the opposable sclerite (*Os*).

At the point of entry of the penis into the penis-bearing sclerite, this sclerite in all species of both genera (excepting *Amphibdelloides narcine*) whether it be hooked and on the parasite's left or trumpet-shaped and on the parasite's right, receives the duct of a very prominent 'penis gland' (*Pg*).

Within each of the two genera *Amphibdelloides* and *Amphibdella* the specific differences in the male copulatory apparatus are mainly of size, as illustrated in Text-figs. 16–21. In *Amphibdella*, however, there is a further difference in

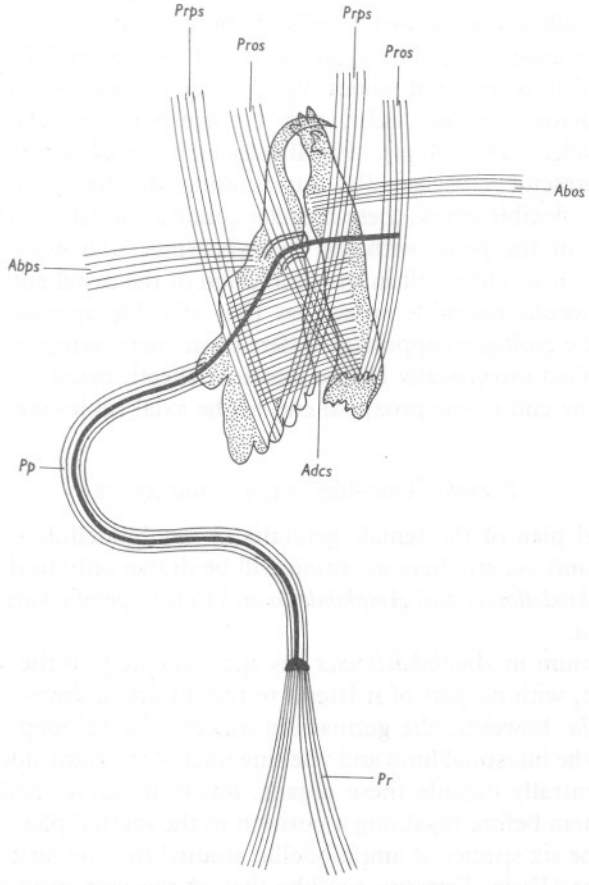


Text-figs. 16–21. Male copulatory apparatus of amphibdellids in dorsal view, all drawn to same scale. Figs. 16–18. *Amphibdelloides*: Fig. 16. *A. maccallumi*. Fig. 17. *A. vallei*. Fig. 18. *A. narcine*. Figs. 19–21. *Amphibdella*. Fig. 19. *A. flavolineata*. Fig. 20. *A. torpedinis*. Fig. 21. *A. paronaperugiae*. *Os*, opposable sclerite; *P*, penis; *Pg*, penis gland; *Ps*, penis-bearing sclerite; *T*, tubercled lip region of penis-bearing sclerite of *Amphibdella flavolineata*.

that while the distal end of the penis-bearing sclerite of *A. flavolineata* has a prominent tubercled 'lower-lip' region (*T* in Text-fig. 19), such a feature is absent from *A. torpedinis* (Text-fig. 20) and *A. paronaperugiae* (Text-fig. 21). In *Amphibdelloides narcine*, Hargis (1955) did not report, nor have I been able to find, a penis gland. Again in *A. narcine* the accessory sclerites were described by Hargis as being only 18–31 μ in length, but in well-flattened specimens, or in specimens in which the copulatory sclerites can be seen in side view, I have found the opposable sclerite to be 37 (36–40) μ long.

The copulatory apparatus of amphibdellids is provided with various muscles, the most prominent of which are indicated in Text-fig. 22, which was constructed from observations of whole mount specimens of *A. maccallumi*

seen in polarized light. Smaller muscles, which appear to be antagonists to some of the larger ones included in Text-fig. 22, are also present, but they have been omitted from the diagram to reduce confusion. A special hazard in the determination of the distribution of the muscles of the copulatory



Text-fig. 22. The male copulatory apparatus of *Amphibdelloides maccallumi*, accessory sclerites somewhat displaced to permit illustration of muscles. *Abos*, abductor of opposable sclerite; *Abps*, abductor of penis-bearing sclerite; *Adcs*, adductor of copulatory sclerites; *Pp*, protractors of penis; *Pr*, retractors of penis; *Pros*, protractors of opposable sclerite; *Prps*, protractors of penis-bearing sclerite.

apparatus was the presence of sphincter muscles (not shown in Text-fig. 22) surrounding the opening of the genital atrium and lying immediately ventral to the distal ends of the copulatory sclerites.

The copulatory apparatus has not been seen working, but from a consideration of the spatial relationships between the various parts in *A. mac-*

callumi it seems likely that its mode of action is as follows. With the distal end of the penis still contained within the penis-bearing sclerite, the distal ends of the two copulatory sclerites are extruded through the opening of the common genital atrium by the contraction of the protractor muscles, of which each copulatory sclerite has a pair (*Pros*, *Prps*). Next the abductor muscles (*Abos*, *Abps*) pull apart the distal ends of the copulatory sclerites as a preliminary to the grasping of the vaginal region of the body of the co-copulant, an action which is brought about by the contraction of the proximally situated adductor muscles (*Adcs*) and a corresponding relaxation of the abductor muscles (*Abos*, *Abps*). Finally, there is a contraction of the loose sleeve of protractor muscles (*Pp*) surrounding the long, slender, curved sclerotized but flexible penis; these muscles connect the sclerotized disc at the proximal end of the penis with the penis-bearing copulatory sclerite, and their contraction would result in the protrusion of the distal end of the penis. Such action would resemble somewhat that of cable-operated mechanical devices, but the biological apparatus differs from engineering ones in that the power is supplied intrinsically by the sleeve or sheath being itself contractile and fixed at one end to the proximal end of the axial cable-like penis.

Female (Text-figs. 14, 15, and 23–28)

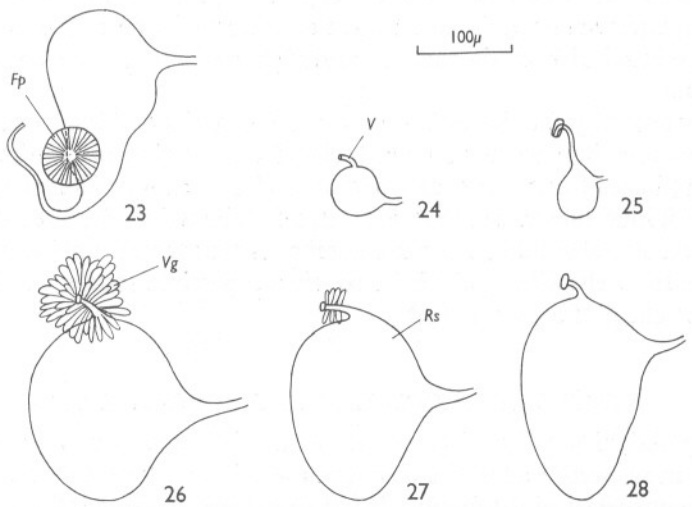
The general plan of the female genitalia in amphibdellids is as shown in Text-figs. 14 and 15, and here attention will be drawn only to the differences between *Amphibdelloides* and *Amphibdella* and to the specific variations within the two genera.

The germarium in *Amphibdelloides* lies approximately in the sagittal plane of the parasite, with no part of it lateral to the intestinal limbs and vitellaria. In *Amphibdella*, however, the germarium makes a lateral loop which passes first dorsal to the intestinal limb and vitelline tract of the right side of the body, then turns ventrally outside these organs, finally to curve medially to pass ventrally to them before regaining a position in the sagittal plane of the body.

In five of the six species of amphibdellid studied the vitellarium was found to be follicular (*Vi* in Text-fig. 14) like that of the vast majority of monogeneans, but in *A. flavolineata* the vitellarium was found to consist of two long tubes exhibiting only a very slight degree of lobing. Paraffin sections of *A flavolineata* showed no trace of a follicular organization inside the vitellarium.

In *Amphibdelloides* the vagina opens on the dorso-lateral surface of the body, but in *Amphibdella* it opens on the ventro-lateral surface. Within each of the two genera, the main variations in the female genitalia are as follows: differences in the length of the sclerotized vagina; variations in the site of origin of the vagina from the receptaculum seminis; differences in the form of the distal end of the vagina, whether a simple tube or whether provided with an

expanded sclerite; the presence or otherwise, and the degree of development of, a vaginal gland; and the size, and sometimes the shape, of the receptaculum seminis. With regard to the last character, it must be pointed out that in most species the receptaculum seminis in life is probably spherical, but that it suffers considerable change when specimens are flattened. In *Amphibdelloides maccallumi*, however, the receptaculum seminis is characteristically pyriform with the narrow end directed posteriorly. Moreover, a special organ ('fibrous pad') is present in this species, and will be described below. The particular form of the female copulatory apparatus in the various amphibdellids is illustrated in Text-figs. 22–28, and will be referred to in the specific diagnoses on pp. 580–2.



Text-figs. 23–28. Female copulatory apparatus of amphibdellids in dorsal view, all drawn to same scale. Figs. 23–25. *Amphibdelloides*. Fig. 23. *A. maccallumi*. Fig. 24. *A. vallei*. Fig. 25. *A. narcine*. Figs. 26–28. *Amphibdella*. Fig. 26. *A. flavolineata*. Fig. 27. *A. torpedinis*. Fig. 28. *A. paronaperugiae*. *Fp*, fibrous pad; *Rs*, receptaculum seminis; *V*, vagina; *Vg*, vaginal gland.

Near to the vaginal opening in *A. maccallumi* there is a thick disc of fibrous tissue simulating somewhat the appearance of a sucker (Text-figs. 14, 23). In this disc the fibres are arranged perpendicularly to the body surface of the parasite, but they are not bounded from the underlying tissue by a basement membrane. Moreover, there appears to be no trace of a concavity on the outer surface of the organ such as is present in ordinary acetabulate suckers. It is necessary to point out too that this fibrous disc lies to one side of (and so does not surround) the vaginal opening as it was described to do so by Alexander (1954) in *A. maccallumi* from *Torpedo californica*. The fibrous disc is not easily seen in whole specimens except when observed by phase contrast

microscopy, but it is readily seen in sections (Pl. II, fig. 1 on the dorsal surface of the parasite, one-quarter of the length of the animal from the anterior end). Dr Alexander was kind enough to lend me some of his specimens of *A. maccallumi* from *Torpedo californica*, and I have confirmed that the position of the fibrous disc in these specimens is the same as in Plymouth specimens of *Amphibdelloides maccallumi*. There is no trace of a corresponding organ in the other amphibdellids studied.

If the fibrous disc is in fact a sucker, then its special function would appear to be that of attaching the vaginal region of the parasite to the genital atrial region (i.e. the region of the extruded accessory copulatory sclerites) of the co-copulant. But if the organ is not a sucker, as indeed seems the more likely, then it is possible that it serves as a 'toughened pad' which may be gripped firmly by, and even be perforated by, the accessory sclerites of the co-copulant with a reduced risk of damage to underlying organs such as the gut or vitellarium.

It is noteworthy that in both *Amphibdelloides* and *Amphibdella* the sperms in the receptaculum are not randomly distributed as they are in the vesicula seminalis; instead they are aggregated around spherical or elongated masses of an acidiphilic substance (Text-figs. 14, 15). The walls of the receptaculum seminis are not glandular, and the inference is that the acidiphilic substance has come from elsewhere; if this be so, then a possible source would be the 'prostate' gland of a co-copulant.

STATUS OF BLOOD-LIVING AMPHIBDELLIDS

The amphibdellids collected from the hearts of electric rays were examined carefully in respect of all of the characters which have been found to vary in the different species of the family. It was found that specimens from the heart of *Torpedo nobiliana* were very similar to specimens of *Amphibdella flavolineata* from the parietal mucosa of the gills of the same host, differing only in their smaller size, in the absence of enlarged hooklet-bearing lobes, in the absence of vitellaria, and in the presence of only a rudimentary germarium. The size and shape of the accessory sclerites of the male copulatory apparatus, including the tubercled trumpet-shaped opening of the penis-bearing sclerite, was identical in the blood stream and gill mucosa forms, as also were the position of the ventrally opening vagina anterior to the receptaculum seminis, the presence of a dilatation in the vas deferens immediately preceding the vesicula seminalis, the shape of the large hooks, and the absence of a transverse bar and a posterior gland.

An almost parallel situation was present in the amphibdellids from the heart of *Torpedo marmorata*, but here a rudimentary posterior gland was present, and the shape and size of the hooklet-bearing lobes of the haptor was as in *Amphibdella torpedinis* from the parietal mucosa of the gills.

It is noteworthy that in the amphibdellids from the hearts of both *Torpedo nobiliana* and *T. marmorata*, while the female gonads were invariably undeveloped, in all specimens examined the vesicula seminalis was full of sperms showing that the testis was already functional. Moreover, the receptaculum seminis was invariably well filled with sperms, indicating that copulation had probably taken place.

The obvious inference is that these amphibdellids from the blood systems of their hosts are 'juvenile' specimens of the *Amphibdella* species which attaches itself to the gill mucosa of the particular host species. The blood parasites are juvenile in that the female genitalia are as yet immature, but the male genitalia are already mature. An alternative view would be to regard the blood-living parasites as protandrous adults.

The advantage of a protandrous stage living freely in the blood stream would be in the greatly improved opportunities for meeting a partner and so of permitting cross-fertilization to take place. Copulation between gill specimens permanently anchored in the subcutaneous tissues of the host would be restricted to those specimens happening to lie very near to each other. Such a distribution has been observed occasionally in *A. torpedinis*, but in none of the specimens of *A. flavolineata* that I have collected from the gills would copulation have been possible.

The life-cycle of species of the genus *Amphibdella* then would appear to be as follows. Free-living sixteen-hooked oncomiracidia encounter the appropriate torpedinid host and, instead of settling permanently on the superficial gill tissues as other monogenean gill parasites are thought to do, penetrate into the blood vessels of the gills. The larva is carried around in the blood stream and develops until eventually it exchanges sperms with a co-copulant. It would then emerge, anterior end first, through the gill mucosa (the parasite being too big to enter the capillaries of the secondary lamellae), thus exposing the uterine aperture for oviposition, and with the posterior end remaining within the host tissues. It seems unlikely that the parasite would emerge completely and then re-insert the posterior end of its body into the host, for there appears to be no boring apparatus present; 'posterior glands' of uncertain function are indeed present in *A. torpedinis* and *A. paronaperugiae* but are absent from *A. flavolineata*. Ruszkowski (1931) found egg-laying specimens and free egg capsules of *A. paronaperugiae* in the blood system of *Torpedo torpedo*; but he also reported (p. 163) individuals of the same species as living on the gills; it is possible that the egg-capsules in the blood system were merely an example of precocious egg-laying.

TAXONOMY

The preceding comparisons of amphibdellids from various micro-habitats on various torpedinid host species have made necessary certain taxonomic revisions; these are given below.

Family: AMPHIBDELLIDAE Bychowsky, 1957 emend.

Tetraonchidea (Bychowsky, 1957) with bifurcate but otherwise unbranched intestine; adults with two pairs of large hooks, with or without a single supporting bar; sixteen persistent oncomiracidial hooklets arranged as five lateral pairs including four marginal pairs and one submarginal pair, and two median pairs including one posterior terminal pair and one centrally placed pair; eyes absent in oncomiracidium and adult; adults parasitic on secondary gill lamellae or gill mucosa of Torpedinidae, but juveniles of some species endoparasitic in blood system of host. Type genus: *Amphibdella* Chatin, 1874.

The above family diagnosis differs from that given by Bychowsky in that it recognizes that the supporting bar is absent from half of the known species, and in that it gives more details about the distribution of persistent oncomiracidial hooks in the adult, and about the micro-habitats of the parasites. Since the type genus is *Amphibdella*, the family name should be Amphibdellidae not 'Amphibdellatidae' as given by Bychowsky.

Genus: **Amphibdella** Chatin, 1874

Amphibdellidae without transverse bar supporting the large hooks; posterior gland present or absent; germarium loops around right intestinal limb; vitellarium follicular or tubular; vaginal opening on ventro-lateral surface of body; with or without vaginal gland; vagina arising from anterior end of receptaculum seminis; with dilatation in vas deferens immediately preceding vesicula seminalis; right male copulatory sclerite trumpet-shaped and serving as penis-bearer, left male copulatory sclerite with terminal hook; adults parasitic on mucosa of gills, but some development, involving protandry, takes place in blood system of host. Type species: *Amphibdella torpedinis* Chatin, 1874.

Amphibdella torpedinis Chatin, 1874

Length 4·45 (3·20–5·68) mm, width 0·68 (0·60–0·80) mm; haptor not separated from remainder of body by a narrow neck; hooklet-bearing lobes not greatly enlarged; large hooks 155 (136–172) μ long, of characteristic shape illustrated in Text-figs. 12A, B and lacking a distinct shoulder at the junction of the broad flattened part with the curved slender part; with posterior gland; penis-bearing copulatory sclerite 64 (60–78) μ long and with smooth trumpet; vaginal gland poorly developed; distal end of vagina slightly swollen to about 8–10 μ external diameter; parasites of gill mucosa of *Torpedo marmorata* with part of juvenile development in blood system of same host.

Amphibdella paronaperugiae sp.nov.

Length 3·82 (2·60–4·80) mm, width 0·37 (0·24–0·46) mm; large hooks 138 (132–148) μ long, with distinct shoulder at junction of broad flattened part with curved slender part as illustrated in Text-figs. 13A, B; vaginal gland absent; distal end of vagina swollen to 12–16 μ external diameter; penis-bearing copulatory sclerite 54 (48–58) μ long; parasites of gill mucosa of *Torpedo torpedo*, but some egg-laying adults, probably precociously developed, have been reported from the blood system of the host. Other characters as in *Amphibdella torpedinis*.

Amphibdella flavolineata MacCallum, 1916

Length 4·85 (3·20–6·60) mm, width 0·75 (0·40–1·20) mm; haptor separated from remainder of body by a narrow neck; two median pairs of hooklet-bearing lobes greatly expanded; large hooks 156 (152–160) μ long and lacking distinct shoulder at junction of broad flattened part with curved slender part as illustrated in Text-figs. 11A, B; without posterior gland; vitellarium tubular and not follicular; penis-bearing copulatory sclerite 102 (96–116) μ long with tubercled lip to trumpet as illustrated in Text-fig. 19; with very well-developed vaginal gland; distal end of vagina only very slightly swollen to about 6–8 μ external diameter; parasites of gill mucosa of *Torpedo nobiliana*, with part of juvenile development in blood system of same host.

Genus: **Amphibdelloides** Price, 1937

Amphibdellidae with transverse bar supporting the large hooks; posterior gland present; germarium lying entirely within the intercaecal field; vitellarium always follicular; vagina opening on dorso-lateral surface of the body; without vaginal gland; vagina arising from anterior or posterior end of receptaculum seminis; without dilatation in vas deferens; left copulatory sclerite hook-shaped and serving as penis-bearer, right copulatory sclerite another hook, sometimes with terminal prongs; adults parasitic on secondary gill lamellae of hosts, juvenile development not known. Type species: *Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price 1937.

Amphibdelloides maccallumi (Johnston & Tiegs, 1922) Price, 1937

Length 2·66 (2·00–3·00) mm, width 0·45 (0·32–0·58) mm; large hooks 172 (160–194) μ long, of characteristic shape illustrated in Text-figs. 8A, B and supported by a transverse bar 79 (72–84) μ long; with fibrous pad near vaginal aperture; vagina arising from posterior end of receptaculum seminis and ending in a simple tubular opening; receptaculum seminis pyriform with narrow end directed posteriorly; penis-bearing copulatory sclerite 140 (130–160) μ long; parasitic on *Torpedo nobiliana* and *T. californica*.

Amphibdelloides vallei sp.nov.

Length 0·86 (0·60–1·20) mm, width 0·14 (0·10–0·24) mm; large hooks 100 (92–104) μ long, of characteristic shape illustrated in Text-figs. 9A, B and supported by a transverse bar 44 (42–48) μ long; without fibrous pad near vaginal opening; vagina arising from anterior end of receptaculum seminis and ending in a simple tubular opening; receptaculum seminis spherical; penis-bearing copulatory sclerite 37 (35–38) μ long; parasitic on *Torpedo marmorata*.

Amphibdelloides narcine Hargis, 1955 (diagnosis based mainly on Hargis, 1955)

Length 0·90 (0·79–1·87) mm, width 0·16 (0·15–0·19) mm; large hooks 97 (85–108) μ long, of characteristic shape illustrated in Text-figs. 10A, B and supported by a transverse bar 35 (26–51) μ long; without fibrous pad near vaginal opening; vagina arising from anterior end of receptaculum seminis and ending in a sclerotized plate about 18 (16–20) μ long by 10 (8–12) μ wide (in the illustration of the sclerotized plate of the vagina by Hargis, 1955, fig. 18, the scale is erroneously magnified by a factor of about 5); receptaculum seminis slightly pyriform with narrow end directed anteriorly; penis-bearing copulatory sclerite 37 (36–40) μ long (see p. 574); parasitic on *Narcine brasiliensis*.

Other species of the Amphibdellidae

Both Monticelli (1890) and Ruszkowski (1931, footnote to p. 164) have referred to what is likely to be a new species of *Amphibdelloides* from the secondary gill lamellae of *Torpedo torpedo*.

Bychowsky (1957) has referred to an amphibdellid from the gills of *T. smithi* from the Arabian Sea, Baluchistan.

I have had an opportunity of seeing a new species of *Amphibdella* from the gills of *Narcine timlei* from South India; this amphibdellid was found by and will be described by Mr R. V. Unnithan.

On the basis of the above classificatory scheme, it is now proposed to review the taxonomic histories of the various amphibdellid species.

The first monogenean from an electric ray was described by Chatin (1874) as *Amphibdella torpedinis* (without a transverse bar in the adhesive apparatus) and was collected from the gills of *Torpedo marmorata* at Naples. Chatin's description was vague and inaccurate, and a more detailed diagnosis of the species, based on specimens collected from the same host species at Sète (Mediterranean, Gulf of Lyons), is given in the present paper.

Monogeneans were also found on this same host *T. marmorata* at Trieste by Valle, who sent the parasites to Genoa, where they were described by Perugia and Parona (1890) under the name of '*Amphibdella torpedinis* Chatin'. Valle's specimens were said to have one transverse bar in the adhesive apparatus, but in a later paper (Parona & Perugia, 1890) this observation was qualified: it was now stated that there were really two bars present, one of them having been omitted from the illustration in the earlier paper for the sake of simplicity. In describing two bars as being present, however, Parona & Perugia were almost certainly mistaken: as pointed out by Bychowsky (1957), what was thought to be the second transverse bar was very probably the muscle connecting the anterior ends of one of the pairs of hooks. A corresponding muscle (*Bm*) in *Amphibdelloides maccallumi* is illustrated in Text-fig. 7. This second amphibdellid (with one transverse bar) from *Torpedo marmorata* has been designated in the present study a new species *Amphibdelloides vallei*.

Following their description (written in November 1889) of Valle's amphibdellids from *Torpedo marmorata*, Parona and Perugia (1890) themselves

collected and described in April 1890 some monogeneans from *T. torpedo* (syn. *T. narce*) at Genoa. These parasites were collected not from the gill lamellae, but from the parietal mucosa of the gill chamber, and were found to be without a transverse bar. Though Parona & Perugia described the parasites from the parietal mucosa of *T. torpedo* as *Amphibdella torpedinis* Chatin, their specimens (from the C.E.C.I., Naples) have been re-examined in the course of the present study and were found to belong in fact to a new species (without bar) for which the name *A. paronaperugiae* has been proposed. The same species was collected from the gills of *Torpedo torpedo* (syn. *T. ocellata*) at Naples by Ruszkowski (1931, p. 163), and also from the heart and urinogenital system of this host, the specimens being identified by Ruszkowski as Chatin's '*Amphibdella torpedinis*'.

At about the same time that Parona & Perugia discovered the amphibdellid *without* a transverse bar on the parietal mucosa of the gills of *Torpedo torpedo* at Genoa, Monticelli (1890) recorded under the name of '*Tetraonchus torpedinis* Chatin' what is probably a second species (*with* a transverse bar) from the same host species *Torpedo torpedo* (syn. *T. narce*) at Naples; this same species was probably recorded again from the same host *T. torpedo* (syn. *T. ocellata*) at Naples by Ruszkowski (1931, footnote to p. 164). Monticelli referred to the presence of two transverse bars, but in this he almost certainly made a mistake similar to that made by Parona & Perugia (1890) and referred to above. Thus it is highly desirable that the gills of *T. torpedo* be searched again for a second species of amphibdellid and that the parasite be described in detail.

MacCallum (1916) discovered two species of amphibdellids on the gills of *T. nobiliana* (syn. *Tetranarce occidentalis*) from Woods Hole, U.S.A., and identified one of them (*with* a transverse bar!) as Chatin's *Amphibdella torpedinis* and the other (without a transverse bar) as a new species *A. flavolineata*. Johnston & Tiegs (1922) proposed a new species *A. maccallumi* for MacCallum's specimens of '*A torpedinis*' and later Price (1937) made this species the type of a new genus *Amphibdelloides* characterized by the presence of a transverse bar. In the course of the present study MacCallum's specimens have been borrowed from the United States National Helminthological Collection and have been compared with specimens of *A. maccallumi* and *Amphibdella flavolineata* from the same host *Torpedo nobiliana* captured in Europe (Plymouth, Irish Sea, Irish Atlantic Slope, and Mediterranean), and have been found to be identical. It is concluded that Price's recognition of two distinct genera according to the presence or absence of a transverse bar is basically sound, but that Price's second character, namely, that concerning the lobing of the posterior adhesive apparatus, needs considerable modification. Such a modification, together with some new generic characters, is proposed on pp. 580–2.

Palombi (1949), in his review of trematodes from Italy, regarded all amphi-

bdellids previously recorded from Mediterranean hosts as belonging to one species *Amphibdella torpedinis* in which a transverse bar was constantly present and distinct in small specimens, but absent from large specimens.

Recently Alexander (1954) has recorded and redescribed *Amphibdelloides maccallumi* from *Torpedo californica* from California. I have compared some of Alexander's actual specimens with MacCallum's specimens and also with specimens of *Amphibdelloides maccallumi* from *Torpedo nobiliana* (i.e. the same host species as that from which MacCallum's material was collected) from various European localities, but can find no significant differences between any of them. Then in spite of the strongly suggestive evidence from the difference in host species and the difference in geographical distribution, on morphological grounds the amphibdellids with a transverse bar from *T. californica* and *T. nobiliana* must both be recognized as *Amphibdelloides maccallumi*. The inference from this parasitological evidence is that the divergence between *Torpedo californica* and *T. nobiliana* took place very recently, and support is thus given to the view of Fraser-Brunner (1949) who placed both *T. nobiliana* and *T. californica* in the subgenus *Tetronarce*, whereas *T. torpedo* and *T. marmorata* were regarded as belonging to the subgenus *Torpedo*.

Hargis (1955) described a new species *Amphibdelloides narcine* from *Narcine brasiliensis* from the Gulf of Mexico, and Euzet (1957) described the oncomiracidium of what he regarded at that time as *Amphibdelloides maccallumi* from the gills of *Torpedo marmorata* and *T. nobiliana* but which the present study has shown might properly belong either to *A. maccallumi* or to the new species *A. vallei*.

Bychowsky (1957) in surveying the systematics of the Monogenea, found previous work on amphibdellids to be inaccurate and contradictory, and in an attempt to clear up the confusion, studied specimens, some of them living, from *Torpedo marmorata*, *T. torpedo* (syn. *T. ocellata*), *T. californica* and *T. smithi*. He confirmed the observations of Ruszkowski and Palombi that there were sixteen hooklets on the haptor, and properly emphasized the phylogenetic significance of this observation. But Bychowsky refuted Price's (1937) recognition of two amphibdellid genera separated from each other by the presence or absence of a transverse bar and by the lobed or unlobed condition of the haptor, claiming that a transverse bar was always present but that it may be inconspicuous in older specimens, and that the lobing of the haptor could be greatly affected by histological fixation. The present study of the functional morphology of the adhesive apparatus has shown that the transverse bar is an integral part of the adhesive apparatus of those amphibdellids which hook themselves to secondary gill lamellae, and that it is absent from those amphibdellids which 'root' themselves subcutaneously in the gill mucosa. Thus Price's view that the presence or absence of the transverse bar was of taxonomic significance was well-founded. At the same time the

present study agrees with Bychowsky's rejection of the second generic character used by Price, namely, the alleged unlobed condition of the haptor in *Amphibdelloides*. In place of Price's recognition of two genera of *Amphibdellidae* based on two characters (one of which was mis-interpreted), and of Bychowsky's recognition of a single genus, the present study accepts the same two genera as those accepted by Price, but on a basis of at least six contrasting characters, only one of which had been used by Price.

PHYLOGENY

On the basis of the above comparative morphological and taxonomic studies of the Amphibdellidae it is proposed now to speculate on the probable lines of evolutionary development within the group.

On the grounds of the very widespread occurrence of modern Tetraonchideans on the secondary gill lamellae of their hosts it may be assumed that the ancestral amphibdellid lived in a similar micro-habitat. It was attached to its host by a haptor provided with sixteen hooklet-bearing lobes, a posterior gland, and two pairs of unsupported hooks (i.e. without a transverse bar) operated by extrinsic muscles and tendons threaded through loops on the ventral hooks; such a haptor survives with least change in the present-day *Amphibdella torpedinis* and *A. paronaperugiae*. The male copulatory apparatus consisted of a pair of opposable sclerites, one on the left with a hook, and one on the right consisting of a simple bar, with the penis lying freely between them.

The dominating environmental hazard was the gill ventilating current of the host, and the parasite began to meet the problem in two different ways. One way was to make the hook apparatus more efficient by developing an accessory transverse supporting bar (the ancestral *Amphibdelloides*); the other was to relieve the hooks of some of their burden by 'rooting' the haptor subcutaneously in the host (the ancestral *Amphibdella*). In the second method it was an advantage to move from the relatively thin and delicate secondary lamellae to the more robust adjacent mucosa.

The dominating evolutionary trend now became towards increased efficiency of the copulatory apparatus. This took the form of a closer association of the penis with one of the accessory sclerites so that the latter acted as a guide. However, in the diverging *Amphibdelloides* and *Amphibdella* stocks different sclerites were used for the development of such a guide: in *Amphibdelloides* the left, hooked sclerite became the guide, with the penis emerging from the side of the sclerite, but in *Amphibdella* the right sclerite became tubular with the penis emerging through its distal end, the left sclerite retaining its more primitive function of acting as an opposable hook. Associated with these divergences in the male copulatory organs were some changes in the female copulatory organs: in *Amphibdella* the vaginal opening became ventro-

lateral, but in *Amphibdelloides* it became dorso-lateral. Larval or juvenile forms of *Amphibdella* now took to invading the blood system of the host, perhaps to provide greater opportunities for cross-fertilization among its protandrous developmental stages (see p.579), perhaps to facilitate taking up the definitive manner of attachment (see Pl. II, fig. 2), or perhaps merely to provide a relatively sheltered environment for larval development.

At this stage there was a divergence in the host stock, on the one hand (Fraser-Brunner, 1949) into *Tetronarce* (from which the modern *Torpedo nobiliana* and *T. californica* have descended) and on the other into *Torpedo* which has given rise to the present-day *T. torpedo* and *T. marmorata*. The gills of *T. nobiliana* have become relatively large and support the relatively large parasites *Amphibdella flavolineata* and *Amphibdelloides maccallumi*, and those of *Torpedo marmorata* are relatively small and support the smaller parasites *Amphibdella torpedinis* and *Amphibdelloides vallei*.

Following this divergence in the ancestral torpedinid stock, no further speciation took place on the *Tetronarce* line of descent for a long time, and under these relatively stable conditions the amphibdelloid parasites became increasingly specialized. In *Amphibdella flavolineata* the haptor was buried more deeply in the host tissues, and some of the hooklet-bearing lobes became greatly expanded, simulating the roots of a tree in providing more efficient anchorage. The increase in the 'rooting' component of the adhesive apparatus was accompanied by a gradual decrease in the efficiency of the hook apparatus, and the muscles have become correspondingly simplified; moreover, the posterior gland was lost. While the haptor was evolving thus, the trumpet of the penis-bearing sclerite developed a roughened surface to maintain more secure coverage of the vaginal opening of the co-copulant. In *Amphibdelloides maccallumi* the main specializations were the acquisition of a fibrous pad in association with the vaginal opening, and the development of a 'catch' mechanism to lock the adductor muscles of the large hooks.

Accompanying the relatively recent speciation of the *Tetronarce* stock to give rise to the modern *Torpedo nobiliana* and *T. californica*, we would expect corresponding speciation among the amphibdellid parasites, but in the limited sample of parasites from the gill lamellae of *T. californica* there was no evidence for this; it is possible that an examination of a larger sample of fresh material from *T. californica* might reveal evidence of at least incipient speciation in *Amphibdelloides maccallumi*. No specimens of *Amphibdella flavolineata* have yet been recorded from *Torpedo californica*.

In the *Torpedo* line of host descent, speciation into *T. marmorata* and *T. torpedo* took place long enough ago to have allowed divergences to become manifest also in the amphibdellid parasites. *Amphibdella torpedinis* (without shoulders to its hooks and with a relatively simple vaginal aperture) from *Torpedo marmorata* differs from *Amphibdella paronaperugiae* (with shoulders to its hooks and with the terminal part of the vaginal sclerite enlarged) from

Torpedo torpedo. No information is available yet about the divergences which may have occurred between the corresponding *Amphibdelloides* parasites: *A. vallei* is known from *Torpedo marmorata* but the parasite from the gill lamellae of *T. torpedo* has not yet been described.

The Director and Staff of the Plymouth Laboratory have very kindly made available to me most of the rather rare electric rays brought in by the research vessels in recent years, and as always have provided excellent working facilities; Dr Louis Euzet of Sète has made special collections of specimens for me and has given me much of his own material; and the following have either arranged loans or presented me with specimens: Dr C. G. Alexander of California, Dr W. J. Hargis of Virginia, Dr M. Sara of the University of Naples, Dr H. H. Williams of Cardiff, and the United States National Museum.

SUPPLEMENTARY NOTE

In April 1960, by kind permission of Prof. P. Mathias, I was able to visit the Station Biologique at Sète, where the following observations were made.

Torpedo marmorata. (*a*) A freshly killed specimen was found to have nine very active juvenile specimens of *Amphibdella torpedinis* in its heart; these parasites were seen to move in a leech-like manner.

(*b*) Sections of the heart of a young host, prepared by and kindly shown to me by M. André Raibaut, were seen to contain a pair of juveniles of *A. torpedinis* in copulation.

Torpedo torpedo. (*a*) A single preserved specimen (caught at Sète in November 1959) was found to bear over fifty adult specimens of *Amphibdella paronaperugiae* all resembling exactly the specimens collected by Parona & Perugia and described in the paper above; all these parasites were deeply embedded in the proximal gill mucosa as described and illustrated above for *A. flavolineata*.

(*b*) In the heart of the same host specimen were three juveniles of *A. paronaperugiae*, but no adults.

(*c*) No amphibdellids were found on the secondary gill lamellae.

SUMMARY

Comparative studies of the functional morphology of the adhesive organs and the genitalia of amphibdellid parasites from various micro-habitats on five species of electric rays have resulted in the proposal of several taxonomic revisions.

The family name Amphibdellidae has been substituted for the 'Amphibdellatidae' of Bychowsky, with an amended diagnosis. Revised diagnoses have been give also for the genera *Amphibdella* Chatin and *Amphibdelloides* Price, and specific diagnoses for *Amphibdella torpedinis* Chatin, *A. flavolineata* MacCallum, *A. paronaperugiae* n.sp., *Amphibdelloides maccallumi* (Johnston & Tiegs), *A. vallei* n.sp., and *A. narcine* Hargis.

Amphibdella spp. live partly embedded subcutaneously in the gill mucosa of

their hosts, and *Amphibdelloides* spp. hooked to the secondary lamellae; there are corresponding differences in the basically complex adhesive apparatus.

There is strong evidence that juvenile development in *Amphibdella* involves a protandrous form living endoparasitically in the blood system of the host.

Speculations have been made on the phylogeny of the group.

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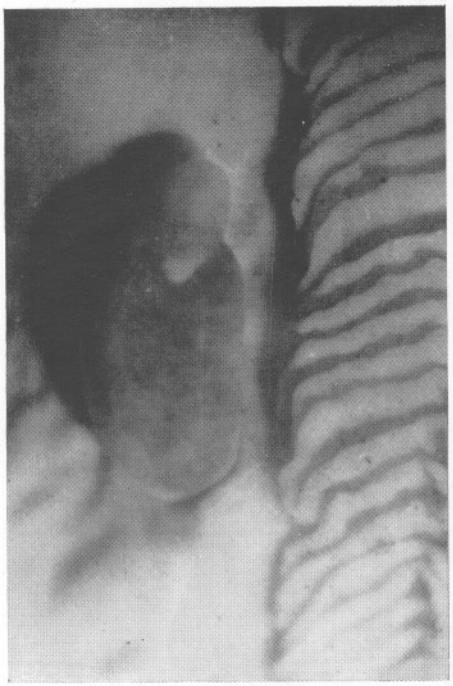

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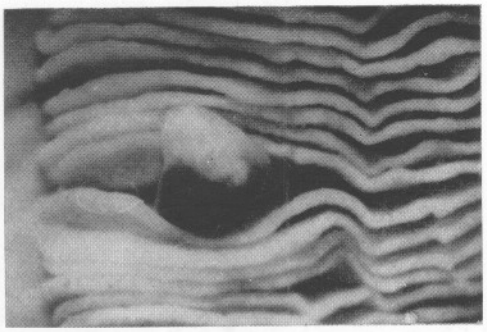

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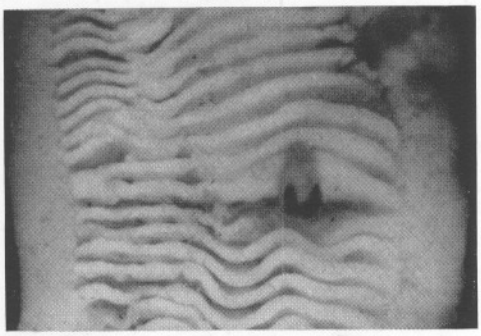

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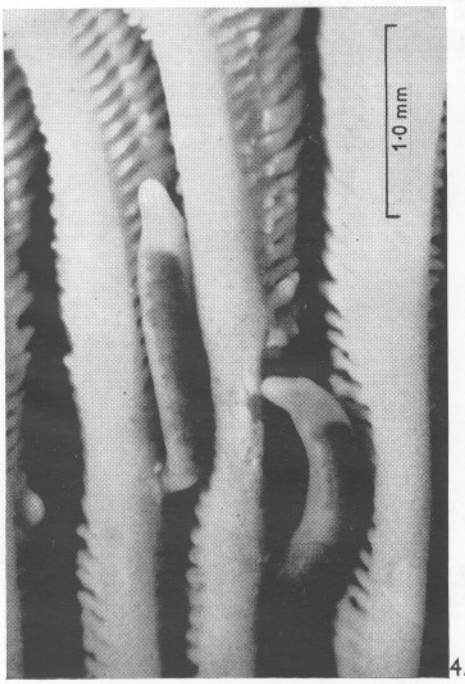

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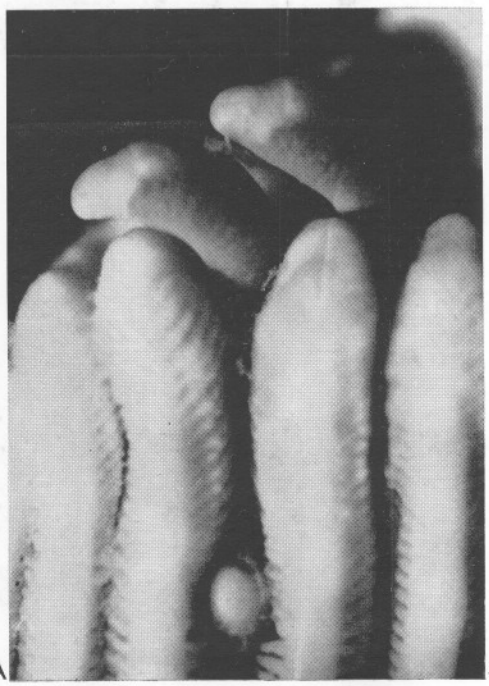

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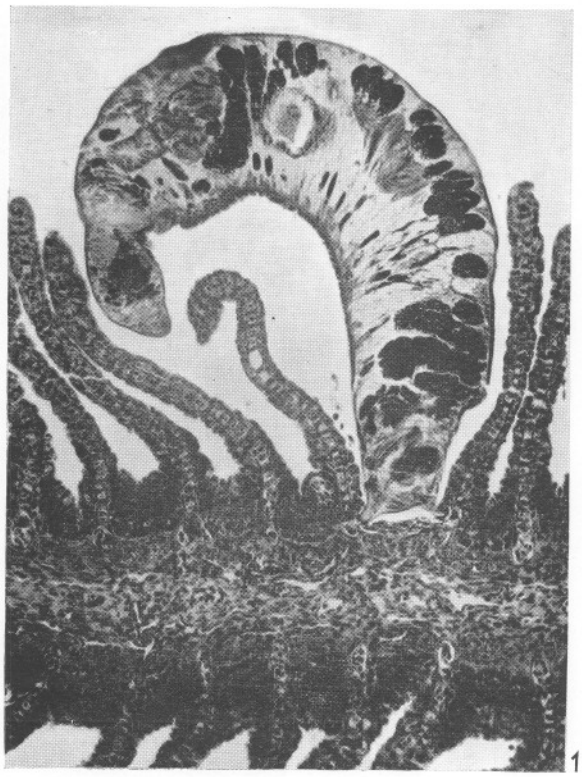

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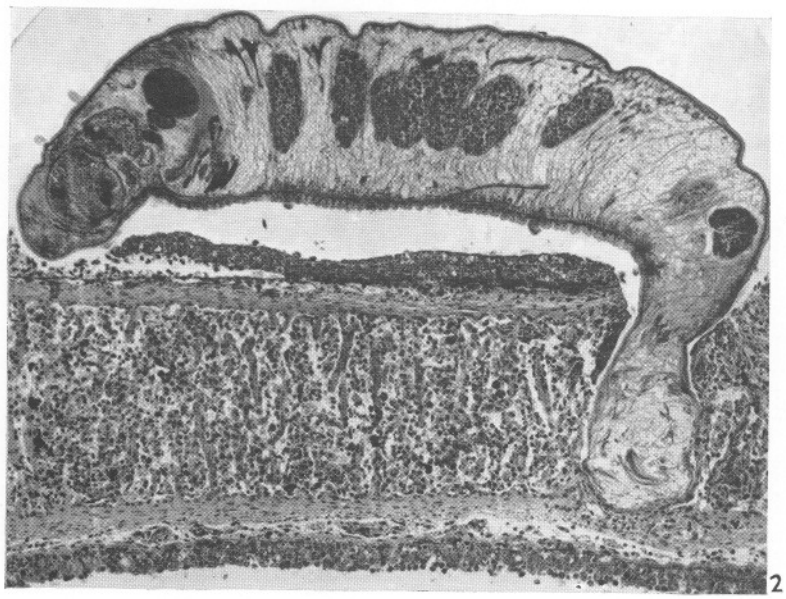

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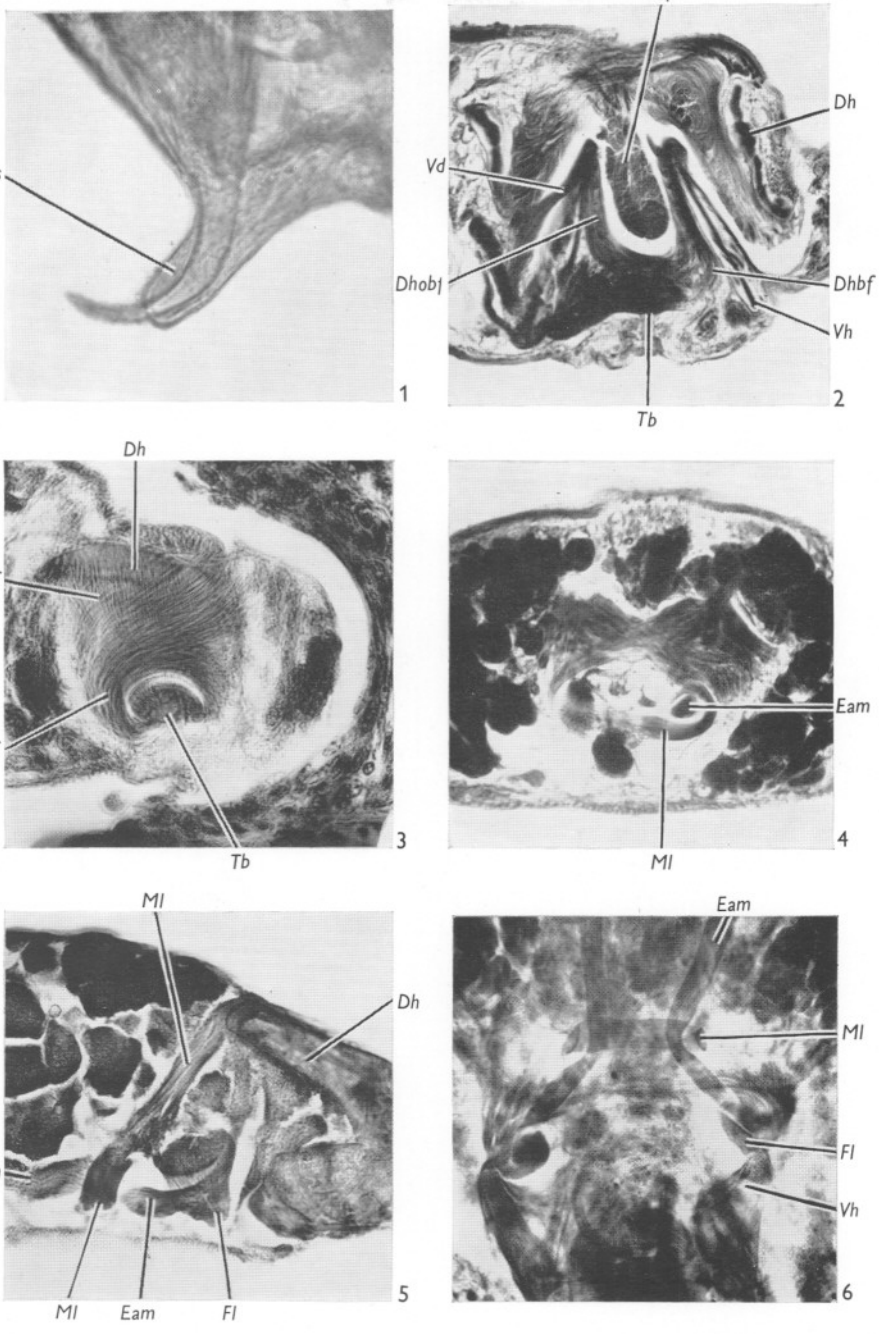
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EXPLANATION OF PLATES

PLATE I

The micro-habitats of amphibdellids.

(All photographs to the same scale.)

Fig. 1. *Amphibdella flavolineata* on the gill mucosa of *Torpedo nobiliana*. Fig. 2. *Amphibdelloides maccallumi* on the secondary gill lamellae of *Torpedo nobiliana*. Fig. 3. *Amphibdelloides vallei* on the secondary gill lamellae of *Torpedo marmorata*. Figs. 4A, B. *Amphibdella torpedinis* on the gill mucosa of *Torpedo marmorata*; 4A, two specimens on the distal, free border of a primary lamella; 4B, three specimens on the proximal mucosa adjacent to the gill arch.

PLATE II

The attachment of amphibdellids to their hosts.

Fig. 1. *Amphibdelloides maccallumi* hooked to the secondary gill lamellae of *Torpedo nobiliana*. Fig. 2. *Amphibdella flavolineata* 'rooted' subcutaneously in the gill mucosa of *Torpedo nobiliana*.

PLATE III

The hook apparatus of *Amphibdelloides maccallumi*.

For explanation of lettering see text pp. 566–9 and compare with Text-fig. 7. Fig. 1. The muscle sheath surrounding the base of the curved part of the hook. Living specimen. Figs. 2–5. Paraffin sections of haptor. Fig. 2. Transverse section in plane of transverse bar. Fig. 3. Sagittal section. Fig. 4. Transverse section at level of median loop. Fig. 5. Parasagittal section in plane of dorsal hook. Fig. 6. Balsam preparation of whole specimen stained in chlorocarmine.

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THE EFFECTS OF SALINITY ON THE DEVELOPING EGGS AND LARVAE OF THE HERRING

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(Text-figs. 1–8)

The herring (*Clupea harengus* L.) deposits its eggs in the coastal waters around the North Atlantic Ocean, North Sea, and Baltic Sea. The salinity on the spawning grounds may vary from about 35‰ to 5‰. For instance, Brandhorst (1959) reports that successful spawning took place in the Kiel Canal in salinities down to 5‰, and Ford (1929) records that ripe herring have been found in the Tamar estuary. In a series of experiments Ford found that the eggs of herring could be successfully fertilized and incubated even in a salinity of 4·8‰. McMynn & Hoar (1953) investigated the effect of salinity on the development of the Pacific herring *C. pallasii* and found it had a wide tolerance, the lower level being somewhere between 0 and 6‰.

The experiments now described were carried out as part of an investigation into osmoregulation in the herring, and particularly to find the range of conditions which herring eggs and larvae might tolerate both in nature and in rearing tanks. An extension of this work into the temperature tolerance of herring larvae is described by Blaxter (1960).

MATERIALS AND METHODS

Ripe gonads were obtained from herring caught in the Firth of Clyde in February and off the Scottish East Coast in September and the eggs fertilized in the laboratory. The techniques of storage and fertilization are described by Blaxter (1955). After fertilization, eggs were incubated in sea water of salinity 31–32‰ at temperatures of 11·2–11·7° C in 50 l. glass tanks. Smaller numbers of larvae were incubated in water of other salinities in 500 ml. jars; the water in these jars was changed every second day. Low salinity water was made up by adding distilled water to sea water and high salinity water by adding sodium chloride to sea water.

Most of the experiments were carried out on the spring-spawned larvae while a few confirmatory ones were done in the autumn.

FERTILIZATION

Prior to fertilization both eggs and sperm normally undergo changes of environment, i.e. from the body fluids of the parent to sea water. In addition the sperm then penetrate the eggs. Thus the gametes must be resistant to osmotic stress, especially the sperm; its large surface/volume ratio and small diffusion pathways would seem to make it particularly susceptible.

To find out the tolerance of the gametes to salinity, fertilizations were carried out in salinities of 5·9, 11·5, 22·7, 33·6, 41·6, 45·0 and 52·5‰; the results are shown in Fig. 1. Fertilization was complete in salinities 22·7–52·5‰. It fell off in salinities 11·5 and 5·9‰.

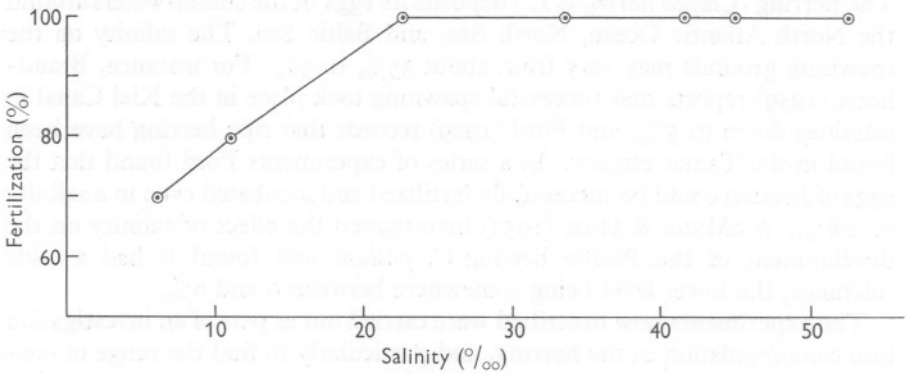

Fig. 1. Percentage fertilization of eggs.

EMBRYONIC DEVELOPMENT AND HATCHING

Krogh (1939), in a review on the subject, concludes that the developing teleost egg is not independent of the environmental salinity. In these experiments a number of observations were made to test this dependence in the herring egg.

Size of egg. The average diameter of eggs incubated in different salinities is shown in Fig. 2. It will be seen that the diameter increases in the lower salinities, due to an increase in water content.

Osmotic concentration of the eggs. Experiments were done to test whether the osmotic concentration (and therefore the proportion of water) varied in eggs incubated in different salinities. Freezing-point depressions (Δ) were determined for the perivitelline fluid and the embryonic fluid, using the apparatus described by Ramsay (1949) and Ramsay & Brown (1955).

Samples of the egg contents were taken after placing the egg under medicinal paraffin in a watch-glass coated with a lacquer of bakelite damada. A fine capillary, made of silica glass, was inserted into the perivitelline fluid and a

small sample sucked in. This sample was sealed between two layers of paraffin by sucking paraffin into the capillary before and after taking the sample.

It was much more difficult to sample the body fluid of the embryo. The embryo was removed from the egg (under paraffin) and cleared of perivitelline fluid. The capillary was inserted into the posterior trunk region. Due to the difficulty of avoiding contamination with yolk many samples had to be discarded.

The results are shown in Table 1.

TABLE 1. OSMOTIC CONCENTRATIONS OF EGGS

(7–8 days post-fertilization.)

Salinity ‰ (Δ)		Perivitelline fluid		Embryonic fluid	
Fertilization	Incubation	Δ	‰ NaCl	Δ	‰ NaCl
10·9 (0·65)	10·9 (0·65)	0·56	9·3	0·70	11·66
		0·57	9·5	0·68	11·33
32·3 (1·94)	10·9 (0·65)	0·64	10·7	0·68	11·33
		0·67	11·2	0·69	11·50
32·3 (1·94)	32·3 (1·94)	1·60	26·7	—	—
		1·67	27·8	—	—
32·3 (1·94)	47·8 (2·87)	2·07	34·5	0·90	15·0
		2·09	34·8	—	—
47·8 (2·87)	47·8 (2·87)	2·73	45·5	—	—
		2·69	44·8	—	—

TABLE 2. OSMOTIC CONCENTRATION OF EGGS AFTER TRANSFER

Salinity ‰ (Δ)		Time after transfer	Perivitelline fluid		Embryonic fluid	
Incubation	Transfer	(h)	Δ	‰ NaCl	Δ	‰ NaCl
32·3 (1·94)	10·9 (0·65)	24	0·64	10·7	0·63	10·5
	32·3 (1·94)	24	1·67	27·8	—	—
	47·8 (2·87)	24	2·46	41·0	—	—
	10·9 (0·65)	48	0·61	10·2	—	—
	32·3 (1·94)	48	1·70	28·3	—	—
	47·8 (2·87)	48	2·70	45·0	—	—

The water content of the perivitelline fluid is higher in eggs incubated at the low salinities. This content, however, also depends on the salinity at fertilization. Very limited readings for the embryos suggest that their water content is also higher at the lower salinities.

Eggs were also transferred from sea water to a higher and a lower salinity before hatching, and freezing-point determinations made after 24 and 48 h. The results are shown in Table 2. The concentration of the perivitelline fluid seems to be greatly dependent on that of the environment but there does seem to be a slight measure of regulation. Unfortunately the samples from the embryos had nearly all to be discarded.

Time to hatching and percentage hatching. The time from fertilization to that when 50% of the larvae hatched was the same (11 days) for all salinities

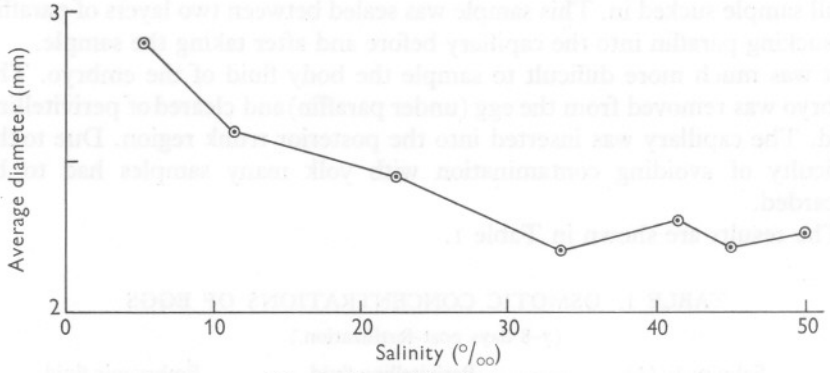

Fig. 2. Size of developing eggs.

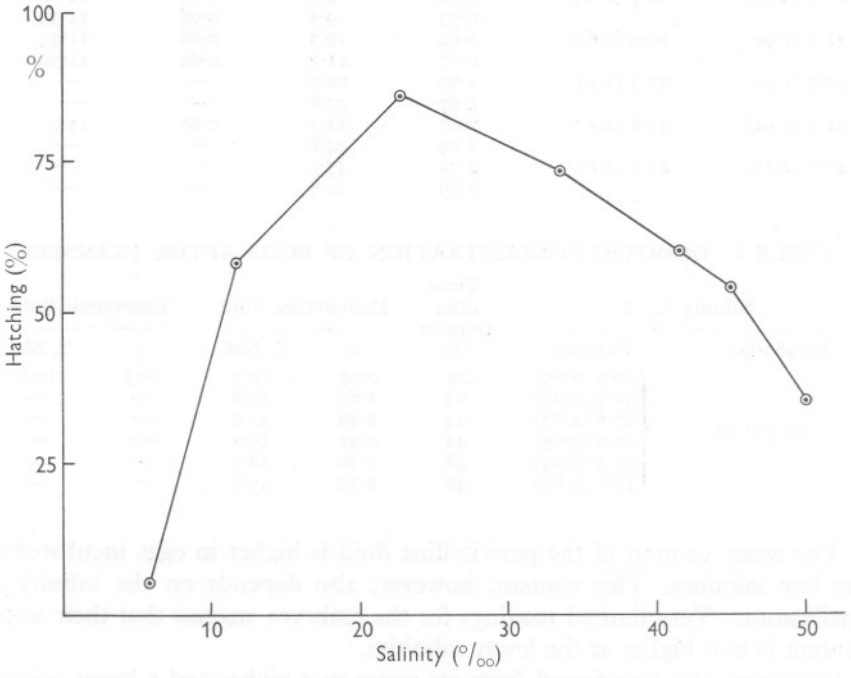

Fig. 3. Percentage hatching of eggs.

of incubation except 5·9 and 11·5‰, where the time to hatching was about 2 days longer.

The percentage hatching in different salinities is shown in Fig. 3. There appears to be an optimum range of salinity from about 20 to 35‰ and it appears that extremes of salinity impose more limitations on development.

LARVAE

Morphological characters. Observations were made on length, weight, appearance and activity of larvae on hatching. The results are shown in Table 3.

TABLE 3. LENGTH, WEIGHT AND APPEARANCE OF NEWLY HATCHED LARVAE

(Each value is the mean of ten larvae.)

Incubation salinity (‰)	Mean length (mm) (and S.E.)	Mean weight (mg)	Colour and shape of yolk sac
5·9	8·75 ± 0·037	0·90	Pale yellow; oval
11·5	7·85 ± 0·085	0·90	
22·7	7·90 ± 0·10	0·84	
33·6	6·43 ± 0·075	0·75	Dark yellow; spherical
41·6	6·70 ± 0·16	0·70	
45·0	6·90 ± 0·11	0·71	
52·5	6·75 ± 0·053	0·60	Intense yellow, shrunken and hard

The larvae hatched in salinities of 5·9, 11·5 and 22·7‰ were larger but the time to hatching tended to be longer in the lower salinities. There was, however, a negative correlation between weight and salinity. This was probably a reflexion of water content (see later description of freezing-point determinations) as larvae in high salinities would have a tendency to be dehydrated. This probably also explains the difference in appearance of the yolk sac and Ford's (1929) observations that a decrease in the specific gravity of larvae took place with reduced salinity of incubation.

Salinity tolerance. The range of salinities in which survival is possible is restricted to those in which the regulatory mechanisms of the animal can maintain the body fluids within certain limits. Outside this range, despite the functioning of the regulatory mechanisms, there is a continuous change of the body fluids from normal. The survival time will then depend, first, on the speed of the change, which will be greatest in the more extremes of salinity, and secondly, on the ability of the cells to function in conditions which are not optimum. Larvae were transferred in batches of ten from incubation salinities of 11·5, 20·5, 33·6 and 52·5‰ to 500 ml. jars holding a wide range of salinities from 0 to 70‰. The criteria of tolerance used were that 50% of the larvae should survive 24, 48 or 168 h immersion in the particular salinity. Thus the upper and lower limits of tolerance for 24 h may be considered as the high and low lethal salinities for herring larvae on the same basis used by Blaxter (1960) for temperature tolerance.

The results for these experiments are shown in Fig. 4. The most striking result is the extremely wide salinity tolerance, from 1·4 to 60‰, over 24 h to 2·5–52·5‰ over 168 h. A few larvae even survived in 60‰ for 168 h. At the end of the 24 h period some larvae were still alive (i.e. the heart was

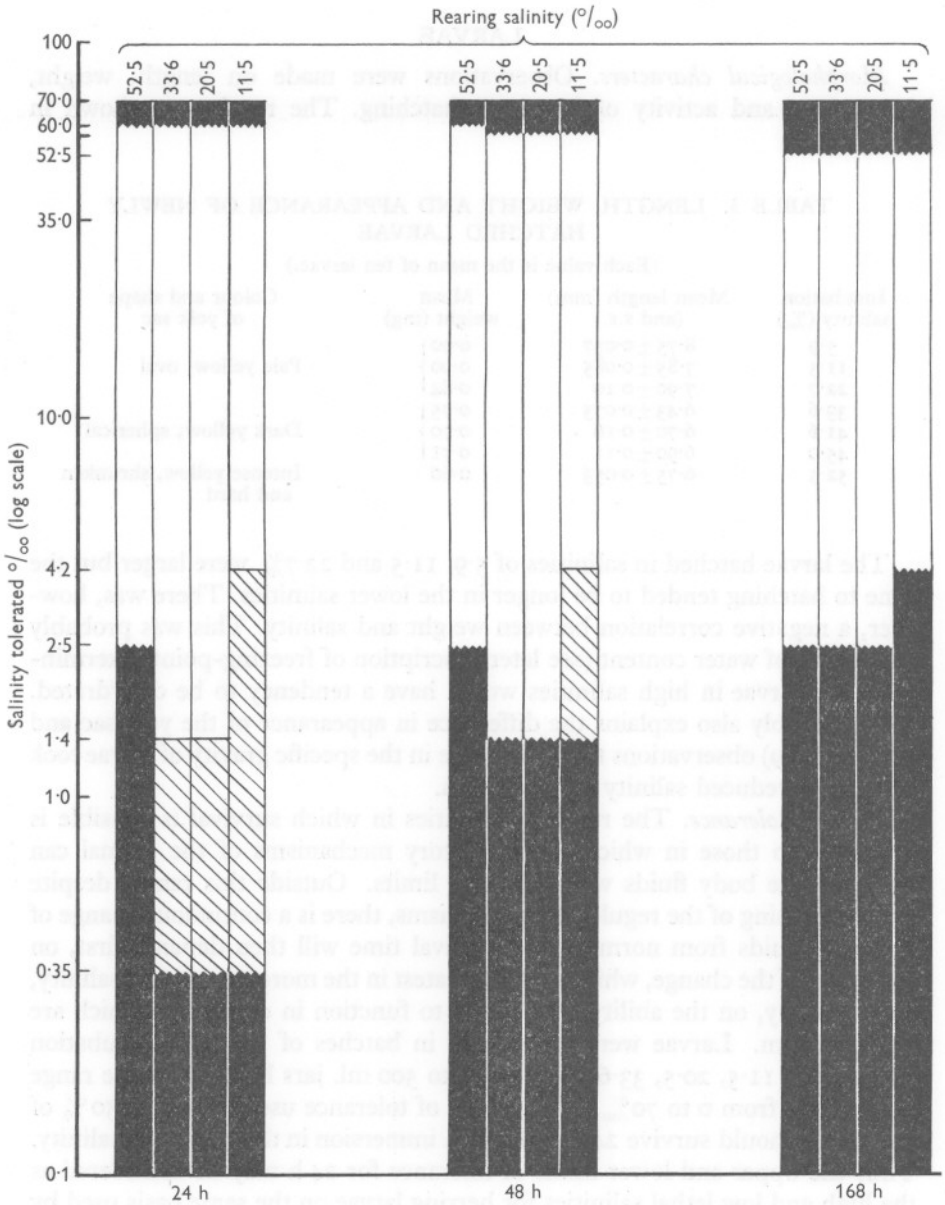

Fig. 4. Salinity tolerance of herring larvae. Shaded areas, < 50 % survival. Unshaded areas, > 50 % survival. Hatched areas, > 50 % survival, inactive but heart beating.

beating) but inactive, between salinities from 0·35 to 1·4‰. This is also shown in Fig. 4. There is a tendency for larvae incubated in the low salinities to have a greater tolerance of low salinities and larvae incubated in high salinities to have a greater tolerance of high salinities, but this is not consistent. There was very little tolerance of distilled water; the larvae either died or became inactive within 45 min. In this period of inactivity, which sometimes lasted for as long as 18 h before death, the rate of heart beat was reduced from a normal average rate of about 1·1 beats/second to an average of 0·7 beats/second. The body, and in particular the eyes swelled considerably before death. However, larvae recovered if they were transferred back to sea water within 18 h of being put in distilled water.

No difference was found between the salinity tolerance of spring- and autumn-spawned larvae.

Weight changes. It is well known (Summer, 1905; Black, 1948) that when fish are transferred from one salinity to another they undergo weight changes which correspond with movements of water into and out of the body.

Batches of fifty larvae were transferred from a salinity of 33·6‰ to salinities of 3·0, 11·4, 33·6 (control), 45·0 and 56·3‰. The weight of the larvae at the start of the experiment was measured by taking two samples of twenty larvae straight from 33·6‰. All weighings involved killing the larvae, and were done in a consistent manner. The larvae were removed from the water and placed on filter-paper to absorb excess water. For each sample identical methods of handling and exposure to the air were used. The change in weight in the different salinities is shown in Fig. 5, weighings being carried out after 6 and 24 h on samples of twenty larvae. There were changes in weight after 6 h consistent with water entering the body in salinities up to 11·4‰ and being lost in higher salinities. There is a tendency for loss of water at these higher salinities to be corrected after 24 h.

Osmotic concentrations. Freezing-point determinations (Δ) were made on larvae which had experienced different salinities to see whether these could be correlated with weight changes and salinity tolerance.

TABLE 4. OSMOTIC CONCENTRATIONS OF NEWLY HATCHED LARVAE

Incubation salinity ‰	(Δ)	No. of observations	Δ (and S.E.)	‰ NaCl
10·9	(0·65)	8	0·64 ± 0·002	10·7
32·3	(1·94)	10	0·74 ± 0·003	12·3
47·8	(2·87)	10	0·82 ± 0·012	13·7

First, the mean Δ's for ten larvae from each of three incubation salinities (10·9, 32·3 and 47·8‰) were measured. These are shown in Table 4. They show that the concentration of the internal body fluids does vary with the external salinity but in high salinities it is regulated and is well below the external salinity. The body-fluid concentration in sea water (here 32·3‰) is

equivalent to 12·3‰ of salt. This may be taken as about the normal level for herring larvae in the sea.

Secondly, Δ's were determined on larvae which had been transferred from one salinity to another. Three series of experiments were carried out. In the first larvae were transferred from a salinity of 32·3‰ to a range of salinities

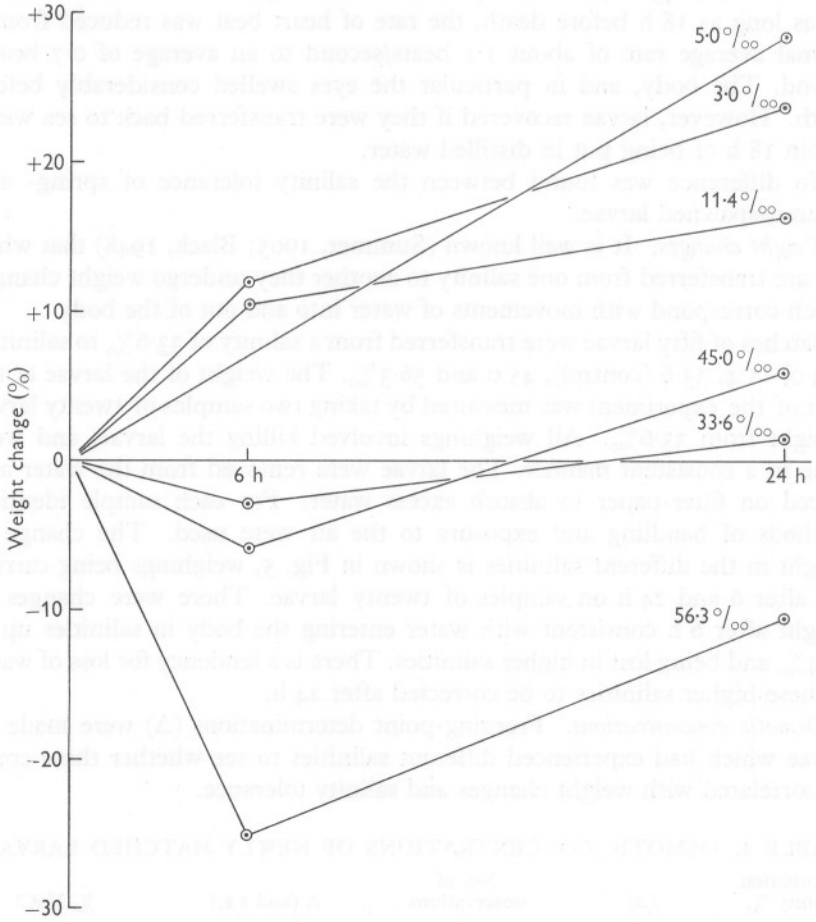

Fig. 5. Changes in weight of larvae when transferred from sea water to the given salinity.

from 3·3 to 60·1‰, body-fluid samples being taken after 3, 24 and 48 h. The results are shown in Fig. 6. In the second, larvae were transferred from 32·3‰ to distilled water, 3·3 and 60·1‰ and samples taken after 30 min, 1 h and 3 h. The results are shown in Fig. 7. Finally larvae from 11·2‰ were transferred to a range of salinities from 3·3 to 60·1‰ and samples of body fluids taken after 24 h (see Fig. 8).

The results show that there are considerable changes in the concentration of the body fluids when larvae are transferred, though regulation starts to take place within about 3 h. As samples were only taken from healthy larvae, the tissues of the body can presumably withstand these extremes of 'salinity' which may be as high as 27·5‰ and as low as 8·7‰ (the normal level being 12·3‰).

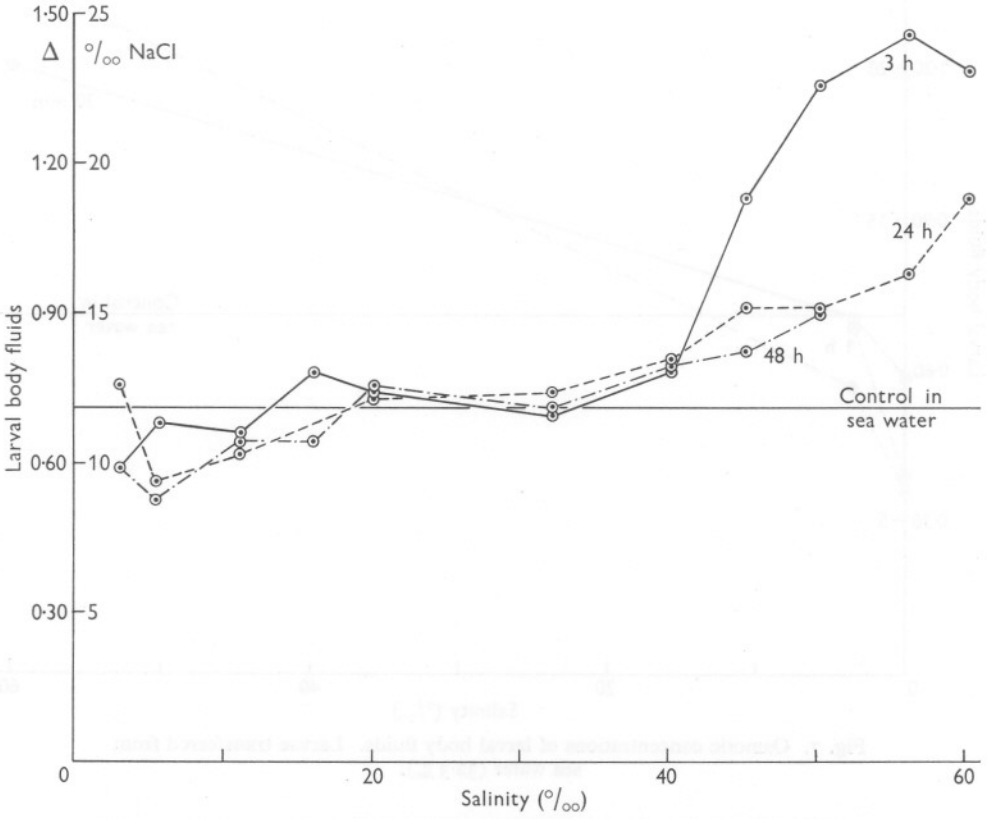

Fig. 6. Osmotic concentrations of larval body fluids. Larvae transferred from sea water (32·3‰).

The levels at which the body fluid concentrations become lethal seem to be equivalent to about 6 and 30‰ NaCl.

Sites and mechanisms of regulation. These are considered in adult fish to be the kidney and an extra-renal route for salt exchange, probably in the gill membranes. Very little is known about regulation in fish larvae.

Holstvoogd (1957) found a well-developed pronephric glomerulus and archinephric duct in herring larvae 10 mm long. Serial longitudinal and

vertical sections were cut of larvae used in these experiments (up to 8·5 mm long). No sign of a kidney could be found, nor had the gills developed at this stage.

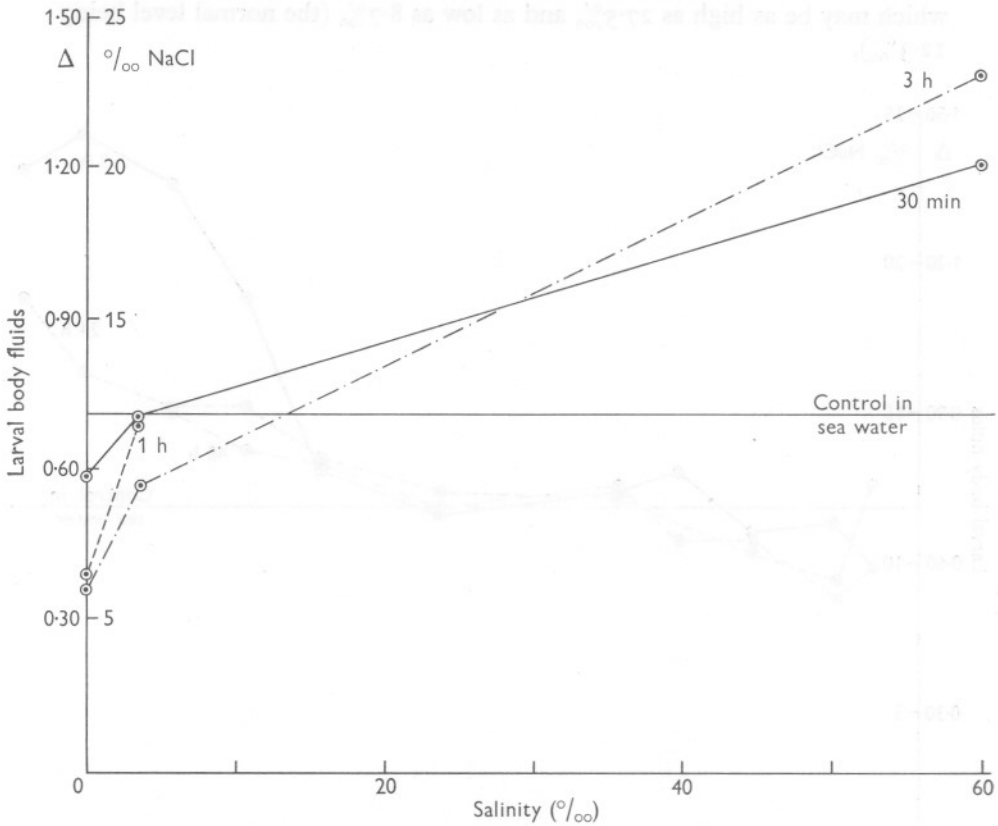

Fig. 7. Osmotic concentrations of larval body fluids. Larvae transferred from sea water (32·3‰).

DISCUSSION

The most striking results which came from this work are, first, that herring larvae can withstand external salinities ranging from 1·4 to 60·1‰ for 24 h and that they have a slightly reduced range of tolerance over longer periods. Secondly, the tissues themselves can withstand for a short time internal concentrations equivalent to salinities of about 9–28‰ though the normal value in sea water is 12‰. Thirdly, they have a mechanism for regulating the body-fluid concentration. Thus, when larvae are transferred to salinities within the range of 2·5–52·5‰, the body fluids are regulated to equivalent salinities 9·8–15·0‰. The salinity tolerance of newly hatched larvae is, in fact, wider

than that of the adult (Holliday & Blaxter—unpublished to date), although the adult has well-developed sites for regulation. The wider salinity tolerance of the larvae, despite its lack of kidney and gill membranes, is probably due to the greater tolerance of the individual tissues as well as some presumed regulatory process.

The sites of this regulation have not yet been determined; Shelbourne (1957*a*) suggests the epidermis as a site for the regulation of salt in plaice larvae. The technique used to demonstrate this is not completely specific,

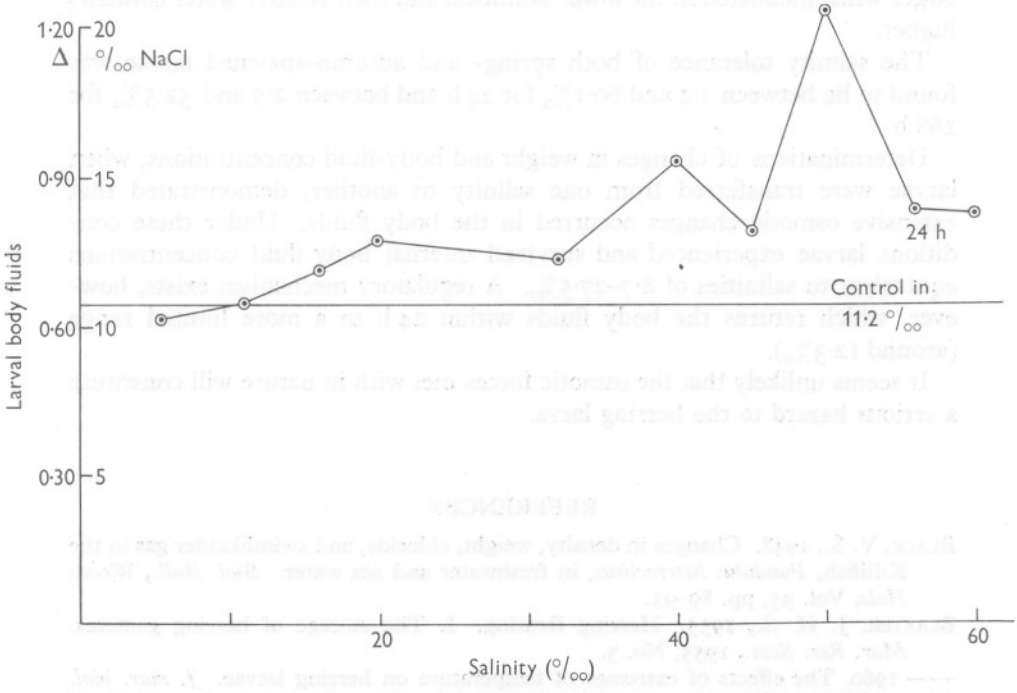

Fig. 8. Osmotic concentrations of larval body fluids. Larvae transferred from salinity 11·2‰.

however, so that the issue is not yet decided. Shanklin (1954) showed in *Fundulus* embryos that if the glycolytic pathways of metabolism were blocked by specific inhibitors, the embryos failed to osmoregulate, whereas they could normally survive in salinities from tap water to double strength sea water.

The conclusion may be reached that herring larvae are relatively independent of salinity and that they are unlikely to be adversely affected by any salinity change which might take place in the sea or in rearing tanks. They are also more tolerant to salinity than the adult. This is in contrast to Shelbourne's (1957*b*) conclusions based on work with plaice. He considers that the osmotic hazard is one of the greatest dangers facing plaice larvae and that this danger decreases in the adult stage.

We should like to thank Dr G. Parry of the Ministry of Agriculture, Fisheries and Food Freshwater Fisheries Laboratory for much advice and help, and to Mr Parrish of this laboratory for his encouragement and advice.

SUMMARY

Fertilization, development and hatching of herring eggs occurred in salinities ranging from 5·9 to 52·5‰. Both the developing eggs and the larvae were larger when incubated in the lower salinities, and their relative water contents higher.

The salinity tolerance of both spring- and autumn-spawned larvae was found to lie between 1·4 and 60·1‰ for 24 h and between 2·5 and 52·5‰ for 168 h.

Determinations of changes in weight and body-fluid concentrations, when larvae were transferred from one salinity to another, demonstrated that extensive osmotic changes occurred in the body fluids. Under these conditions larvae experienced and survived internal body fluid concentrations equivalent to salinities of 8·7–27·5‰. A regulatory mechanism exists, however, which returns the body fluids within 24 h to a more limited range (around 12·3‰).

It seems unlikely that the osmotic forces met with in nature will constitute a serious hazard to the herring larva.

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THE EFFECT OF EXTREMES OF TEMPERATURE ON HERRING LARVAE

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(Text-fig. 1)

Most of the work on temperatures lethal to fish has been reviewed by Brett (1956). Most of the fish have been adults of freshwater species, and it has been found that both upper and lower lethal temperatures vary with the species, the temperature of acclimatization and the duration of time the fish are subjected to the test temperature.

Experiments on the upper and lower lethal temperatures for herring larvae (*Clupea harengus* L.) were started for three reasons: (1) to find out the range of temperature the larvae could withstand in rearing experiments at different acclimatization temperatures, this being part of a programme to determine the tolerance of herring larvae to a number of environmental factors (Holliday & Blaxter, 1960); (2) to look for possible differences in temperature tolerance between larvae from spring- and autumn-spawned herring (see Blaxter, 1958, for a discussion of this problem); and (3) to obtain some idea of what danger larvae might experience if subjected to rises of temperature in the sea caused by effluents or hot weather.

MATERIALS AND METHODS

Ripe gonads were dissected from spring-spawning herring caught in the Firth of Clyde in February 1957 and from autumn-spawning herring caught off the East Coast of Scotland in September 1957. The gonads were stored at 4° C (Blaxter, 1955) and transported to the laboratory, where the eggs were fertilized and hatched in tanks holding 50 l. of sea water (Blaxter, 1956). In February three tanks were used and maintained at different incubation temperatures (7·5, 11·0, 15·0° C). In September tanks at temperatures of 11 and 15·5° C only were used. These were also the acclimatization temperatures for the succeeding experiments.

Hatching occurred 7–15 days after fertilization, depending on the incubation temperature. The larvae were then 6–8 mm long and possessed yolk sacs. Within 2 days of hatching batches of ten larvae were transferred by a pipette from the incubation tanks to jars holding 500 ml. of sea water at the temperature of incubation. These jars were then placed in baths holding water

at the test temperatures. The high-temperature baths, for testing the upper lethal temperatures, were maintained at their temperature by low-power immersion heaters controlled by thermostats. The low-temperature baths were either kept in a refrigerator or were cooled by glycerol from a refrigeration unit. The glycerol was circulated through a cooling coil by a small centrifugal pump controlled by a thermostat.

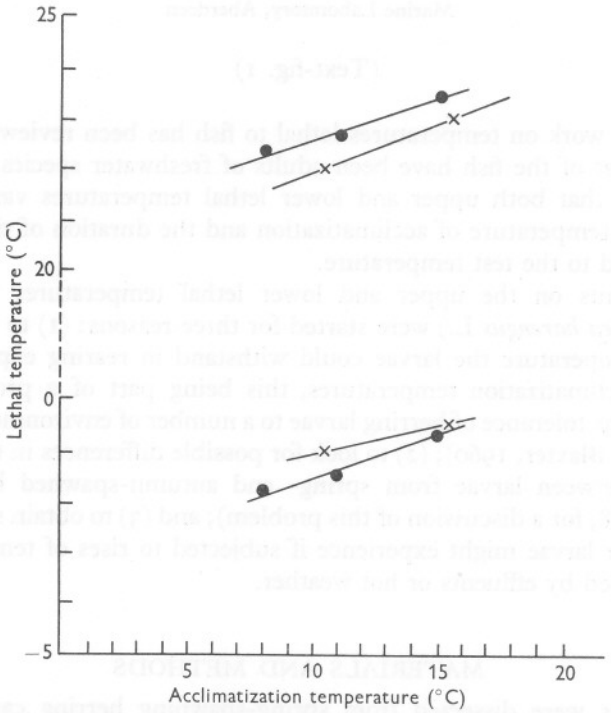

Fig. 1. Lethal temperatures for spring-spawned herring larvae (●—●) and autumn-spawned larvae (×—×) at different acclimatization temperatures.

The temperature of the water in the 500 ml. jars reached the test temperature within 1 h. Although continuous records were not kept, no observation of the test temperature showed a fluctuation greater than $\pm 0{\cdot}1^{\circ}$ C during an experiment.

The numbers of larvae which were moribund or dead after 24 h at the test temperatures were counted. Larvae were called moribund when they had started to turn opaque though the heart continued to beat. Tests showed that this condition was not reversible. The scale of test temperatures (each one differing by about $0{\cdot}5^{\circ}$ C from the next) was such that at one end all the larvae survived and at the other at least 50% were moribund or dead.

RESULTS

The lethal temperatures, in this case defined as the temperature at which 50% of the larvae died or became moribund after a 24 h period of exposure, were determined in the following way. For each acclimatization temperature a graph was drawn of the percentage of larvae dead or moribund after 24 h at each test temperature. By interpolation the temperature at which 50% died or became moribund was determined. The lethal temperatures for both spring- and autumn-spawned larvae are plotted against the acclimatization temperature in Fig. 1. It will be seen that the range of lethal temperature is less for autumn- than for spring-spawned larvae. This difference was checked by probit analysis and found to be not significant.

DISCUSSION

The upper lethal temperatures (22–24° C) for herring larvae acclimatized to 7·5–15·5° C are very similar to those (22–25° C, over the same acclimatization range) for five species of salmonid fry studied by Brett (1952). The lower lethal temperatures for the herring larvae are, however, −0·75° C to −1·8° C, compared with 1–5° C for the salmonid species. Colton (1959) observed mortality at sea among the larvae of *Limanda ferruginea* and *Merluccius bilinearis* when they had probably been subjected to a rise in temperature from 6·7 to 17·8° C in 24 h. Kuthalingam (1959) found that the tolerance range for the larvae of ten species of tropical fish was very narrow, the upper lethal temperature varying from 30 to 31° C and the lower one from 27 to 29° C.

Although the test period of 24 h used in these experiments is an arbitrary one, it has been quite generally used in the past. Since the work of Doudoroff (1945) and Fry, Hart & Walker (1946) it has been more usual to determine the lethal temperatures by plotting the percentage dying at a given temperature against time. These authors found in nearly every test that all deaths occurred within the first 24 h at upper lethal temperatures. For lower lethal temperatures, deaths may continue to occur for up to 5 or 6 days depending on the test temperature. It has not been practicable to use this technique for herring larvae on hatching as they only survive this stage for about 1 week to 10 days and a sufficient number of experiments could not be carried out in this time. The upper lethal temperatures obtained in these experiments, then, may be compared with those determined by different criteria, but the lower lethal temperatures are probably rather lower than might be obtained by longer-term experiments.

Although the lethal temperature differences between spring- and autumn-spawned larvae are not significant, other physiological differences have been shown between larvae from spring- and autumn-spawning herring (Blaxter,

1956), and both Hart (1952) and McCauley (1958) have shown that lethal temperatures may vary in different races of the same species.

Thanks are due to my colleague Mr W. Hall for his help with the statistical treatment of the results.

SUMMARY

For herring larvae 6–8 mm long, acclimatized to temperatures between 7·5 and 15·5° C, the upper lethal temperature (defined as that temperature at which 50% of the fish die or become moribund after 24 h) varies from 22 to 24° C and the lower lethal temperature from −0·75 to −1·8° C.

The range of temperature tolerance is slightly less for autumn-spawned larvae than for spring-spawned larvae though this difference is not significant.

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DIRECT OBSERVATIONS ON SOME MANX SUBLITTORAL ALGAE

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(Text-figs. 1 and 2)

The recent spread of the free-diving technique has made direct contact with the sublittoral environment relatively simple. The advantages of this to the ecologist need not be stressed.

The rather more cumbersome and expensive standard diving method had had already been used by Gislén (1930), Kitching, Macan & Gilson (1934), Kitching (1937, 1941), Zalokar (1942), Bursa, Wojtusiak & Wojtusiak (1948) and Waern (1952). Drach (1948*a*, *b*, 1949, 1951) was the first to exploit free diving for ecological purposes and was followed by Forster (1954, 1955, 1958), Pérès & Piccard (1949), Ernst (1955), Laborel & Vacelet (1958), Knight-Jones & Clifford Jones (1956) and Aleem (1956).

Compared with the littoral region, the sublittoral of the British coast has been necessarily neglected. A certain amount of information has been collected by mechanical means (Chapman, 1947; Walker, 1947; Lodge, 1954), and where the bottom is smooth and the algae attached to small stones or unattached (Burrows, 1958) a grab can be as reliable as a diver. It is the detailed flora of the uneven rock surfaces which, with the exception of Kitching's admirable studies with a diving helmet, has defied description. Forster has included the more important plants in his studies, and Knight-Jones has made small collections.

It is clear that these studies are still in the descriptive stage. A certain amount of description of the flora must precede any attempt at distinguishing the factors. It is for this reason that the preliminary picture which has been obtained of the sublittoral algae of some parts of the south end of the Isle of Man is being presented here. This should be more than of local interest; it should give an indication of the type of vegetation which exists below low water on rocky coasts of Britain. A general qualitative description of the distribution of the more important algae with depth on the rocky parts of the coast was all that was attempted at first.

The nomenclature used is that given in the 'Preliminary Check List' (Parke, 1953) and the corrections to it (Parke, 1956, 1957). Where reliable taxonomic information was lacking, aggregates were used. Thus plants of *Nitophyllum* and *Polyneura* were grouped under *Nitophyllum* agg.; four-siphoned plants

of *Polysiphonia*, other than *P. elongata*, were called *P. urceolata* agg. when ecorticate and *P. violacea* agg. when corticate.

METHODS

In order to cover as much ground as possible in this preliminary survey it was necessary to employ a sampling technique that was simple and rapid.

The depth was measured with a metre-long capillary tube gauge and expressed as metres below 'extreme low-water springs' (ELWS) by allowing for the height of the tide at the time of the dive. This was calculated in advance, using the data given by the *Admiralty Tide Tables* and Southward (1953), and corrected for deviation from the predicted height from observation of the Port Erin tide pole.

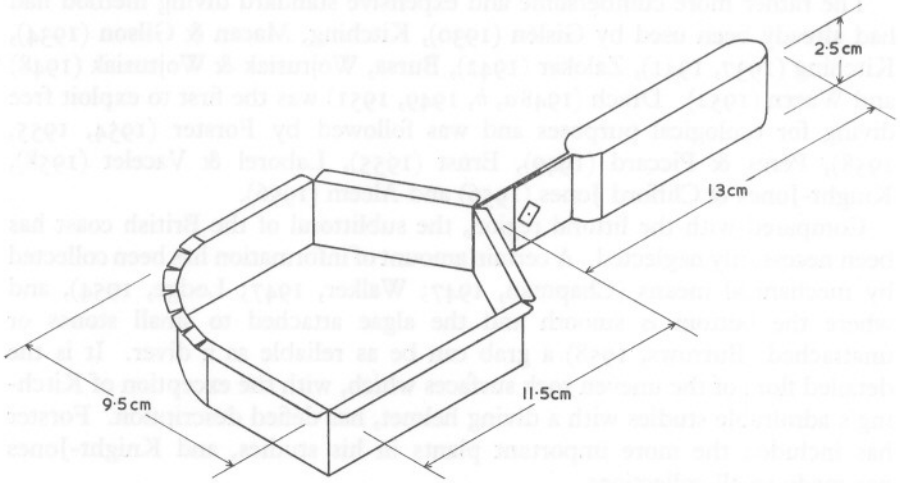


Fig. 1. Diagram of the scraper used, without the net bag.

The algae were removed from the rock with the aid of a scraper (Fig. 1), shaped somewhat like a miniature dredge. This was made from strip iron, had the lower leading edges sharpened, and bore a flange around the upper edges. A bag made from mosquito netting and measuring 40 cm in circumference and 66 cm in length had its neck drawn in by elastic cord. This fitted over the flange on the scraper and could easily be removed and replaced under water. The net had a wooden clothes peg attached near the neck and a roughened plastic label. The sharpened edge of the scraper easily removed the bases of most algae, except encrusting calcareous forms and large laminarians. The thalli so released passed into the net bag and were held there by the water passing through as the instrument was moved.

A rapid survey of a chosen place was made by collecting samples of the flora from several rock faces at intervals of approximately 1 m of depth from ELWS to the lowest level of the rock itself. The net bag on the scraper was changed between each sample, the depth and substratum noted on the label and the bag attached by means of the clothes peg to a carrier. Each sample was examined in the laboratory and the species listed with notes on reproductive structures and a subjective abundance score. An exhaustive search for species was not made. *Lithothamnion* and related genera were ignored.

To show how far results were repeatable six levels at Port Erin breakwater were sampled twice within a few days. The general picture given of the distribution of the main species was similar in the two surveys, but the danger of attaching too much importance to the abundance scoring was emphasized by the apparent commonness of one species (*Delesseria sanguinea*) in one survey and its rarity in the other. Most of the places were sampled at one season of the year only, but Port Erin breakwater was sampled at regular intervals for one year for an indication of seasonal changes.

THE REGION

The places sampled all lie off the south-west end of the Isle of Man between Niarbyl and Langness (Fig. 2). This part of the coast is mainly rocky, with sand or shingle in the bays of Fleshwick, Port Erin, Perwick, Port St Mary, and Castletown. The sublittoral flora of these bays, where the bottom is relatively flat, forms a study in itself (Burrows, 1958) and has not been included here. Along much of the rest of the coast there are cliffs, varying in height and steepness. Below these sublittorally there are usually boulders, varying in size and extent with the topography of the cliffs. Opposite gullies the boulders have accumulated; below sheer cliffs they are fewer and more steeply stacked. In no place so far visited, however, do vertical cliffs extend for more than a few metres below ELWS; the slope of the rock is always more gentle. In certain places there are outcrops of solid rock either amongst the boulders or offshore from them. These form reefs of various shapes. The rocky bottom, whether formed of solid rock or boulders, always gives way at a depth of 8–21 m (mainly at about 12 m) below ELWS to an unstable bottom of gravel or sand. Where the boulder bed slopes gently this change is gradual, there being gravel between the boulders for some distance before the gravel bed itself.

The principal factors likely to be important in the sublittoral environment will be briefly reviewed. They are, of course, interrelated.

The temperature of the sea varies between about 6° and 15° C (Slinn, 1959). Except occasionally in the sheltered bays, and on rare occasions offshore in unusual weather conditions, there is little temperature stratification in this region. Taken by itself, therefore, temperature cannot be a factor determining the position of sublittoral species. The same applies to the concentrations of the major nutrients.

The substratum, on the other hand, is an extremely important factor in determining the algal distribution. As has been seen, the extent of rock surface suitable for colonization is very limited; much of the bottom is occupied by gravel. This latter may on occasion provide a suitable substratum for certain forms, but it seems likely that for much of the year not only is it uninhabitable itself, but its presence may reduce the suitability of some parts of the rock surfaces. The general topography of the rocks

is important, the slope and aspect clearly affect the light intensity received, and may also have a bearing on the possible effect of the settling or scouring by sand or gravel. The type of surface does not vary a great deal and does not seem greatly to affect colonization.

It is likely that water movements affect algal distribution in a variety of ways. The tidal streams are in some places fairly strong, reaching 5 knots at springs in the vicinity of Calf Sound, and in other places are negligible. They may have some effect on

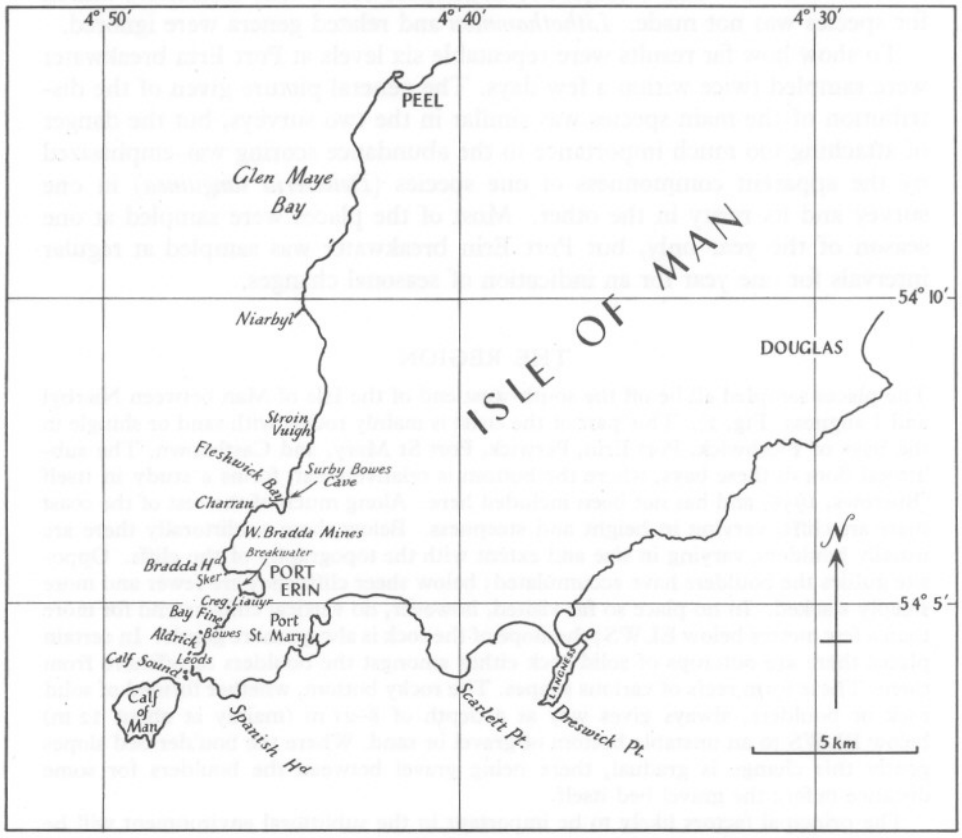


Fig. 2. Outline map of the south end of the Isle of Man.

the distribution of spores, and where they are strong growth may be affected through the provision of nutrient. The turbidity of the water and thus the light penetration is slightly increased at spring tides, but there is not the marked variation in underwater visibility that is so noticeable on other coasts.

Water movement of what is probably a more important type is caused by wave action. This is a notoriously difficult factor to measure on the shore and it is not any easier sublittorally. Its importance for a considerable depth below ELWS is beyond doubt during gales, as large quantities of sublittoral vegetation are washed on shore. It is possible that under more extreme conditions the water motion and the movement

of solid material could be very considerable in the depth range under consideration. The movement of solid material could have indirect effects both on water turbidity and thus light penetration, and possibly through scouring action or settling on rock surfaces. The effects of gales on turbidity is just noticeable subjectively, but is not marked because there is no reservoir of suspendable material in the form of shallow water mud beds.

Light is clearly an important factor affecting algal distribution with depth. Direct measurements in these waters have only just begun and cannot yet be presented. It must now suffice to say that compared with many British waters the transmission is high and the compensation point for many algae subsequently deep. During the day there is sufficient light to see clearly at 35 m in summer, though of course it is virtually monochromatic.

ROCKY BOTTOMS

The places that have been studied will be described in turn around the coast. The records for all the species are given in Tables 1–3.

Niarbyl

At Niarbyl there is a conspicuous reef extending south-westwards from the shore, much of it above high-water level. The sublittoral part of the reef extends farther south-westwards and is highly dissected, there being a number of knolls with nearly vertical sides, about 8 m high, set on a smooth rock plateau at about 10 m below ELWS. This plateau extends farther south-westwards for at least 100 m, gently sloping and reaching a depth of 16 m. On the lower parts gravel lies in slight fissures, and most of the surface is occupied by an ophiuroid bed. The point is subjected to fairly strong tidal streams.

The algae were sampled in May 1958 (Table 1). The vertical and upward-facing slopes of the rocky knolls were occupied by typical laminarian forest, with *Laminaria hyperborea* dominant. An undergrowth to this was formed by *Dictyota dichotoma* (particularly abundant here), *Desmarestia aculeata*, *Cryptopleura ramosa*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte and other species in smaller quantities. No *Callophyllis laciniata* was found here, though it was abundant in the forest farther south. *Alaria esculenta* occurred in places near the tops. The overhanging faces of the knolls bore few algae and were mainly occupied by the coelenterate *Alcyonium*. The zone of *Laminaria* had its lower limit at about 6–7 m below ELWS, leaving a gap of at least 2 m above the horizontal rock plateau. Most of the other common algae extended down through this region and also occupied much of the plateau. *Saccorhiza polyschides*, common in the lower parts of the *Laminaria* zone, tended to dominate just below it, both on the vertical rock faces and on the shallowest parts of the plateau at about 10 m. *Dictyota* was also abundant in these lower parts, together with large bushes of *Desmarestia*. The vegetation gradually thinned out along the lower slopes of the plateau and was very sparse at the outer end of the reef.

Stroin Vuigh

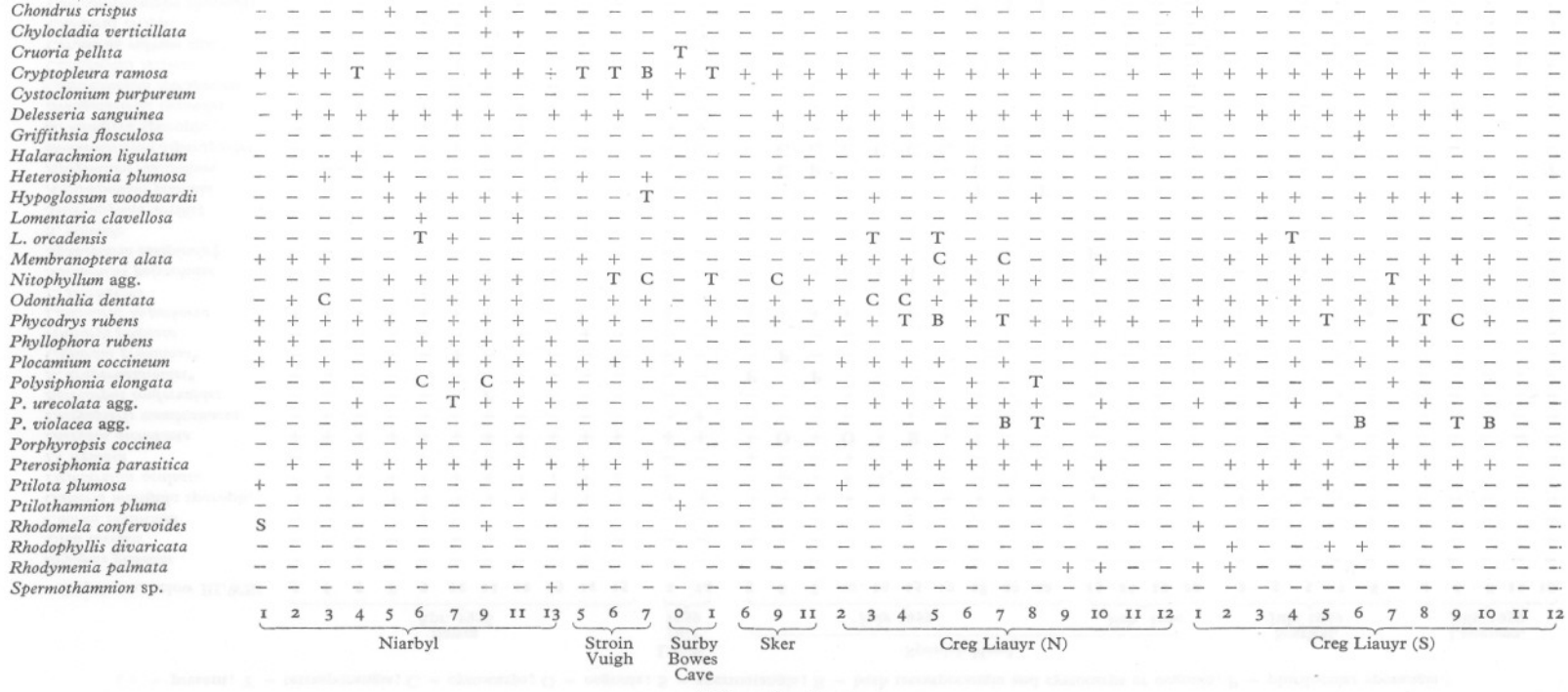
A ridge of boulders runs out from the shore between Niarbyl Bay and Fleshwick Bay. The solid rock of the shore itself extends to about 7 m below ELWS, with occasional knolls. The boulders are numerous at this level but thin out gradually farther offshore, until they are only occasional at 10 m, imbedded in fairly fine gravel. There is little or no tidal stream along this part of the coast.

The algae were sampled in July 1959 (Table 1). The usual *Laminaria hyperborea*

TABLE 1. THE SPECIES OCCURRING IN SAMPLES FROM ROCKY PLACES BETWEEN NIARBYL AND BAY FINE, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C = cystocarps; B = both tetrasporangia and cystocarps; P = plurilocular sporangia; p = propagules.)

	Niarbyl May 1958										Stroin Vuigh, July 1959			Surby Bowes Cave, Oct. 1959		Sker, May 1959			Creg Liauyr (N), Apr. 1958										Creg Liauyr (S), Apr. 1958										
Depth (m below ELWS)	1	2	3	4	5	6	7	9	11	13	5	6	7	0	1	6	9	11	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12
Chaetomorpha melagonium	+	–	+	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Ulva lactuca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–
Alaria esculenta	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
*Chorda tomentosa**	–	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Cutleria multifida sporoph.	–	+	+	+	+	+	+	+	+	+	+	+	+	–	–	?	?	?	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+
Desmarestia aculeata	–	+	–	+	+	+	–	+	+	–	–	–	+	–	–	+	+	+	–	–	+	–	+	+	+	+	+	–	–	–	+	–	+	–	+	+	+	+	+	–	–
D. ligulata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dictyota dichotoma	–	+	+	+	+	+	+	+	+	+	+	+	T	–	–	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	+	+	+	+	+	+	+	–	–	–	–
*Ectocarpus confervoides**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
*Giffordia hincksiae**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Halidrys siliquosa	–	–	–	–	+	–	–	+	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Laminaria hyperborea	+	+	+	+	+	–	–	–	–	–	+	+	–	–	–	+	–	–	+	+	+	+	+	+	–	–	–	–	–	+	+	+	+	+	+	–	–	–	–	–	–
L. saccharina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Pylaiella littoralis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Saccorhiza polyschides	–	+	+	+	+	+	+	+	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	+	+	+	+	–	–	–	–
Sphacelaria pennata†	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. plumula†	–	–	–	–	–	–	–	p	p	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	p	–	–	–	–	–
Spongonema tomentosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apoglossum ruscifolium	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–
Bonnemaisonia asparagoides	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. hamifera sporoph.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	+
Brongniartella byssoides	–	+	–	–	+	+	+	+	+	+	T	–	T	–	–	+	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Callithamnion hookeri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Callophyllis laciniata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	+	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Ceramium rubrum agg.	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	+	+	–	C	–	+

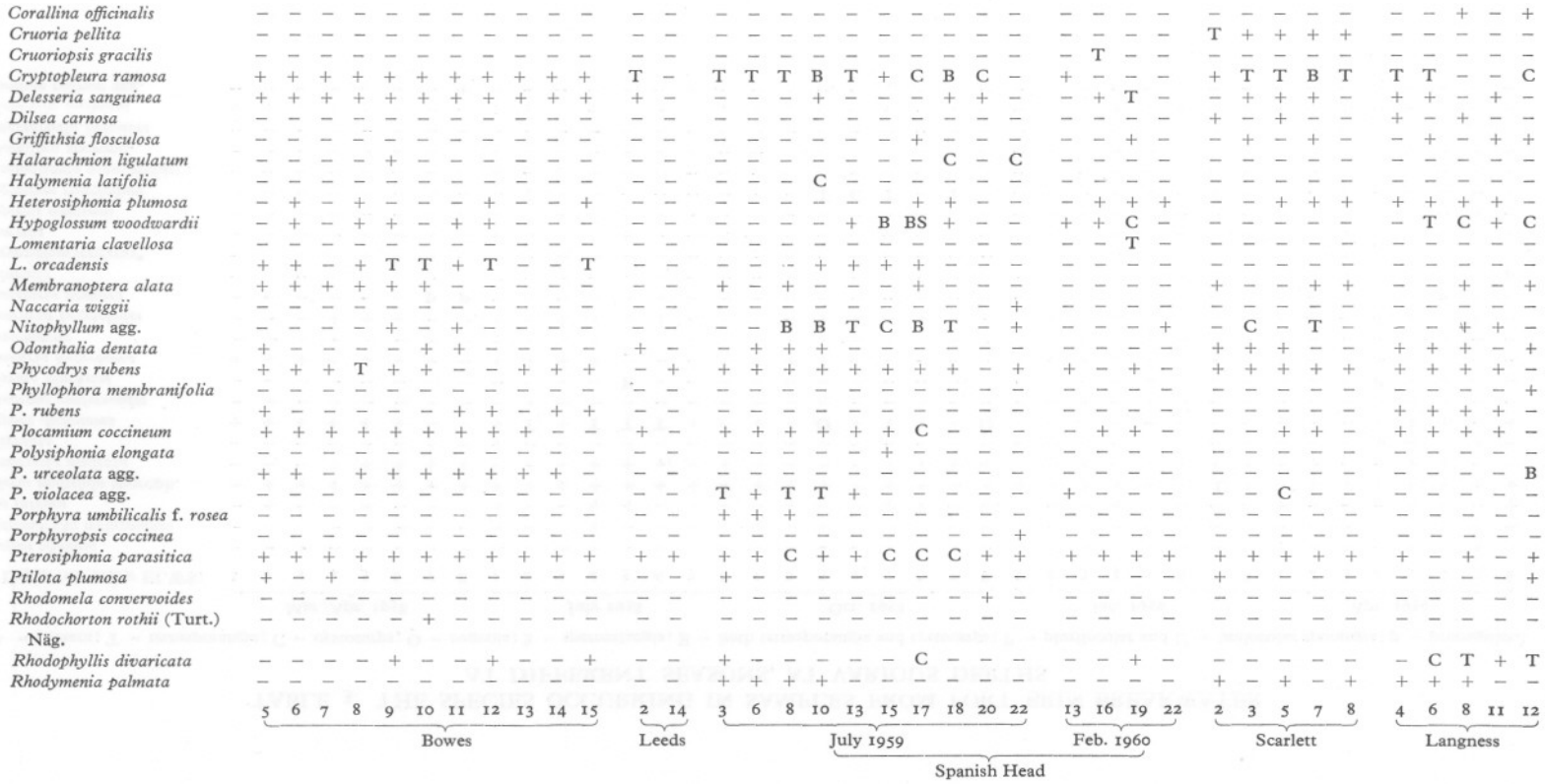


* *Sensu* Hamel, 1931–9.
† *Sensu* Irvine, 1956.

TABLE 2. THE SPECIES OCCURRING IN SAMPLES FROM ROCKY PLACES BETWEEN BAY FINE AND LANGNESS, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C = cystocarps; O = oogonia; S = spermatangia; B = both tetrasporangia and cystocarps or oogonia; P = plurilocular sporangia.)

	Bowes, Apr. 1958											Leods, July 1959		Spanish Head, July 1959									Spanish Head, Feb. 1960				Scarlett, July 1959					Langness, July 1959				
Depth (m. below ELWS)	5	6	7	8	9	10	11	12	13	14	15	2	14	3	6	8	10	13	15	17	18	20	22	13	16	19	22	2	3	5	7	8	4	6	8	11	12
Bryopsis plumosa	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ulva lactuca	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chorda tomentosa	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cutleria multifida sporoph.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	–	–	–	–	–
Desmarestia aculeata	–	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
D. ligulata	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dictyota dichotoma	+	+	+	+	+	+	+	+	+	+	+	+	+	+	O	+	O	+	B	+	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Dictyopteris membranacea	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ectocarpus confervoides	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*E. drapernaldioides**	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*Giffordia granulosa**	–	–	–	–	–	+	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Halidrys siliquosa	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Laminaria hyperborea	+	+	+	+	+	+	–	–	–	–	–	+	–	+	+	+	+	+	–	–	–	–	–	+	.	.	–	+	+	+	+	+	+	+	–	+	–
L. saccharina	–	+	+	–	+	+	+	–	+	–	–	–	–	–	–	–	+	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Saccorhiza polyschides	–	–	–	–	+	–	+	+	+	–	–	–	–	+	–	+	+	+	+	+	+	–	–	+	+	.	–	–	–	+	+	–	–	–	–	–	–
Sphacelaria caespitula†	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–
S. plumula	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stictyosiphon tortilis‡	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Antithamnion plumula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	T	+	T	–	–	+	–	–	–	–	T	–	–	–	–	–	–
Apoglossum ruscifolium	–	–	+	+	–	–	–	–	–	–	–	–	–	–	C	B	–	–	–	–	C	–	–	–	–	–	–	–	C	–	+	–	–	–	C	–	T
Bonnemaisonia asparagoides	+	–	+	–	+	+	+	+	+	–	–	–	C	–	C	C	C	C	C	C	C	C	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. hamifera sporoph.	–	–	+	+	+	+	+	+	+	–	+	–	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–
Brongniartella byssoides	–	+	+	–	+	+	+	+	+	–	+	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	T	–	–	–
Callithamnion tetragonum	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	C	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Callophyllis laciniata	+	+	+	+	+	+	+	–	+	–	–	+	–	–	+	+	+	+	+	+	–	–	+	–	+	+	–	+	–	+	+	–	+	+	+	+	+
Ceramium rubrum agg.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Chondrus crispus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Composothamnion thuyoides	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	T	T	T	–	–	–	–	–	–	–	–	–	–	–	+	–	+

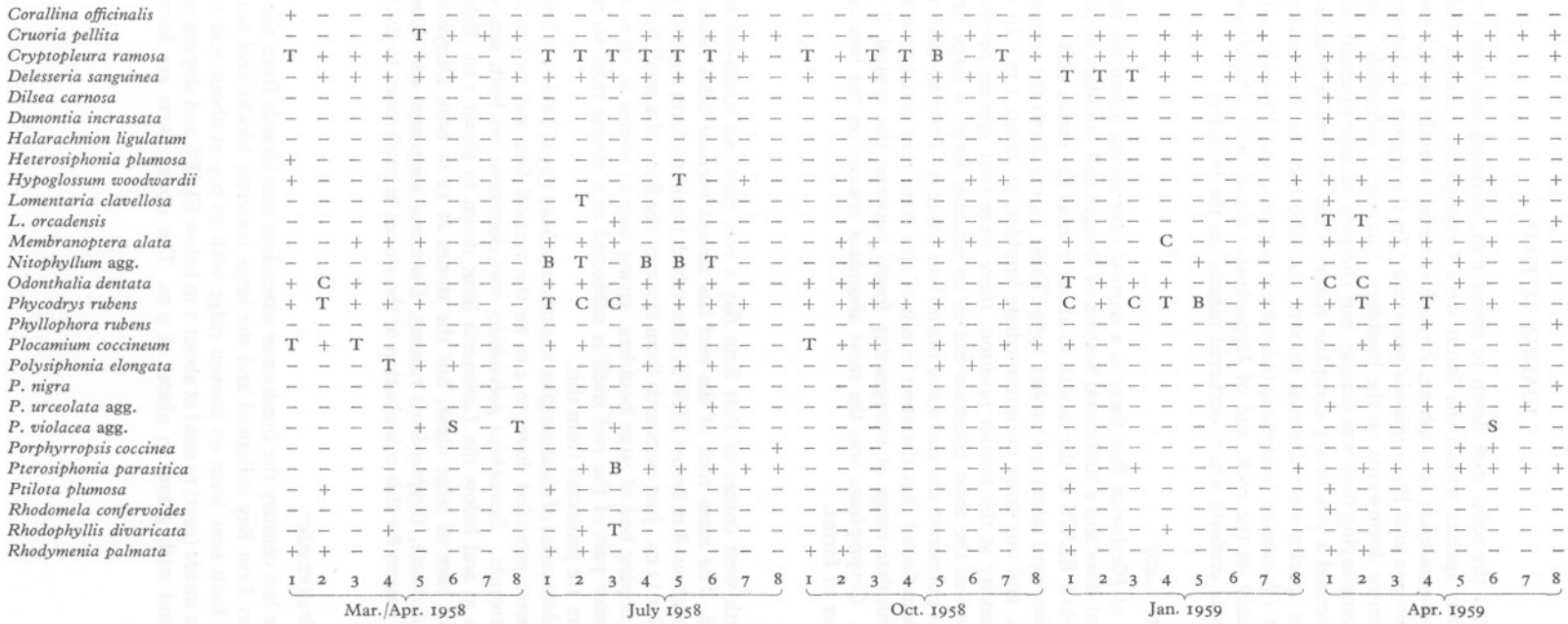


* *Sensu* Hamel † *sensu* Irvine ‡ *sensu* Naylor, 1958.

TABLE 3. THE SPECIES OCCURRING IN SAMPLES FROM PORT ERIN BREAKWATER AT DIFFERENT SEASONS, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C = cystocarps; O = oogonia; S = spermatangia; B = both tetrasporangia and cystocarps; P = plurilocular and U = unilocular sporangia; p = propagules.)

	Mar./Apr. 1958								July 1958								Oct. 1958								Jan. 1959								Apr. 1959							
Depth (m. below ELWS)	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Bryopsis plumosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	+	–
Chaetomorpha melagonium	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ulva lactuca	–	+	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	+	+	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+
Cutleria multifida sporoph.	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	U	+	–	+	+	+	+	+	+	+
Desmarestia aculeata	–	–	–	+	+	+	+	+	–	–	+	+	+	+	–	+	–	–	–	–	+	+	+	+	–	–	+	–	+	+	+	+	+	+	–	–	+	+	–	–
D. ligulata	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–
Dictyota dichotoma	+	+	+	+	+	+	–	–	+	T	+	T	T	T	+	–	+	–	O	+	T	+	+	O	–	–	–	–	–	–	–	–	+	–	–	+	+	+	–	+
Ectocarpus confervoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Giffordia hincksiae	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–
Laminaria hyperborea	+	+	+	+	+	–	–	–	+	+	+	+	–	–	–	–	+	+	+	+	+	–	–	–	+	+	+	+	+	–	–	–	+	+	+	+	–	–	–	–
L. saccharina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–
Saccorhiza polyschides	–	–	–	+	+	+	–	–	+	+	+	+	+	+	–	–	–	–	+	+	+	+	–	–	–	+	–	+	+	+	–	–	+	+	–	+	+	–	+	–
Sphacelaria pennata	–	–	–	–	–	–	p	p	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	p	–	–
S. plumula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	p
*Stictyosiphon soriferus**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
S. tortilis	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tilopteris mertensii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Apoglossum ruscifolium	–	–	–	–	–	–	–	–	–	T	–	–	–	–	–	–	–	–	T	C	T	–	T	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Bonnemaisonia asparagoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
B. hamifera sporoph.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+
Brongniartella byssoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–
Callophyllis laciniata	+	+	+	–	–	–	–	–	+	+	–	+	–	–	–	+	+	+	+	+	+	–	+	–	+	+	–	+	+	+	–	+	+	+	+	–	–	–	–	–
Ceramium rubrum agg.	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–



* *Sensu* Naylor.

forest occupied the solid rock down to about 6 m, thinning out down to 8 m. The most important species within the forest were *Cryptopleura ramosa*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte, *Phycodrys rubens* (mainly on *Laminaria* stipes), *Dictyota dichotoma* and *Pterosiphonia parasitica*. In the region of thinner forest and for some distance downwards on the boulders, *Saccorhiza polyschides* was dominant. Here the accompanying flora was similar, but *Dictyota* became gradually more abundant until it formed a practically complete cover of the outermost boulders. Most of the important species were common to both the solid rock or the boulders, with the exceptions of *Plocamium coccinium*, *Odonthalia dentata*, and *Phycodrys rubens* which occurred mainly on the rock, and of *Hypoglossum woodwardii*, *Polysiphonia elongata* and *Desmarestia aculeata* which occurred mainly on the boulders.

Surby Bowes Cave

Just north of Fleshwick Bay there is a narrow cave facing about north-west, with almost vertical sides and a sublittoral bottom of shingle and boulders sloping up from about 3 m below ELWS at the mouth to about 1 m at the inside end.

Two samples were taken in October 1959 (Table 1), one from the vertical end wall, at about 0 m, and one from an intermediate boulder, at about 1 m. In spite of the low light intensity at the former position, there were four species present. *Cryptopleura ramosa* was the most common but in an unusual form; a large proportion of the frond was polystromatic and some plants had tendrils. *Ptilothamnion* was present here: Dr Dixon found that the erect fronds of this were very variable in appearance, showing a complete range of intergrading forms between the typical *P. pluma* and *P. lucifugum*. *Cryptopleura* was the most abundant species on the boulder, where it took a number of forms.

The Sker

At the north-west corner of Port Erin Bay a reef runs out south-westwards from Bradda Head. The main rock of the reef has almost vertical sides from above high water down to about 8 m below ELWS, after which boulders form a gently sloping bed down to sand at 11 m. Just eastwards from this reef the floor of a small bay is occupied by a steeply sloping bed of large boulders, giving way to stones at 10 m and sand at 11 m. The outer part of the reef itself is subjected to a strong tidal stream, but the inner boulders are protected from this.

An incomplete series of algal samples was taken in May 1959 (Table 1). The *Laminaria hyperborea* forest extended down to 4 m on the vertical face and to 5 m on the large boulders eastwards. *Saccorhiza polyschides* was dominant on both sets of boulders in the region at and below the *Laminaria* limit down to about 7 m. Below that the boulders were bare of large algae, but the stones at 11 m bore *Dictyota dichotoma*, *Desmarestia aculeata*, *Cryptopleura ramosa*, *Delesseria sanguinea* and *Laminaria saccharina*. The reason for this colonization of the stones in preference to the rocks is not yet certain.

Port Erin Breakwater

During the last century the breakwater extending northwards from the south-west corner of Port Erin Bay collapsed and the large concrete blocks and boulders from which it was built now form an uneven ridge with its top at about mid-tide, sloping steeply on the inside (east) to sand at about 7 m below ELWS and sloping gently on the outside to sand with gravel in places at 9 m. The upper parts are formed only of

concrete blocks about 2 m long, while the lower parts have boulders mixed with the blocks. Tidal streams are weak and effect only the top and end.

Sampling has been carried out at three-monthly intervals throughout a year on the outer (western) side. The records are given in Table 3. The *Laminaria hyperborea* forest was thick on the upper surface of the concrete blocks down to 5–6 m. At this level *Saccorhiza polyschides* dominated at all times of year. The most abundant smaller plants at all levels were *Cryptopleura ramosa*, *Delesseria sanguinea*, *Dictyota dichotoma*, *Phycodrys rubens*, *Cutleria multifida* sporophyte, *Desmarestia aculeata* and *Odonthalia dentata*. There was no marked change in the qualitative composition of the flora during the year, except for the apparently complete absence of *Dictyota* in January. That the disappearance of this species from sublittoral rocks in winter is a regular occurrence was confirmed the following year. The forms of many of the species showed a seasonal change, the fronds of such plants as *Delesseria* and *Odonthalia* becoming denuded in the autumn and regenerated in January. There was no suggestion of a summer annual flora. More species were recorded in April 1959 than April 1958; this may have been a reflexion of improved technique rather than a difference between the years.

Creg Liauyr

Between Port Erin breakwater and Bay Fine an exposed reef extends west-north-west from the shore. Beyond this, under water, there are a number of isolated rocky knolls with steep sides, surrounded by large boulders which slope steeply to the level of the gravel, at 13·5 m, where they stop abruptly. Just south-west of the reef the boulders are smaller, 1–2 m across, and slope more gently down to the gravel. The region is subjected to some tidal stream at springs but very little at neaps.

Two series of samples were taken, one ('north') on the rocky knolls and large boulders, and the other ('south') on the continuous boulder bed, in April–June 1958 (Table 1). In both places there was the usual thick forest of *Laminaria hyperborea* which faded out between 6 and 8 m below ELWS. Again *Saccorhiza polyschides* was most abundant at this level. The undergrowth flora in both places consisted mainly of *Phycodrys rubens* (mostly on *Laminaria* stipes), *Cryptopleura ramosa*, *Delesseria sanguinea*, *Dictyota dichotoma*, *Cutleria multifida* sporophyte, *Desmarestia aculeata*, *Odonthalia dentata*, *Pterosiphonia parasitica*, *Plocamium coccineum*, *Membranoptera alata* and *Callophyllis laciniata*. Most of these extended below the *Laminaria* forest for about 2 m but the *Cutleria* sporophyte was the principal occupier (though not forming a continuous cover) of the lowest boulders at 11–12 m. There was little difference between the main constituents of the flora of the two regions, but the smaller boulders south showed a greater variety in the more occasional species.

The Bowes

Between Bay Fine and Aldrick a rocky reef lies just off the shore, and is known as Halfway Rocks or the Bowes. Part of this is visible at all stages of the tide, but offshore from it there is an extensive submerged rock with its pinnacle at 5 m below ELWS. The gravel bed lies deeper here than nearer Port Erin, with the result that there are rocky surfaces down to 16 m below ELWS. The reef itself is very uneven with ledges, cliffs and overhangs. The reef is subjected to fairly strong tidal streams even at neaps.

The main sampling series was made in April–May 1958 (Table 2). The *Laminaria hyperborea* was as dense as found in the previous places mentioned, and thinned out between 10 and 12 m. Here again *Saccorhiza polyschides* formed a dominant zone at the lower limit of *Laminaria*. The associated flora was also similar. The similarity of the flora to that of the breakwater and Creg Liauyr is remarkable in that the whole

spectrum is 4–5 m lower. The top of the Bowes rock is at the same level as the lower limit of *Laminaria* at the breakwater, but the forest is thick for another 5 m downwards. Some algae were present on the lowest rock surfaces at 16 m, though the cover was sparse; the most common were *Desmarestia aculeata*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte, and *Heterosiphonia plumosa*. In December the only occupant of this level had been *Cutleria* sporophyte.

The Leods

Near the entrance to Calf Sound a reef known as the Heifer Rocks or the Leods lies offshore with its top just above LWS. The main shore is steep at this point, with some boulders at the base. The channel between here and the reef is narrow with a rocky bottom at about 10 m below ELWS. The side of this formed by the reef is slightly overhanging, while the south-western side of the reef is about vertical with a boulder bed at its base at 14 m, sloping gently down to the gravel at 17 m. The northern side of the reef is also a sloping boulder bed. The reef is subjected to strong tidal streams.

An incomplete series of samples was taken in July 1958 and 1959 (Table 2). *Laminaria hyperborea* extended to 6–10 m. The steep inner side of the reef was occupied by *Alcyonium* below about 3 m where it overhangs. The flora in the *Laminaria* forest had the usual composition, while the south-west boulders at 14 m were occupied mainly by *Dictyopteris membranacea*, *Dictyota dichotoma*, *Cutleria multifida* sporophyte, *Bonnemaisonia asparagoides* and *B. hamifera* sporophyte.

Spanish Head

Spanish Head lies on the other side of Calf Sound and consists of steep cliffs with large boulders (2–3 m across) below them under water. These slope steeply (at about 1 in 5) into deep water and provide the deepest rock so far encountered on the island at 22 m below ELWS. The Head is subjected to very strong tidal streams on both flood and ebb.

Sampling was first carried out in July 1959 (Table 2). The *Laminaria hyperborea* plants were large and the forest started thinning at about 9 m but extended to 14 m below ELWS. *Saccorhiza polyschides* extended over a wide range, down to 19 m, but was again probably most abundant at the lower limit of *Laminaria*. The main species occurring within the forest and some distance below it were *Cryptopleura ramosa*, *Phycodrys rubens*, *Plocamium coccineum*, *Cutleria multifida* sporophyte, *Pterosiphonia parasitica*, *Desmarestia aculeata*, *Dictyota dichotoma*, *Callophyllis laciniata* and *Nitophyllum* agg. Those confined to above 10 m were *Rhodymenia palmata*, *Callithamnion tetragonium* and *Porphyra umbilicalis* f. *rosea* (all on *Laminaria* fronds), *Desmarestia ligulata* and *Odonthalia dentata*. Below 10 m the vegetation became sparse and irregular; some of the boulders had a fair cover of small forms, some were bare and some were colonized by *Alcyonium*. From 10 to 18 m the most important species were *Bonnemaisonia asparagoides*, *B. hamifera* sporophyte and *Hypoglossum woodwardii*, in addition to those already mentioned. Below this the vegetation was very sparse indeed and a close search was necessary to detect it. Even so, there were still eleven species present on the lowest boulders at 22 m, the most important being *Antithamnion plumula*, *Bonnemaisonia hamifera* sporophyte, *Compsothamnion thuyoides*, *Pterosiphonia parasitica* and *Cutleria multifida* sporophyte. The crinoid *Antedon* occupied many of the boulders.

In February 1960 further sampling was carried out on the lower boulders in order to determine whether the sparse algal cover was confined to the summer. Although the vegetation was considerably reduced in quantity the majority of the species were

still present (Table 2). The most marked absence was of *Dictyota dichotoma*, which also disappeared from other sublittoral rocks in winter. *Bonnemaisonia asparagoides* and *Compsothamnion thuyoides* had also apparently disappeared. Although it was almost too dark to read at the lowest depth, at least five species were still present. *Plocamium coccineum* was abundant at 19 m, where there was also a first year sporeling of *Laminaria hyperborea* (with mucilage canals in the stipe). This was the deepest record for this plant.

Scarlett Point

The shore just east of the southern tip of Scarlett Point is formed of limestone ledges, each ledge being inclined slightly upwards towards the sea. Sublittorally the configuration is very similar, though obscured by the thick forest of *L. hyperborea*. The general slope is very gentle and in places there are patches of gravel. There are also shallow gullies containing boulders.

An incomplete series of samples was taken in July 1959 (Table 2). The *Laminaria* forest was very thick. The rock below was noticeably bare, apart from a cover of *Lithothamnion* and small quantities of the usual species. Even *Cutleria multifida* sporophyte, the most regular species, was present in only very small amounts in the really thick forest at 1–5 m; its place was largely taken by *Cruoria pellita*. All these extended over the depth range sampled (the level of the gravel bed proper was not reached), except for *Odonthalia dentata* which ceased at 5 m. The boulders in the gullies were occupied by *Laminaria saccharina*.

Dreswick Point (Langness)

Langness is a narrow peninsula extending southwards and Dreswick Point is the southern tip of this. Offshore the tidal stream is notoriously strong, but there is little evidence of this inshore. Just west of the lighthouse a gully runs southwards, with boulders on its gently sloping floor and several steep-sided knolls of rock about 8 m high.

An incomplete series of samples was taken from a knoll and the boulders in July 1959 (Table 2). The knoll was occupied by *L. hyperborea* forest as usual, but the associated flora differed somewhat from that common near Port Erin: *Heterosiphonia plumosa* was the most prominent red alga, and neither *Cutleria multifida* sporophyte nor *Dictyota dichotoma* was recorded. The *L. hyperborea* extended to the bottom of the knoll, at 11 m below ELWS, with occasional plants on the boulders. There was no *Saccorhiza polyschides* zone, the boulders being occupied instead by *L. saccharina*. The level of the gravel bed was not reached, though there were patches of coarse sand amongst the boulders.

UNSTABLE BOTTOMS

Over the course of a number of years Lodge (1954) carried out a great many dredging operations around the south end of the Isle of Man and recorded a total of 128 species. Many of these have not been found on the rock surfaces, and as some of the areas which she dredged were gravel beds it seems likely that a considerable flora could develop on the unstable bottom under certain conditions. Little attempt has been made to extend these particular observations using diving equipment, but the few direct records on gravel that have been made (Table 4) may be of interest. It must be emphasized that these algae were attached to superficial stones and were clearly not drifting.

Glen Maye Bay

Glen Maye Bay, just north of Niarbyl, was sampled in July 1959. The bottom consists of small boulders and stones mixed with gravel. At 11 m below ELWS the gravel (diameter 2–30 mm) bore *Chorda filum*, *Brongniartella byssoides*, *Myriocladia?* sp., *Stictyosiphon tortilis*, *Cutleria multifida* gametophyte (male and female), *Sporochnus pedunculatus*, *Cladostephus spongiosus*, *Acrothrix gracilis* and other species. This assemblage clearly differed from those found on the rock reefs. Brown algae were predominant. Further offshore, at 12 m, there were small boulders and these bore many of the species normally inhabiting rock surfaces: *Saccorhiza polyschides*, *Dictyota dichotoma*, *Halidrys siliquosa*, *Heterosiphonia plumosa*, *Cutleria multifida* sporophyte, *Hypoglossum woodwardii*, *Brongniartella byssoides*, *Pterosiphonia parasitica* and *Phycodrys rubens* being the most common.

Stroin Vuigh

In July 1959 the lowermost boulders (10 m) at Stroin Vuigh, already described, bore a flora very similar to that on the Glen Maye boulders. In addition, the gravel between the boulders was occupied by *Myriocladia?* sp., *Chorda filum*, *Enteromorpha clathrata* and *Cutleria multifida* gametophyte. *Myriocladia?* sp. was also found by Parke (private communication) in this region and then ascribed by her to *M. loveni* J. Ag. This was later found to differ from the Swedish material of this species (Parke 1950). Its identity is not yet certain.

Off Bradda Hill

In September 1958 small stones at 15 m below ELWS off the Charran, west of Fleshwick Bay, were occupied by *Brongniartella byssoides*, *Saccorhiza polyschides* sporelings and *Plocamium coccineum*. At 21 m the bottom was sand and gravel and there were no algae.

In August 1959 an extensive search was made at 32 m and at 23 m on the coarse gravel bed off the West Bradda Mines, but no attached algae were found. The calm sunny summer would have resulted in there being growth, given a spore supply, if this were ever possible, but clearly either the depth or tidal streams prevented it.

Off Creg Liauyr

Again in August 1959, somewhat shallower beds off Port Erin breakwater between Bradda Head and Bay Fine, where the tide is less strong, were found to support a fairly rich flora. The most abundant species, on stones of 5–20 cm, mixed with coarse sand, were *Saccorhiza polyschides*, *Stictyosiphon tortilis*, *Sporochnus pedunculatus*, *Arthrocladia villosa*, *Desmarestia aculeata*, *Cutleria multifida* gametophyte, *Bonnemaisonia asparagoides*, *Antithamnion plumula*, *Halarachnion ligulatum* and *Scinaia furcellata*. The gravel at 13 m adjacent to the boulders at Creg Liauyr was found in September 1958 to bear *Scinaia*, *Halarachnion*, *Antithamnion sarniense* and *Sporochnus pedunculatus*.

The same position was visited during the winter, at the end of November 1959, and the flora found to be almost negligible. Clearly the intervening gales had destroyed most of the plants which were dependent on the unstable bottom not being extensively disturbed.

TABLE 4. THE SPECIES OCCURRING IN SAMPLES FROM UNSTABLE BOTTOMS, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C = cystocarps; B = both; S = spermatangia; M = monospores; O = oogonia; A = antheridia; b = both; P = plurilocular and U = unilocular sporangia; p = propagules.)

	Glen Maye Bay, July 1959					Stroin Vuigh, July 1959				Off Charran, Sept. 1958			Off Creg Liauyr 1959			
													Aug.			Nov.
Depth (m below ELWS)	10	11	12	13	14	8	9·6	9·9	10	11	15	21	14	15	15·3	16
Cladophora sp.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Enteromorpha clathrata (sensu Bliding, 1944)	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Ulva lactuca	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Acrothrix gracilis	U	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arthrocladia villosa	–	–	–	–	–	–	–	–	–	–	–	–	–	U	U	–
Chorda filum (sensu Hamel 1931–9)	+	–	–	–	–	–	–	+	–	–	–	–	+	+	–	–
Cladostephus spongiosus (sensu Hamel 1931–9)	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cutleria multifida gametophyte	b	–	–	–	–	–	–	+	–	–	–	–	A	+	+	–
C. multifida sporophyte	–	+	+	+	–	+	+	–	+	–	–	–	–	–	–	–
Desmarestia aculeata	+	–	–	–	–	+	–	–	+	+	–	–	+	+	+	–
Dictyota dichotoma	–	A	+	+	+	+	b	–	O	+	–	–	–	–	+	–
Ectocarpus confervoides	+	–	–	P	–	–	+	–	–	–	–	–	–	–	–	–
Halidrys siliquosa	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–
Laminaria saccharina	–	+	+	–	–	–	–	–	+	+	–	–	–	–	–	+
Myriocladia? sp. (see Parke, 1950)	U	–	–	–	–	–	U	U	–	–	–	–	–	–	–	–
Saccorhiza polyschides	+	+	+	–	–	+	+	–	+	+	+	–	+	+	+	+
Sphacelaria bipinnata	–	–	–	–	PU	–	–	–	–	–	–	–	–	–	–	–
S. pennata	p	–	p	–	–	–	p	–	p	–	–	–	–	–	–	–
S. plumula	–	–	–	–	–	p	–	–	p	–	–	–	–	–	–	–
Sporochnus pedunculatus	+	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–
Stictyosiphon tortilis	+	P	–	–	–	–	–	–	–	–	–	–	–	+	+	–
Antithamnion plumula	–	–	–	–	–	–	–	–	–	–	–	–	B	C	+	–
Bonnemaisonia asparagoides	–	C	C	–	–	–	–	–	C	–	–	–	C	C	C	–
Brongniartella byssoides	+	S	T	+	–	T	T	–	C	–	C	–	–	–	–	–
Callithamnion corymbosum	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Ceramium rubrum agg.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chylocladia verticillata	–	C	T	–	–	–	–	–	–	–	–	–	–	–	–	–
Corynospora pedicellata	–	M	M	–	–	–	–	–	–	–	–	–	–	–	–	–
Cryptopleura ramosa	–	+	+	–	T	T	T	–	T	+	–	–	–	+	+	–
Delesseria sanguinea	–	–	+	–	–	+	+	–	+	+	–	–	–	–	–	–
Halarachnion ligulatum	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–	–
Heterosiphonia plumosa	–	+	+	+	–	–	+	–	+	–	–	–	–	–	–	–
Hypoglossum woodwardii	–	+	T	T	–	+	B	–	B	–	–	–	–	–	–	–
Lomentaria clavellosa	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Membranoptera alata	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Nitophyllum agg.	–	T	T	–	–	B	B	–	T	–	–	–	+	–	–	–
Odonthalia dentata	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Phycodrys rubens	–	+	+	+	+	–	–	–	–	–	–	–	+	–	–	–
Plocamium coccineum	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+
Polysiphonia brodiaei	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
P. elongata	–	+	–	–	–	+	+	–	+	–	–	–	+	+	–	–
P. urecolata agg.	–	–	S	–	–	–	–	–	–	–	–	–	–	–	–	–
P. violacea agg.	C	–	+	–	–	T	–	–	–	–	–	–	T	–	–	–
Pterosiphonia parasitica	–	+	+	+	–	+	+	–	+	–	–	–	–	–	–	–
P. thuyoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Ptilota plumosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Rhodomela confervoides	–	+	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Scinaia furcellata	–	–	–	–	–	–	–	–	–	–	–	–	C	+	–	–
Sphondylothamnion multifidum	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–

DISCUSSION

The aim of a preliminary survey of this nature is the recognition of the ecological problems peculiar to the habitat. The first that arises here concerns what was undoubtedly the most ubiquitous sublittoral plant, the sporophyte of *Cutleria multifida* (*Aglaozonia parvula*). It occurred at virtually every level sampled in all the localities except Langness, on rocky bottoms and on boulders though not on smaller stones. It rarely formed a continuous carpet, but patches could be found on almost all rocks, sometimes several layers thick. Occasionally it was mixed with prostrate *Dictyota dichotoma* but was easily distinguishable from this in transverse section. During the first year of sampling no gametophytes were found. The widespread occurrence of the other generation of the plant was therefore an enigma. Although alternation of generations is supposed to occur, by-passing of the gametophytic stage by the production of an *Aglaozonia*-like phase by zoospores from the sporophyte has been reported (Church, 1898). It was therefore thought likely that this might be the normal occurrence in these waters, and when a reproducing thallus was found on Port Erin breakwater in January 1959 it was kept under observation in the laboratory. The liberation of the spores was induced in culture medium. After 2 weeks they developed into branched filaments floating on the surface. A number of these were washed and transferred to fresh medium where, without exception, they developed into the gametophytic phase; these developed sporangia while still quite small, there being both male and female plants. Later that year gametophytes were first found in the field on Perspex slides which had been left out for some weeks; this suggested that a search of different habitats might reveal the gametophytes, at least during certain seasons. This proved to be so when they were found both in Glen Maye Bay and off Creg Liauyr (Table 4) during the summer. They had disappeared from the latter position by November. It therefore seems likely that the gametophytic stage of this plant exists as a transient population on the extensive gravel beds during the summer, when the relatively calm weather renders this substratum habitable, and then releases sufficient gametes to maintain the existence of the sporophytic phase on the rock surface. Amongst the limited number of gametophytic plants encountered in nature and culture there was no suggestion of a shortage of males as reported by Feldmann (1957) and others.

The second main problem arising is that of zonation. It is apparent that what zonation there is on the rock faces is determined not only by absolute depth but also by the level or proximity of the adjacent gravel bed. This is associated with the distribution of *Laminaria hyperborea*. As this plant is at present the subject of study it will not be further discussed here.

On solid rock and large boulders it is clear that when the absence of *L. hyperborea* allows, the growth of *Saccorhiza* takes place. It is present in some places mixed in with the former species in the forest, but it has its

climax in the zone just below the *Laminaria* limit, where the light is evidently still sufficient for it but where the factor which limits *Laminaria* is evidently ineffective against it. It is probable that through its power of faster growth it can take advantage of transiently good conditions and become established, but because the plants are much less strongly constructed they last for a shorter time. It is worth stressing that the level of *Saccorhiza* dominance is dependent on the level of the *Laminaria*, at whatever depth this is.

The species forming the undergrowth of the *Laminaria* forest are not confined to that region and all extend downwards. The cover gradually becomes thinner, and near to the limit of the rock there are large patches of uninhabited surface. At the breakwater this bare zone is at the same depth as the rich forest flora of the Bowes or Spanish Head. This is in contrast to the situation in the Mediterranean, where Drach (1948*a*) insists that cover is always 100%; where the rock is not occupied by plants it is colonized by animals. It seems that some factor associated with the proximity of the gravel, which inhibits the establishment of algae, also acts on the animals. Where light alone is the limiting factor, on overhangs and possibly the deeper rock at Spanish Head, the place of algae may be taken by *Alcyonium* and sponges.

The presence of a number of algae on the lowest known rock at the darkest time of the year makes the determination of the general lower algal limit for the area impossible.

Thirdly, there arises the question of the effect of depth on reproduction. Jones (1956) suggested that the greater paucity of fertile species at the greater depth of 25 m at Bardsey might reflect a weaker ability to reproduce nearer the limit of the range of a plant, but this cannot be supported by the present records. The reason might be that in most cases in the Isle of Man the lower limit of sublittoral algae is determined by a factor acting not on the growth rate (such as light) but on initial establishment (such as the proximity of the gravel). A second suggestion made by Jones was that carposporic plants of *Brongniartella byssoides* and *Lomentaria clavellosa* grew deeper than tetrasporic plants; this was however based on single samples. All the available records in the present work have been examined with this in mind, but only *Brongniartella* showed any indication of a relationship between reproductive phase and depth. With this species, as at Bardsey, gametophytic plants were confined to deeper water, below 10 m, though there were only three records. There were 6 records of tetrasporic plants and only one of these was deeper than 10 m. This lends support to Jones's evidence.

I am indebted to J. Faragher and L. Collister, crew of the motor-boat 'Cypris', and am particularly grateful to the latter for his unremitting vigilance at the other end of the safety line.

A number of species (though not all) were identified or checked by certain people; very many thanks for this are due to Dr H. Blackler (*Ectocarpus*,

Giffordia), Dr E. M. Burrows (*Enteromorpha*, *Tilopteris*), Dr P. S. Dixon (Rhodophyceae), Dr D. E. G. Irvine (*Sphacelaria*), Dr M. W. Parke (*Myriocladia?*) and Dr M. Roberts (née Naylor) (*Stictyosiphon*).

I am also grateful to Miss W. B. Chapman for help with the maintenance of diving equipment, and would like to thank Professor W. T. Williams for helpful criticism of the manuscript.

SUMMARY

A general survey has been made of the distribution with depth of the main sublittoral algae inhabiting the rock surfaces at ten places around the south end of the Isle of Man, using an aqualung. The region is characterized by the lack of any deep water rock; this is replaced by gravel at a depth of about 12 m in most places. Immediately below ELWS the vegetation was dominated by *Laminaria hyperborea*, forming a thick forest with an undergrowth of smaller brown and red algae. The lower limit of this forest was well defined, and depended not on the absolute depth but on the proximity of the junction of solid rock and the gravel bed. *Saccorhiza polyschides* dominated just below the *Laminaria hyperborea* limit, at whatever depth this was. The smaller algae of the forest extended down on the deeper rock but the cover was reduced as the gravel was approached. Observations were made on one reef throughout the year. Although the abundance and form of the more important species varied, most were present at all times of the year, but *Dictyota dichotoma* was absent in winter. The deepest rock found, at 22 m below ELWS, was colonized by a few algae even in winter. The most ubiquitous plant on the rock was the sporophyte of *Cutleria multifida* which appeared to alternate with sexual plants which formed part of a transient summer population of algae which occupied the gravel bed in places.

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CODIUM AMPHIBIUM: A SPECIES OF DOUBTFUL VALIDITY

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(Text-figs. 1–3)

Codium amphibium was described by Harvey (1844) on the basis of material sent to him by David Moore, who in turn had received it from the collector, William M'Calla. This material was said to grow 'on turfy banks at extreme high-water mark, near Roundstone, county Galway', and was described as comprising numerous erect, small (to $\frac{1}{4}$ in. high), simple, cylindrical or subclavate, obtuse fronds arising from a mass of entangled, divaricately branched filaments densely aggregated into widely spreading patches. Harvey's illustration clearly shows the habit, but his drawing of utricles is neither diagnostic nor accurate [as judged from our study of the type material]. Harvey made particular note of the habitat, which he inferred would place the plant 'beyond the reach of the ordinary sea-level'. In a later work, Harvey (1846, pl. 35B) illustrated this species with similar drawings and added nothing to the description except to extend the maximum height of the fronds to 'nearly half an inch'. Still later, Harvey (1849, p. 194) increased the maximum height of the fronds to an inch, modified 'simple' to 'usually simple, rarely emarginate or forked', added the locality 'at the head of Birtirbui Bay, Galway' and changed the habitat as follows: 'Turf banks, near high-water mark, but washed by every tide...' Kützing (1849, p. 502) furnished a description similar to the original one, based on an Irish specimen sent to him by Berkeley, probably topotype material*. In his illustration of this material, Kützing (1856, pl. 96, fig. á) showed an important character of the utricles: a tendency towards pointed apices.

The first report of *C. amphibium* from some locality other than Ireland was that of Tellam (1883), who collected what he considered to be this species at Falmouth in 1882, growing on a small ledge of rocks near high-water mark to the west of Pendennis Castle, sheltered by higher rocks on the south, but covered by every tide. The fronds were said to be $\frac{1}{4}$–$\frac{3}{8}$ in. high, arising from patches of glossy, dark green filaments which spread through and on the muddy sand covering the rocky ledge. J. Agardh (1887), in his monograph of *Codium*, placed *C. amphibium* in his tribus *Codii tomentosi*. Holmes & Batters

* The three specimens of *C. amphibium* in Kützing's herbarium at Leiden are labelled 'Roundstone Bay', 'Ireland. Harvey. Herb. Kützing' and 'Connemara. Andrews,' respectively.

(1890, p. 77) reduced *C. amphibium* to the status of a form of *C. adhaerens*. Batters (1902, p.22) listed the Isle of Man as an additional locality for *C. amphibium* on the basis of material from Perwick Bay collected by George in 1890. Cotton (1912, p. 113) reported finding this species on a ledge at the mouth of a cave on Clare Island in 1909 and 1911. He also reported that a special search for the plant at Roundstone during September 1911 was without success. Schmidt (1923) included *C. amphibium* in his monograph of the genus solely on the basis of previously published accounts, but in 1939, after having had the opportunity to study material from Port-en-Bassin [Calvados, France, reported earlier by Fortin (1935) as an unnamed variety of *C. tomentosum*] in addition to topotype material from Roundstone, he published a supplementary account of the species. The following secondary references complete the literature for *C. amphibium*: Cocks (1853, p. 77); Gifford (1853, p. 289); Harvey (1857, p. 159, pl. 62, fig. 289); Johnstone & Croall (1860, p. 5); Gatty (1863, p. 123); Gray (1867, p. 243); DeToni (1889, p. 491); Knight & Parke (1931, p. 55); Newton (1931, p. 105); Parke (1953, p. 500).

The amount of information available about *C. amphibium* is not commensurate with the number of published accounts. Up to now neither hairs nor gametangia have been observed. During the last few years one of us (Silva) has had an opportunity to study collections assigned to this species in the major herbaria of the world in addition to liquid-preserved material from Falmouth and from St Andrews, kindly provided by Dr M. A. Wilson and Dr Irvine, respectively. The other of us (Irvine) has been keenly interested in the problem of *C. amphibium* because plants suggestive of this species were growing in tide pools that were the object of an ecological study.

An examination of the type collection in Trinity College, Dublin, confirmed the presence of pointed utricles (Fig. 1, A), as shown first by Kützing (1856) and later by Schmidt (1939). Juvenile plants of *C. fragile* subsp. *atlanticum* (Cotton) Silva are immediately called to mind, and it may be noted that a similar impression was gained by W. A. Setchell from his study of topotype collections of *C. amphibium*. In a letter to A. D. Cotton, dated 10 June 1930, Setchell wrote, 'In all probability this species is simply a depauperate form of your variety [*C. mucronatum* var. *atlanticum*]'. In agreement with the type collection are all topotype collections that we have examined (Fig. 1, B) as well as the Cotton specimens from Clare Island (Fig. 1, C), the George specimens from the Isle of Man (Fig. 1, D), and a collection from Tellam's site near Falmouth (M. A. Wilson, viii.1943; Fig. 2, D).

An opportunity to learn more about *C. amphibium* was provided by the discovery by Dr Helen Blackler at St Andrews of plants referable to this species growing on the vertical sides and the bottom of a few rock pools on the Hind Rock and a neighbouring ridge at M.H.W.N.T. towards M.H.W.S.T. They were first observed in November 1949 and subsequently have been followed

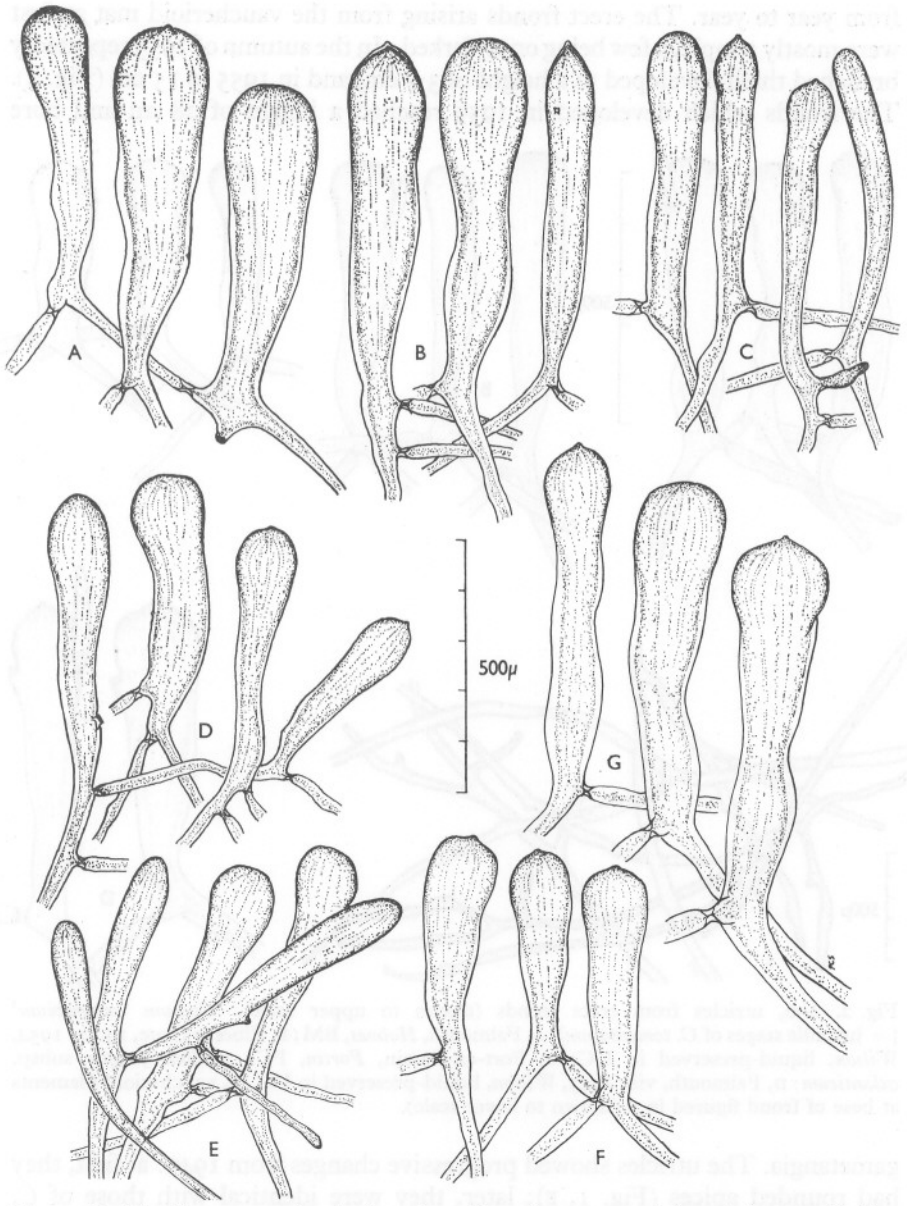

Fig. 1. Utricles from erect fronds (samples taken about 3 mm below tip). A–D, *Codium amphibium*. A, Roundstone Bay, *M'Calla*, TCD = type; B, Connemara, *M'Calla*, K; C, Portlea, Clare Island, viii. 1911, *Cotton* 358, K; D, Perwick Bay, Isle of Man, 3. ix. 1890, *George*, BM. E–G, *Codium fragile* subsp. *atlanticum*. E, St Andrews, 18. ix. 1952, *Irvine*, liquid-preserved in UC, frond 5 mm high; F, St Andrews, xi. 1955, *Blackler*, UC, frond 4 mm high; G, St Andrew, 5. x. 1955, *Blackler*, UC, frond 14 cm high.

from year to year. The erect fronds arising from the vaucherioid mat at first were mostly simple, a few being once-forked. In the autumn of 1953 repeatedly branched thalli developed to a height of 3·5 cm, and in 1955 to 15 cm (Fig. 3). The fronds which developed in 1959 reached a height of 28 cm and bore

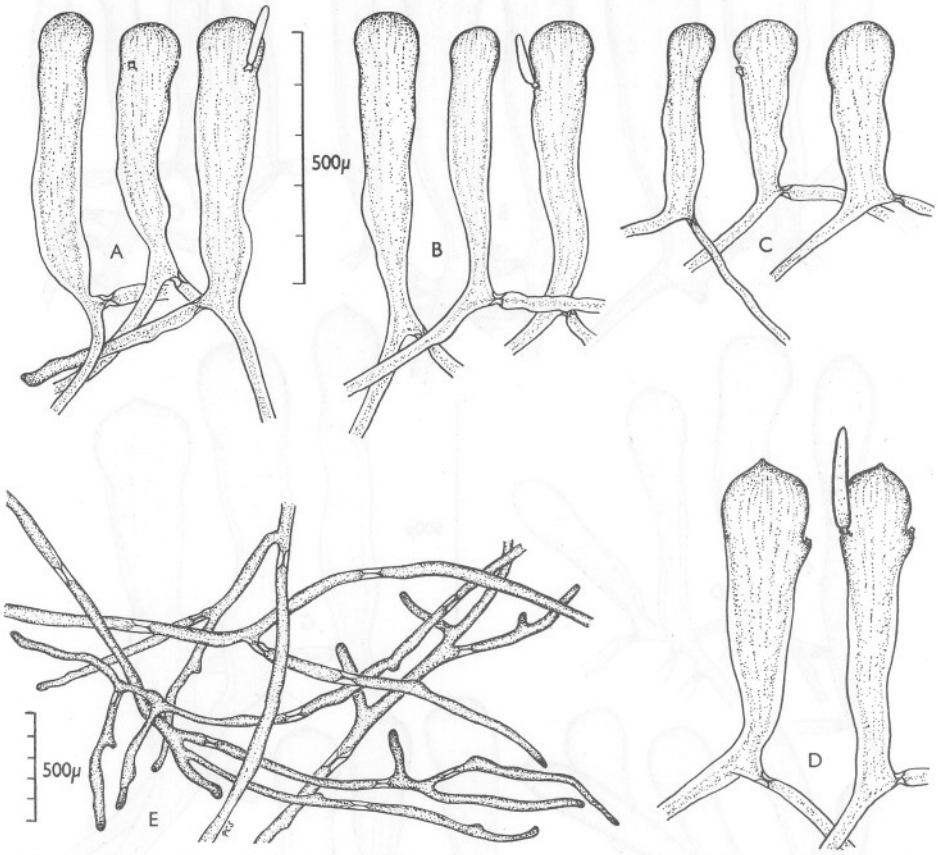

Fig. 2. A–D, utricles from erect fronds (drawn to upper scale). *Codium* '*amphibium*' [= juvenile stages of *C. tomentosum*]: A, Falmouth, *Holmes*, BM; B, Elberry Cove, 14. ix. 1954, *Wilson*, liquid-preserved in UC; C, Port-en-Bassin, *Fortin*, PC. *Codium fragile* subsp. *atlanticum*: D, Falmouth, viii. 1943, *Wilson*, liquid-preserved in UC. E, vaucherioid filaments at base of frond figured in D (drawn to lower scale).

gametangia. The utricles showed progressive changes from 1949: at first, they had rounded apices (Fig. 1, E); later, they were identical with those of *C. fragile* subsp. *atlanticum* (Figs. 1, F and G). The conclusion is drawn that *C. amphibium* at St Andrews is merely a juvenile stage of *C. fragile* subsp. *atlanticum*. Blackler (1956), in collaboration with us, reached the same conclusion. It seems reasonable to suppose that the Irish *C. amphibium* has a similar status, although in the absence of direct proof it must be admitted that

it could be a non-sexually reproducing series of populations maintained in a juvenile stage by the operation of environmental factors related to the purported amphibious habitat.

The development of extensive mossy vaucherioid growths of unconsolidated filaments (Fig. 2, E) is characteristic of members of the Codiaceae (Taylor, Joly & Bernatowicz, 1953). In *Codium* they represent juvenile stages, although not all species, nor all plants of a given species, seem to develop in this manner. Many fronds apparently arise from a spongy crustose base rather

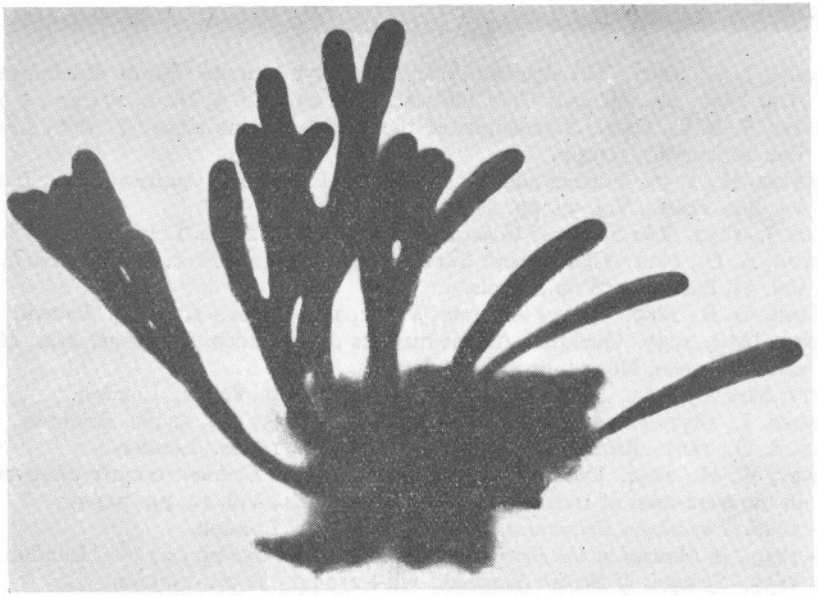

Fig. 3. *Codium fragile* subsp. *atlanticum*, St. Andrews, 1957. Photo: Dr Helen Blackler.

than from a vaucherioid mat, although it is possible that in these instances earlier vaucherioid stages have been overlooked. Morphogenesis in *Codium* has scarcely been studied and holds much promise for future investigation.

A study of some other material agreeing in habit with *C. amphibium* has revealed that *C. tomentosum* also has a vaucherioid juvenile stage. Several collections from Falmouth by Tellam and by Holmes (Fig. 2, A), the one by Fortin from Port-en-Bassin (Fig. 2, C), and one by Dr M. A. Wilson from Elberry Cove, Torbay, Devon (Fig. 2, B) are all referable to *C. tomentosum*.

We are grateful to the directors and curators of the following herbaria for the opportunity to study critical specimens: British Museum (Natural History) (BM); Royal Botanic Gardens, Kew (K); Muséum National

d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris (PC); Trinity College, Dublin (TCD). We wish to thank Dr M. A. Wilson, Dr Mary Parke, and Dr Helen Blackler for their interest and valuable help in this study.

SUMMARY

Plants agreeing in habit with the material originally described as *Codium amphibium* have been shown to be juvenile stages of *C. fragile* subsp. *atlanticum* and *C. tomentosum*. The type specimen is probably a juvenile of the former species. *C. fragile* subsp. *atlanticum* is reported for the first time from Cornwall.

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EXCHANGES OF WATER BETWEEN THE ENGLISH AND BRISTOL CHANNELS AROUND LANDS END

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The Plymouth Laboratory

(Text-figs. 1–11)

An understanding of the oceanography of the Celtic Sea requires an understanding of the exchanges of water around four headlands, Ushant, Lands End, St Davids Head and Carnsore Point. As a sequel to the study on the flow past Ushant already presented (Cooper, 1960*b*), this paper and the following one by Cooper, Lawford & Veley are attempts to achieve a better understanding of the exchanges around Lands End and in the neighbourhood of the Scilly Isles (Fig. 1).

Matthews (1914, p. 20) said: 'The charts published in this report show that the saltest water enters the Irish area between Lands End and the Scilly Islands, and detailed observations made along this line on several cruises at intervals of from half a mile to one mile on the Marine Biological Association's steamers have shown that the axis of highest salinity lies midway between the Longships Rock and the Seven Stones Lightship, that is, at a distance of only a few miles off Lands End. This current of salt warm water is derived from a current which has already entered the English Channel from a south-westerly direction, and has in part turned northwards and north-westwards to escape into the Irish Channel. It is practically certain that this water has come from the mouth of the English Channel and not directly from the open sea because further westwards a great area of lower surface salinity stretches southwards across the fairway and prevents any such direct current.'

Harvey (1925, fig. 19) accepted Matthews' interpretation and later (1929) from a study of geopotential topographies deduced that a residual current ran between Lands End and the Scillies in June 1924 in a N.N.E. direction with a velocity of about $1\frac{1}{2}$ miles per day compared with the water at 60 m. Carruthers (1934) suspected that N.N.E. may be a misprint for N.N.W. but both descriptions could be applied to different parts of the course sketched; N.N.E. applies more nearly in the passage itself.

The current measurements of Carruthers, Lawford & Veley (1951) further discussed in the following paper (Cooper, Lawford & Veley, 1960) cannot be gainsaid but appeared gravely to conflict with the deductions of Matthews and of Harvey.

Lumby (1935, p. 33) also remarked that 'an area of small extent (in the neighbourhood of the 'Seven Stones') appears to have a different régime from the rest of the Channel, according to the fluctuations of salinity from year to year. The same probably applies also to the seasonal variation.' Lumby & Carruthers *et al.* are thus in agreement. If measurements of current, temperature and salinity at the Seven Stones Light Vessel are considered to represent the whole of the Lands End–Scilly passage, we have no choice but to reject the deductions of Matthews and Harvey.

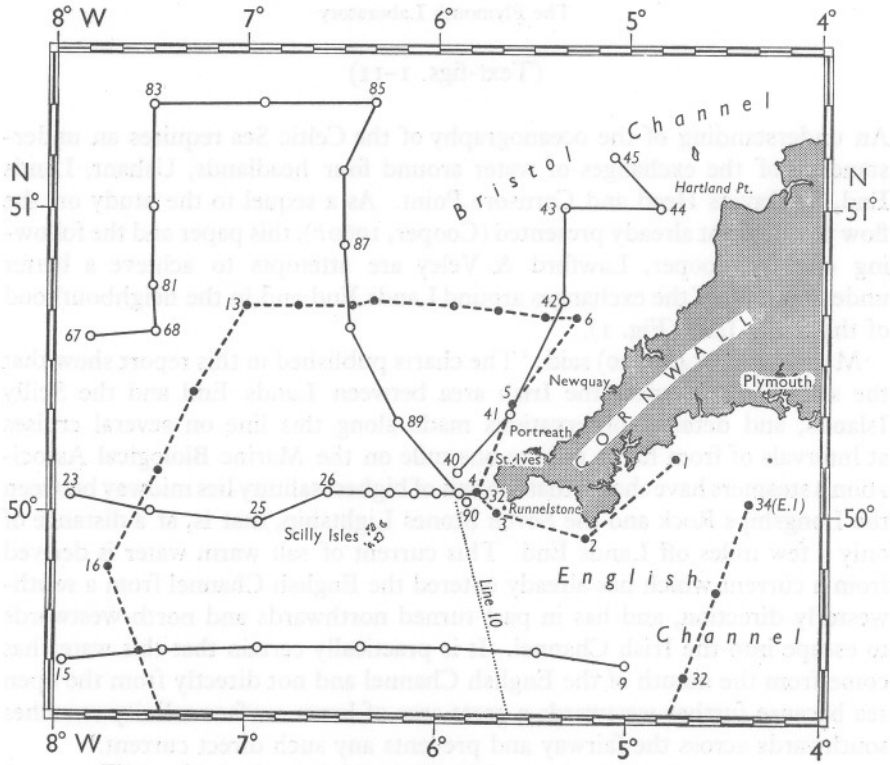

Fig. 1. Chart of area discussed and stations worked in April (full lines) and June 1950 (pecked lines).

The conflict may be resolved if we assume, as Matthews implied, that measurements at the light vessel may not be representative of the whole width of the passage and that a narrow corner current with other characteristics may flow snugly around Lands End from the south coast to the north coast of Cornwall. This was the state of our knowledge when our 1950 cruises were planned. The results, as first appreciated, were equivocal.

But let us start by examining the observations of salinity and temperature at the Seven Stones Light Vessel; as observations, these have quite exceptional homogeneity and apparent reliability.

TABLE 1. THE MEAN TEMPERATURE AND SALINITY IN REGION 5 (= SEVEN STONES LIGHT VESSEL) FOR MONTHS AND YEARS OF THE PERIOD 1928–58

Continuation of Lumby (1935; Table 16)

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year mean
						Temperature							
1928	10·29	9·75	9·85	10·62	12·15	13·06	15·74	16·42	15·74	14·19	12·51	11·09	12·62
1929	9·86	9·59	9·29	9·94	10·81	13·35	14·26	16·36	16·28	13·78	12·06	10·52	12·18
1930	9·95	9·19	9·09	9·78	11·30	14·20	15·36	15·00	14·91	13·45	12·48	11·19	12·16
1931	10·14	9·19	8·75	9·72	10·72	13·39	15·24	14·75	14·21	13·75	12·52	11·64	12·00
1932	10·72	9·74	9·46	9·51	10·62	14·22	15·45	17·62	16·31	13·18	12·19	11·19	12·52
1933	10·36	9·54	9·59	10·36	12·00	13·74	16·50	17·28	16·11	14·24	12·38	10·80	12·74
1934	10·01	9·32	9·14	9·25	10·44	14·70	16·96	15·74	14·76	13·32	11·91	11·22	12·23
1935	10·28	9·65	9·38	9·89	10·55	12·32	15·49	16·59	14·86	13·36	11·99	10·61	12·08
1936	9·90	9·58	9·60	10·26	11·30	13·82	15·19	15·31	16·19	13·95	12·55	11·08	12·39
1937	10·21	9·84	9·28	9·79	11·66	14·38	15·80	17·70	15·65	13·64	12·21	11·00	12·60
1938	10·00	9·38	9·48	9·88	10·90	12·65	13·98	15·38	14·28	13·56	12·85	11·22	11·96
1939	9·99	9·52	9·09	9·62	10·92	13·59	14·51	15·20	15·66	13·21	—	—	—
1940–46	—	—	—	—	—	—	—	—	—	—	—	—	—
1947	—	—	—	—	10·71	12·68	14·61	17·49	17·34	14·65	13·61	12·00	—
1948	10·72	9·75	9·95	10·18	11·74	13·14	13·89	16·01	14·79	14·01	12·84	11·89	12·41
1949	10·70	10·26	10·14	10·45	11·38	14·22	16·86	17·39	17·19	15·60	13·29	11·90	13·28
1950	10·94	10·01	10·11	10·35	11·09	14·38	16·08	16·35	15·26	13·59	12·41	10·40	12·58
1951	9·68	9·14	8·80	9·24	10·20	12·58	15·49	15·84	14·50	13·74	12·91	11·61	11·98
1952	10·38	9·08	9·36	10·00	11·96	13·49	15·48	15·74	14·86	13·04	11·90	11·00	12·19
1953	9·82	9·16	9·18	9·62	11·01	13·00	15·34	16·34	15·34	14·02	12·52	12·19	12·30
1954	11·10	9·94	9·68	10·04	10·85	13·15	14·05	14·79	14·56	13·99	12·54	11·28	12·16
1955	10·59	9·28	8·68	9·11	10·50	12·60	16·19	17·68	16·48	13·69	12·39	11·82	12·42
1956	10·70	9·45	8·95	9·54	10·72	13·09	14·19	15·21	13·80	13·41	12·30	11·42	11·90
1957	10·29	9·60	9·86	10·50	11·44	14·02	15·86	15·60	15·14	13·54	12·19	11·10	12·43
1958	10·16	9·72	9·49	9·98	11·76	13·64	15·25	15·80	16·40	14·62	13·80	12·74	12·78
						Salinity							
1928	35·341	35·404	35·309	35·330	35·174	35·086	35·291	35·214	35·161	35·232	35·178	35·219	35·245
1929	35·221	35·270	35·278	35·329	35·256	35·232	35·298	35·125	35·234	35·251	35·165	35·154	35·234
1930	35·232	35·250	35·331	35·269	35·321	35·336	35·304	35·106	35·261	35·221	35·184	35·219	35·253
1931	35·190	35·069	35·206	35·305	35·295	35·260	35·238	35·178	35·159	35·211	35·270	35·342	35·227
1932	35·235	35·294	35·384	35·362	35·370	35·385	35·255	35·229	35·184	35·289	35·371	35·322	35·307
1933	35·379	35·404	35·414	35·349	35·312	35·248	35·278	35·198	35·171	35·309	35·416	35·394	35·323
1934	35·530	35·502	35·452	35·526	35·420	35·425	35·338	35·461	35·378	35·376	35·366	35·352	35·427
1935	35·325	35·286	35·326	35·345	35·391	35·288	35·365	35·294	35·262	35·281	35·226	35·218	35·300
1936	35·215	35·221	35·008	34·840	34·826	34·864	34·821	34·952	34·966	35·162	35·191	35·180	35·020
1937	35·149	35·110	35·096	35·209	35·264	35·269	35·232	35·268	35·145	35·222	35·301	35·325	35·216
1938	35·275	35·259	35·264	35·310	35·349	35·296	35·306	35·296	35·301	35·171	35·230	35·188	35·270
1939	35·211	35·298	35·199	35·184	35·274	35·341	35·226	35·166	35·219	35·266	—	—	—
1940–46	—	—	—	—	—	—	—	—	—	—	—	—	—
1947	—	—	—	—	35·334	35·286	35·171	35·125	35·029	35·206	35·349	35·324	—
1948	35·301	35·269	35·396	35·304	35·389	35·334	35·266	35·145	35·191	35·221	35·345	35·289	35·288
1949	35·248	35·259	35·249	35·136	35·112	35·159	35·254	35·229	35·200	35·155	35·216	35·184	35·200
1950	35·136	35·270	35·206	35·155	35·159	35·169	35·155	35·282	35·106	35·105	35·171	35·152	35·172
1951	35·131	35·174	35·175	35·278	35·294	35·285	35·322	35·234	35·208	35·298	35·366	35·350	35·260
1952	35·282	35·231	35·218	35·340	35·269	35·250	35·201	35·214	35·241	35·265	35·335	35·369	35·268
1953	35·321	35·326	35·385	35·341	35·295	35·318	35·121	34·961	34·978	35·122	35·325	35·291	35·232
1954	35·299	35·274	35·284	35·205	35·248	35·215	35·134	34·899	34·985	35·040	35·152	35·111	35·154
1955	35·202	35·158	35·218	35·238	35·148	35·096	34·994	34·995	35·122	35·165	35·264	35·290	35·158
1956	35·260	35·265	35·278	35·275	35·245	35·101	34·998	34·926	35·214	35·249	35·312	35·271	35·200
1957	35·259	35·225	35·162	35·151	35·252	35·221	35·219	35·149	35·084	35·151	35·135	35·174	35·182
1958	35·217	35·208	35·089	35·229	35·195	35·191	35·216	35·094	35·068	35·222	35·254	35·339	35·194

Temperature and salinity at the Seven Stones Light Vessel, 1928–58

The light vessel is moored in about 40 fm. of water about 2 miles north-eastward of the Seven Stones, about 14 miles west of Lands End and immediately south of station 29 in Fig. 1. After sporadic observations from May 1903, systematic observations were started in October 1905, at the rate of four per month. In 1912 observations every 4 days were initiated and this level of sampling has been maintained except for a break from 17 October 1939 to 16 March 1947. They provide a base to which all other observations in the area may be referred and are maintained by the Fisheries Laboratory, Lowestoft.

The observations up to 1927 have been very thoroughly reviewed by Lumby (1935) who treated the Seven Stones as 'Region no. 5'. The continuation of these Tables is presented here as Table 1. The monthly mean for three periods are presented in Table 2.

TABLE 2. LONG-TERM MEANS FOR TEMPERATURE AND SALINITY AT THE SURFACE AT SEVEN STONES LIGHT VESSEL (50° 03′ N., 6° 05′ W.)

	Temperature (°C)			Salinity (‰)		
Month	1905–27	1928–39	1947–58	1904–27	1928–39	1947–58
January	9·95	10·14	10·46	35·261	35·275	35·241
February	9·38	9·55	9·59	35·256	35·291	35·241
March	9·18	9·33	9·47	35·248	35·272	35·242
April	9·55	9·85	9·93	35·245	35·278	35·242
May	10·81	11·11	11·11	35·225	35·270	35·245
June	12·92	13·62	13·33	35·227	35·253	35·219
July	14·90	15·37	15·28	35·213	35·245	35·171
August	15·75	16·22	16·19	35·179	35·207	35·105
September	14·61	15·41	15·50	35·191	35·203	35.118
October	13·28	13·66	13·99	35·238	35·248	35·183
November	11·87	12·33	12·63	35·261	35·264	35·270
December	10·84	11·05	11·51	35·264	35·265	35·255
Year	11·92	12·30	12·42	35·234	35·256	35·211

Changes in the long-term means are set out in Table 3. The warming up in the years 1928–39 was maintained during the years 1947–58 and indeed proceeded even further during the 8 winter months September–April. The Seven Stones region has much changed as a biological habitat since the first quarter of the century.

Salinity did not follow the same pattern. It increased during the period 1928–39 but has since shown a decrease. Such small changes in salinity, unlike those in temperature, are unlikely to have much effect on plants and animals.

Lumby's work covered the period up to 1927. In extending it for the Seven Stones Light Vessel up to 1958 we have adhered as closely as possible to his procedure. The statistical limitations and controls which he described at length apply here also.

TABLE 3. CHANGES IN LONG-TERM MEANS FOR TEMPERATURE AND SALINITY AT THE SURFACE AT SEVEN STONES LIGHT VESSEL (50° 03′ N., 6° 05′ W.)

	Temperature (°C)			Salinity (‰)		
Month	1928–39 less 1905–27	1947–58 less 1928–39	1947–58 less 1905–27	1928–39 less 1904–27	1947–58 less 1928–39	1947–58 less 1904–27
January	+0·19	+0·32	+0·51	+0·014	−0·034	−0·020
February	+0·17	+0·04	+0·21	+0·035	−0·050	−0·015
March	+0·15	+0·14	+0·29	+0·024	−0·030	−0·006
April	+0·30	+0·08	+0·38	+0·033	−0·036	−0·003
May	+0·30	Nil	+0·30	+0·045	−0·025	−0·020
June	+0·70	−0·29	+0·41	+0·026	−0·034	−0·008
July	+0·47	−0·09	+0·38	+0·032	−0·074	−0·042
August	+0·47	−0·03	+0·44	+0·028	−0·102	−0·074
September	+0·80	+0·09	+0·89	+0·012	−0·085	−0·073
October	+0·38	+0·33	+0·71	+0·010	−0·065	−0·055
November	+0·46	+0·30	+0·76	+0·003	+0·006	+0·009
December	+0·21	+0·46	+0·67	+0·001	−0·010	−0·009
Year	+0·38	+0·11	+0·50	+0·022	−0·045	−0·023

Observations in January–March 1950

Throughout 1949 very warm water had been present at the Seven Stones, the maximum deviation from Lumby's monthly means for the years 1905–27, +2·32° C, occurring in October. The whole of 1950 was there to remain warm but less so than 1949 (Table 1, Fig. 2). There may be an oscillation of temperature of approximately fortnightly period, the maximum tending to occur about the day before the new or full moon and the minimum about 5 days afterwards. A statistically sound result requires that data for a considerable number of years shall be examined. Until that is done any attempt to correlate in detail with some of the findings of Cooper, Lawford & Veley (1960) would be forced.

Throughout January water 0·13‰ less saline than average (i.e. water from the northern sectors) was followed by a sudden rise of 0·12‰ between 29 January and 1 February (Fig. 2). This betokened the first arrival at the Seven Stones of a water earlier observed to the southward. The winter minimum temperature of 10·0° C persisted with variations of no more than 0·1° C from 10 February to 15 March while salinity remained high (35·2‰).

The line of surface observations no. 10 from Lands End to Ushant was presented in an earlier paper (Cooper, 1960*b*, Fig. 3). About 12 February there was a narrow current around Lands End, but not including the position of the Seven Stones Light Vessel, of low salinity, relatively cold water from Lyme Bay which had flowed westwards along the coasts of south Devon and Cornwall (Cooper, 1958).

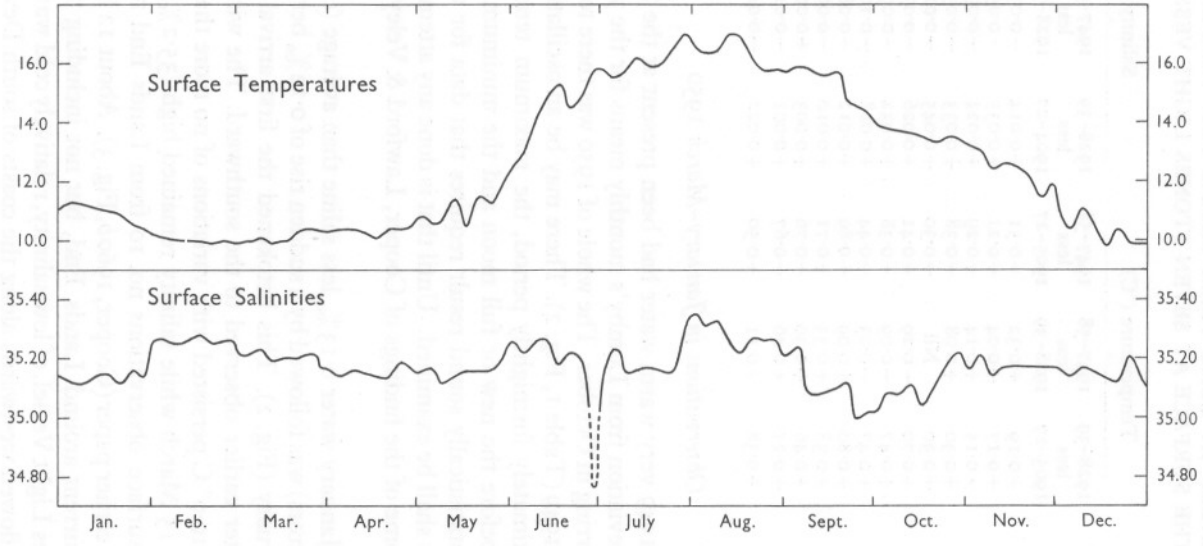

Fig. 2. Temperatures and salinities at the Seven Stones Light Vessel during 1950.

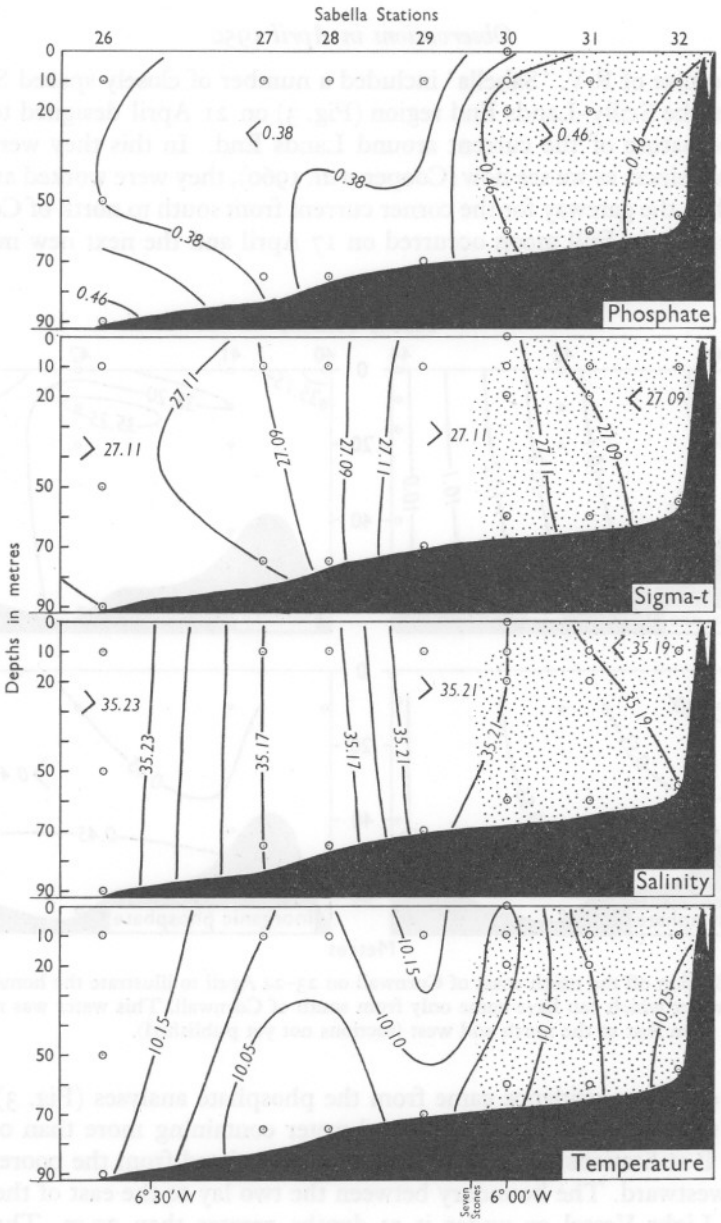

Fig. 3. Section across the Scilly–Lands End passage on 21 April for phosphate, the most informative measurement, for density and salinity, and for temperature which gave no useful information. The south Cornwall coastal water mass, revealed by phosphate, is shown stippled on each diagram.

Observations in April 1950

The cruise of R.V. 'Sabella' included a number of closely spaced Stations 26–32 in the Scilly–Lands End region (Fig. 3) on 21 April designed to elucidate the nature of the current around Lands End. In this they were indeterminate since, as we see now (Cooper *et al.* 1960), they were worked at spring tides when the gateway for the corner current from south to north of Cornwall may be closed. Full moon occurred on 17 April and the next new moon on 2 May.

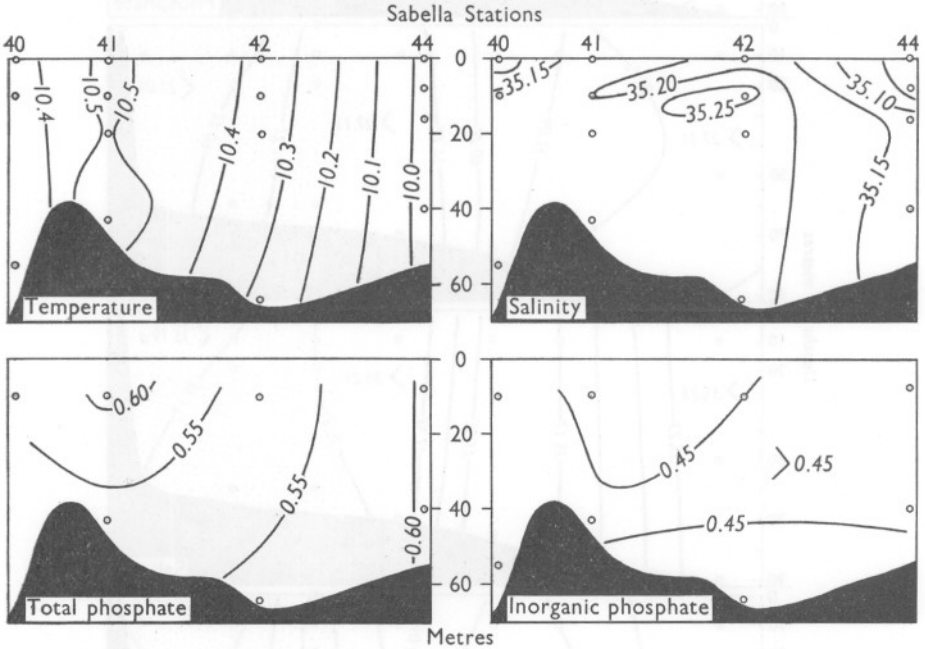

Fig. 4. Section off the north coast of Cornwall on 23–24 April to illustrate the homogeneous mass of water which can have come only from south of Cornwall. This water was markedly different from that to the north and west (sections not yet published).

The only firm evidence came from the phosphate analyses (Fig. 3) which clearly showed south Cornwall coastal water containing more than 0·46 μg-atom/l. P at Stations 30–32 and sharply differentiated from the poorer water to the westward. The boundary between the two lay to the east of the Seven Stones Light Vessel or under it at depths greater than 20 m. The south Cornwall coastal water is stippled in all four panels.

Although density and salinity records showed such small gradients, nevertheless, the boundary indicated by phosphate coincides with the belt of maximum density and salinity. Such a distribution of mass would come about

from a weak counter-current towards the north around Lands End and another weak current towards the south-east running at the surface at the light vessel and at all depths to the westwards. Temperature distribution is not in conflict with such a current system but does not indicate it.

A line of stations off the north coast of Cornwall was run on 23 April (Fig. 4). Water with the properties of Stations 40, 41 and 42 was found nowhere else north of the fiftieth parallel, but its properties were closely similar to those of the waters south of Cornwall in the weeks before (Table 4). Whatever other evidence may suggest, there can be no doubt that there had been a flow of water from the south to the north coast of Cornwall. No such continuity is traceable in any other direction through the close net of stations (Fig. 1 in part). The deductions of Matthews and of Harvey are strongly supported.

TABLE 4. COMPARISON BETWEEN THE WATERS NORTH, WEST AND SOUTH OF CORNWALL, APRIL, 1950

Region ...	South Cornwall				
Ship ...	'Sula'	Interpolated in time	'Sir Lancelot'	'Sabella'	
Station	E1	E1	61	9	10
Date	23. iii.	21. iv.	8. iv.	18. iv.	18. iv.
Latitude °N.	50° 02′	50° 02′	49° 51′	49° 30′	49° 32′
Longitude °W.	4° 22′	4° 22′	4° 00′	5° 00′	5° 28′
Temperature °C	10·15	10·31	10·35	10·43	10·50
Salinity ‰	35·30–35·35	35·20	35·29	35·39	35·35
Density σ_t	27·10–27·20	27·08	27·20	27·20	27·16
Total phosphorus μg-atom/l.	0·53–0·55	0·53	—	0·69	0·63
Phosphate-phosphorus μg-atom/l.	0·43–0·49	—	—	0·40	0·44
Organic phosphorus μg-atom/l.	0·05–0·11	—	—	0·29	0·19

Region ...	Off Lands End			North Cornwall	
Ship ...	'Sabella'			'Sabella'	
Station	31	40	90	41	42
Date	21. iv.	23. iv.	30. iv.	23. iv.	23. iv.
Latitude °N.	50° 04′	50° 08′	50° 02′	50° 20′	50° 42′
Longitude °W.	5° 53′	5° 53′	5° 51′	5° 37′	5° 20′
Temperature °C	10·20	10·33	10·44	10·52	10·35
Salinity ‰	35·20	35·24	35·26	35·22	35·22
Density σ_t	27·10	27·10	27·09	27·05	27·10
Total phosphorus μg-atom/l.	—	0·57	0·56	0·57	0·54
Phosphate-phosphorus μg-atom/l.	0·49	0·47	0·41	0·44	0·43
Organic phosphorus μg-atom/l.	—	0·10	0·15	0·13	0·11

The Seven Stones current measurements held within themselves the probable answer (Cooper *et al.* 1960). The eastern half of the Lands End–Scilly passage may open and close to the passage of water from the south coast of Cornwall to the north like a trap door. It may open when the current at the light vessel sets to the south of its mean direction, an event favoured by neap tides and warm or very wet weather, and close when the current sets to the north of its mean position, an event favoured by spring tides and cold weather.

As we now reconstruct the occasion, water from off the south coast of

Cornwall including the position of station E1 and an interpolated position around 49° 45′ N. lat., 4° 40′ W. long. was being carried north-west as a counter-current towards the Runnelstone and Lands End. In this region mixing both horizontal and vertical was probably greatest at the time of springs while net northerly transport took place at neaps.

For an understanding of the oceanography of the Bristol Channel the sea area within 10 miles of the Lands End promontory is of much importance and deserves much more study than we have been able to give it.

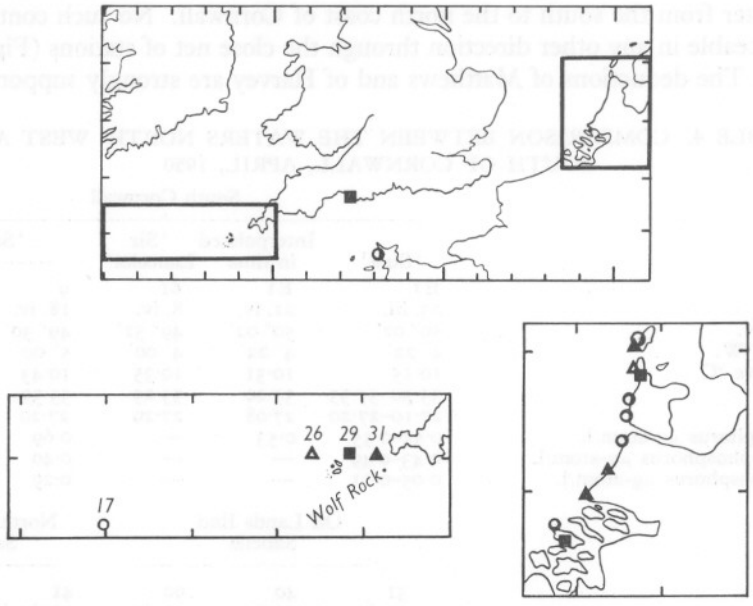

Fig. 5. Direction of surface drift. Four sets of bottles put out on 20–21 April at the positions shown by station numbers in the left inset. All recoveries are shown, most being along the Dutch coast as in the right inset.

Drift-bottle results

Four sets of surface drift bottles, provided by Mr David Vaux of the Lowestoft Laboratory, were put out from R.V. 'Sabella' during the April cruise west of Lands End. The bottles were fitted with 1 m drags of galvanized steel; the metal caps were sealed with pitch and painted white or red. The recoveries reported by Mr Vaux by letter on 29 April 1952 are of much interest (Fig. 5). To facilitate comparison with Carruthers's (1927) work, his position code is included.

At Station 17 (49° 28′ N., 9° 01′ W.) on 20 April 1950 at 00.25 h G.M.T. fifteen bottles were put out, of which six were recovered. Of these one travelled to Cap de la Hague (C55g), 282 miles at a rate of 1·9 miles/day. The other

five grounded on the coast of Holland (J2f, J3b, J5j, J4h, J4h; 511–585 miles) at rates between 2·4 and 3·1 miles per day. Nine bottles were not recovered.

At Station 26 (50° 04′ N., 6° 34′ W., 10 miles N.W. of the Scillies), of five bottles put out on 20 April at 23.50 h G.M.T. only one was recovered near den Helder, Holland (J4c), after a journey of 476 miles at 3·1 miles/day. Four bottles were not recovered.

At station 29 (50° 04′ N., 06° 07′ W., north of the Seven Stones Light Vessel) of five bottles put out on 21 April at 03·20 h G.M.T., one was recovered a few miles east of Bridport, Dorset (B51d) after a minimum journey of 134 miles at a mean speed of only 1·1 miles per day. It is possible that this bottle, like the slow traveller stranded near Cap de la Hague, had travelled a roundabout route. Two more stranded in Holland in the mouth of the Schelde (H2j; 395 miles at 2·8 miles/day). Two bottles were not recovered.

At Station 31 (50° 04′ N., 05° 53′ W., 6 miles west of Lands End and where the corner current is believed to run) five bottles were put out on 21 April at 06.15 h G.M.T., 1½ h before high water Devonport. The tables of tidal streams (positions *E* and *F*) on Admiralty Chart no. 2565 (edition published on 5 August 1955) would suggest the tide would have been making at that time about 0·9 knots towards 40°, but was turning rapidly towards south to reach a maximum of 2 knots towards 195°. The set of the tide was thus such as to carry the bottles well south of the Wolf Rock into the fairway of the English Channel before it turned.

Three bottles were recovered on the coast of Holland between Hook of Holland and Texel (J3g; J2a; J5j) after journeys of 402–458 miles at 2·1, 2·4 and 2·5 miles per day. Two bottles were not recovered.

To sum up, from the thirty bottles put out at four positions in the Celtic Sea, eleven stranded on the coast of Holland, and one each on the mid-Channel coasts of England and France. These had drifted up-Channel with a mean speed of 2·6 miles per day. A surface skin of water had taken about 4 months to pass from end to end of the Channel. No bottles were anywhere recovered to suggest a northerly movement of surface water anywhere in the Celtic Sea. They are completely concordant with Carruthers's (1927) findings and with the pattern of currents which Carruthers *et al.* (1951) drew from their measurements at the Seven Stones Light Vessel.

The remarkably high values for compounds of phosphorus in bottom water at Station 25 on April 20 (Table 5, Fig. 1), and also at Station 26 can have arisen only by regeneration from the muddy deposits around the Labadie Bank or south of Ireland, as at Station 81. Thus west of the Scillies the bottom water was moving in a direction not very different from that shown by the surface drift bottles.

The drift-bottle measurements are also in accord with Russell's (1935) deductions from biological indicators that recruitment into the English Channel

TABLE 5. PROPERTIES OF BOTTOM WATER MOVING SOUTH-SOUTH-EAST TOWARDS THE SCILLY ISLES, 20–29 APRIL 1950

Station no.	Lat. (N.)	Long. (W.)	Depth (m.)	Temperature *in situ* (°C)	Temperature Corr. to 50° N. (°C)	Salinity (‰)	Density σ_t	Phosphorus µg-atom/l. Total	Phosphorus µg-atom/l. Inorganic	Phosphorus µg-atom/l. Organic
81	50° 45′	7° 30′	90	9·80	10·12	35·14	27·11	0·76	—	—
25	49° 58′	6° 56′	95	10·12	10·11	35·26	27·16	0·85	0·83	0·02

in April is of 'western' or 'elegans' type water. Moreover, the direction of flow was closely parallel with that deduced (Cooper, 1960*b*) from the Discovery II stations 100 miles to the southward a fortnight later, i.e. in the approach to the English Channel between 48° 20′ N. and 50° N. lat., the flow of water was everywhere easterly or somewhat south of east.

The drift-bottle results, particularly those from Station 31, combined with so much supporting evidence, are most unfavourable for one of the theses of this paper: that a corner current sets around Lands End from south to north.

The warm high salinity water found off north Cornwall on 23 April 1950 cannot be gainsaid. Any mechanism to get it there has to conflict with much other evidence. It seems inescapable that the current must flow with greatest strength either near the bottom or very close to Lands End, i.e. that it is intermittent and narrow and that the waters around the Longships Lighthouse need close attention.

Observations in June 1950

The 'Sabella' cruise in June 1950 was designed to find the origin and the fate of the nutrient rich water found west of the Scillies in April, to explore the waters lying inshore from the continental edge, to examine further the corner currents around Ushant and Lands End and the waters north and west of Cornwall and of Brittany and to obtain 'elegans' type water for Wilson's (1951) studies on differences between natural waters. The cruise was planned anti-clockwise but worked clockwise. Since the planned stations were not renumbered, we started with Station 34 (identical with E1) and finished with Station 1 (Fig. 1).

Stability and nutrient availability

Information as to potential productivity of different sea areas during the summer months emerges from a comparison of adjacent stations worked on the April and June cruises (Fig. 6, Table 6).

At position *P* well away from the nearest land and with a 1·0 knot spring tide, the temperature below 40 m. depth scarcely increased at all and a very strong thermocline developed (Fig. 7). The stability at positions *Q* and *R*, similarly placed, was nearly as great. Once the spring diatom outburst was

TABLE 6. POSITIONS WORKED IN APRIL AND JUNE 1950, STUDIED FOR STABILITY AND POTENTIAL PRODUCTIVITY

Mean position	Mean lat. (N.)	Mean long. (W.)	Distance of stations apart (miles)	April cruise		June cruise		Rate of tidal streams at springs, knots
				Date	Station no.	Date	Station no.	
P	50° 04′	7° 29′	8	20	24	14	15	1·0
Q	49° 32′	7° 30′	4	19	14	14	17	0·7
R	50° 39′	5° 28′	4	30	88	15	11	1·2
S	49° 29′	4° 51′	12	18	9	13	32	1·5
T	50° 04′	5° 47′	0	21–30	31, 32, 40, 90	16	4	Strong
U	50° 21′	5° 37′	2	23	41	15	5	1·4
V	50° 41′	5° 20′	3	23	42	15	6	1·4

TABLE 7. CONSUMPTION OF PHOSPHORUS COMPOUNDS AT POSITIONS *R*–*V* (μg-atom/l.)

For development of thermocline structure compare Fig. 7.

Sea area	Depth (m)	Total phosphorus		Inorganic phosphate	
		Consumed since April	Remaining on 13–16 June	Consumed since April	Remaining on 13–16 June
Celtic Sea away from coast, position *R*	10	0·28	0·32	0·26	0·14
	20	0·28	0·31	—	—
	40	0·02	0·54	—	—
	70	Nil	0·57	−0·05	0·49
	88	Nil	0·59	—	—
Entrance to English Channel, position *S*	0·5	0·25	0·46	0·24	0·18
	10	0·21	0·50	0·25	0·19
	20	0·17	0·54	0·14	0·25
	50	0·17	0·55	0·09	0·30
	70	0·26	0·42	0·06	0·31
	90	0·19	0·46	0·03	0·32
In Lands End corner current, position *T*	10	0·13	0·37	0·27	0·18
	48	0·20	0·30	0·27	0·18
North-north-east of Lands End, position *U*	10	0·29	0·32	0·24	0·18
	20	0·26	0·31	0·27	0·17
	43	0·19	0·34	0·30	0·16
Position *V*	0·5	0·16	0·36	—	—
	10	0·19	0·33	0·31	0·14
	20	0·21	0·32	0·25	0·19
	30	0·23	0·31	—	—
	61	0·25	0·31	0·21	0·20

over, there could have been little replenishment of the surface water by nutrients from below.

Only at position *R* have we data to illustrate this (Table 7). Below 40 m. where the water had warmed up only 0·3° C there had been no consumption of phosphate. Vertical stability had been sufficient to immobilize the reserves in the deeper water. Only the reserves remaining in the uppermost 20 m were available for plant production which must subsequently have been restricted. The tidal streams around positions *P* and *R* may exceed 1 knot so

that we may conclude that such tides running over a bottom 100 m deep and well away from land are unable to hinder the rapid formation and maintenance of a strong thermocline in late spring and summer.

Earlier (Cooper, 1960*b*) it has been deduced for the area north of Brittany that once the thermocline has developed strongly, vertical exchange across it becomes trifling and temperature in the deeper waters becomes conservative. This conclusion evidently applies at position *P* and to a less degree at positions *Q* and *R*, even in late spring. Moreover, any movement there may have been there between 20 April and 15 June was essentially along a west–east axis.

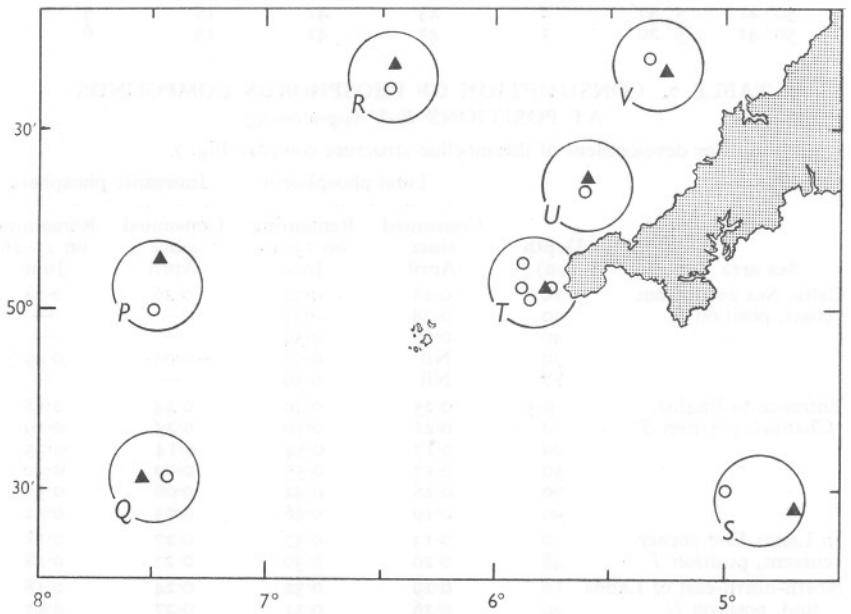

Fig. 6. Positions of stations used for the study of stability and potential productivity; open circles, April; triangles, June.

Position *S* (Fig. 7) was on the centre line of the mouth of the English Channel and spring tides there may reach a rate of 1·5 knots. Hereabouts the deeper water warmed up by 1·4° C and the surface layers only three-fifths as much as in the open Celtic Sea. Total phosphorus (about 0·2 μg-atom/l.) had been withdrawn from the whole water column into forms not sampled with the water. Inorganic phosphate had fallen by only 0·06 μg-atom/l., i.e. about 0·2 μg-atom/l. of phosphorus in organic combination had been regenerated in the deeper water.

Later in the summer it has been shown (Cooper, 1960*b*) that the deeper water around position *S* had warmed up by transport of water, with conservation of properties, from the level of the thermocline west of Ushant.

This movement from the south-west was quite definitely not occurring in May and June 1950. It is much more probable that in spring, in an area where strong tides (1·5 knots at springs) slow down the development of the thermocline, considerable vertical exchange by turbulence between the upper and lower layers may persist longer than where tides do not exceed 1 knot.

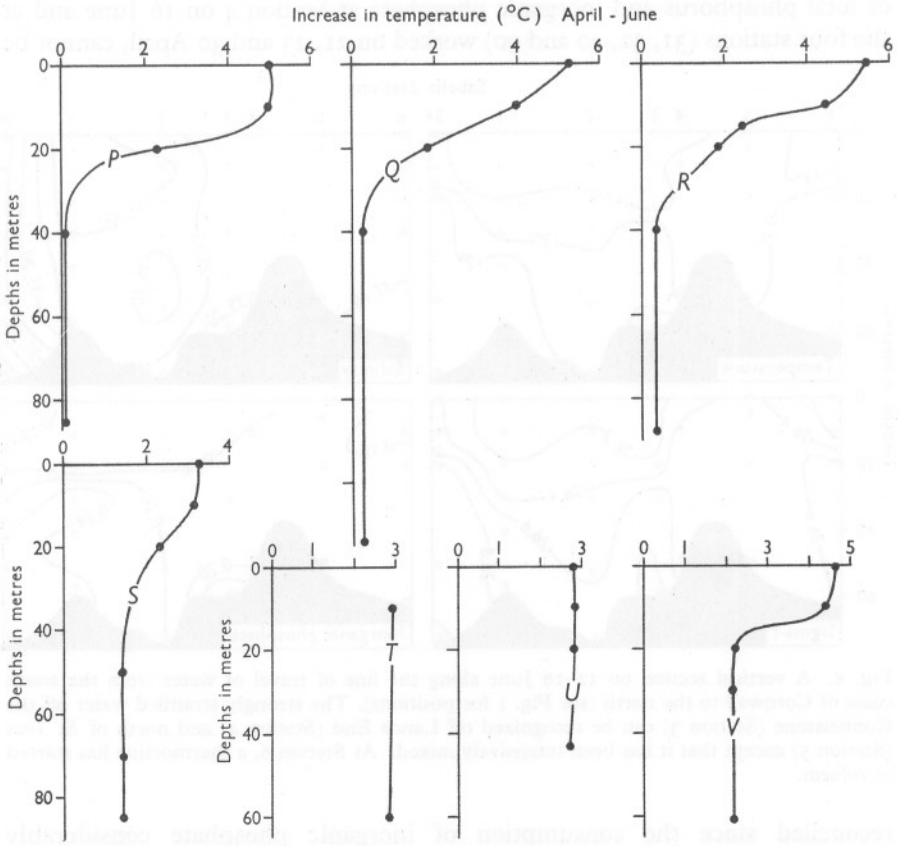

Fig. 7. Increase in temperature at seven positions (Table 6) in the Celtic Sea between 19–30 April and 13–16 June 1950.

Consequently in the mouth of the English Channel turbulent mixing somewhere or other, but not necessarily at the place of observation, is sufficient in spring before the thermocline is fully developed to carry considerable replenishment of phosphate from the deeper reserve to the illuminated upper layers. Moreover, some of this phosphate was passing through a second cycle of utilization. Around midsummer, but not later, the position *S* was likely to be more productive than positions *P*, *Q* and *R*.

The Lands End corner current

Position *T* (Figs. 6, 7, 4 (Station 40) and 8 (Station 4); Tables 6 and 7) was close to Lands End in the corner current in which vertical mixing remained almost complete. The water column in June was almost isothermal (13·05–13·15°), isohaline (35·16–35·19‰) and isopycnal (σ_t 26·50–26·55). Contents of total phosphorus and inorganic phosphate at Station 4 on 16 June and at the four stations (31, 32, 40 and 90) worked on 21, 23 and 30 April, cannot be

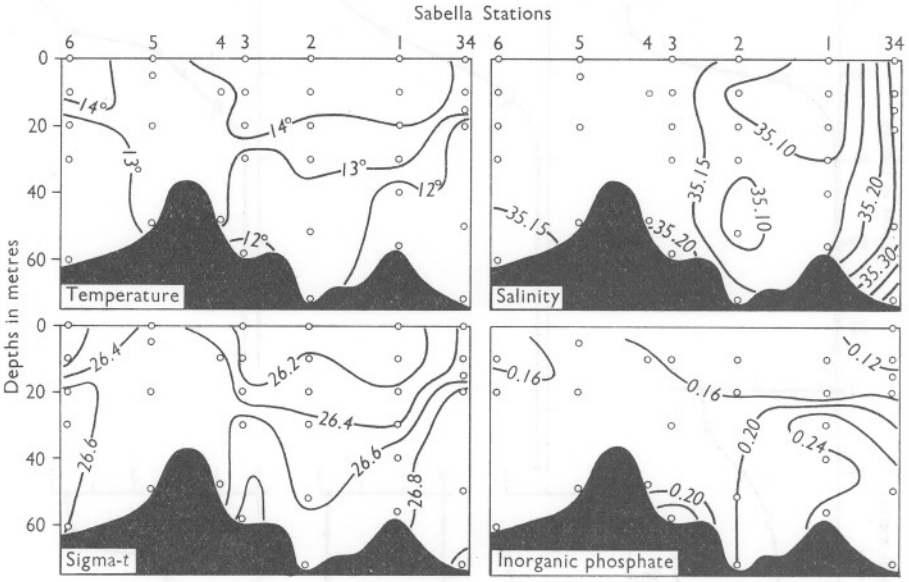

Fig. 8. A vertical section on 12–16 June along the line of travel of water from the south coast of Cornwall to the north (see Fig. 1 for positions). The strongly stratified water off the Runnelstone (Station 3) can be recognized off Lands End (Station 4) and north of St Ives (Station 5) except that it has been intensively mixed. At Station 6, a thermocline has started to reform.

reconciled since the consumption of inorganic phosphate considerably exceeded the consumption of total phosphorus. Sampling in the Lands End corner current, more than in most places, is snap sampling of a highly dynamic system. The water being mixed up in June was of quite different origin from that in April. A small but distinctive water mass is created in the Lands End corner current and its components differ according to the time of year, and probably at different times in the lunar month. Consequently, in the sea area north of Cornwall an assessment of biological productivity in terms of the difference between the winter maximum and the summer minimum of inorganic phosphate is unlikely to be worth while.

The June cruise was laid out to decide whether the water lying close to

Lands End moves north or south. Station 3 was worked one mile south of the Runnelstone. It cannot have failed to sample water escaping to the south, if any there was. The water at Station 3 was as strongly stratified as any other in the northern English Channel (Stations 34–32, 2 and 1; Figs. 1, 8 and 9) and more strongly than most. The water at the Runnelstone was unexceptional English Channel water, probably contributing to the corner current but very definitely receiving nothing from it.

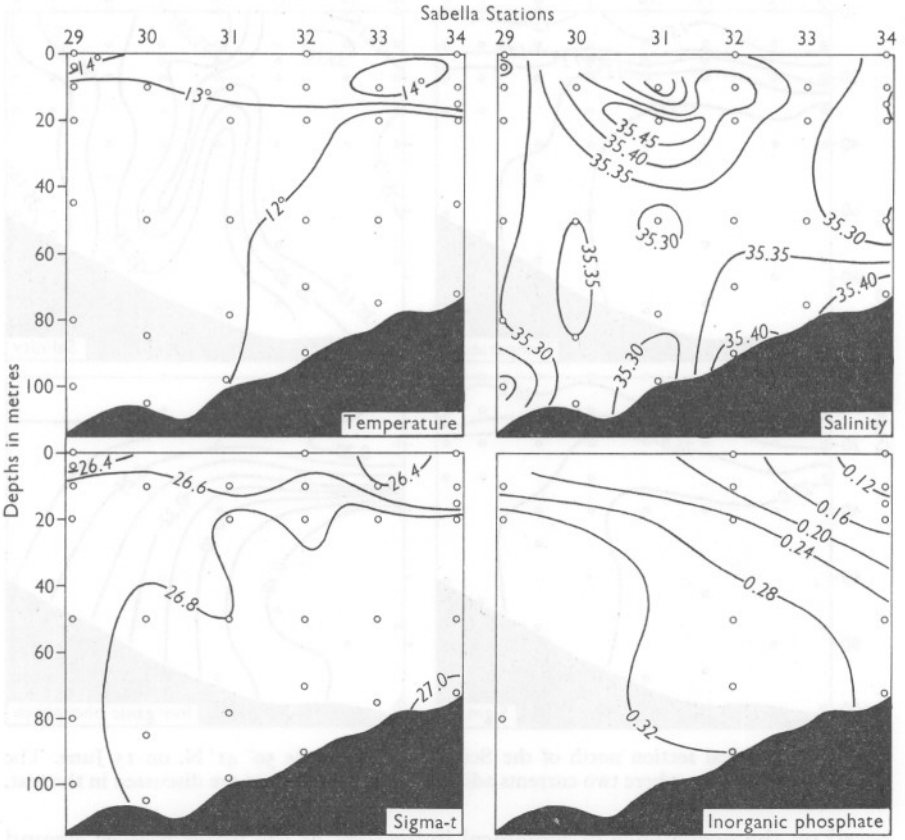

Fig. 9. A vertical section on 12–13 June from near Ushant (Station 29) to E1 (here Station 34).

The north Cornwall water in June 1950

The Stations to the north (here grouped as positions *U* and *V*; Figs. 1, 6, 7, 8 and 10) present a very different story. At position *U* (incorporating June Station 5) the whole homogeneous water column was 2·8° warmer in June than in April. The tidal stream was no stronger than at Station *S*, or off the

Runnelstone. We had here the mixed water produced in the Lands End corner current. Its influence was still very marked at position *V* (incorporating June Station 6) 23 miles on.

The argument for June is quite different from that used in April but is equally convincing. Much of the North Cornwall water had arrived by way of a narrow current around Lands End. Russell's illustration (1936, fig. 6),

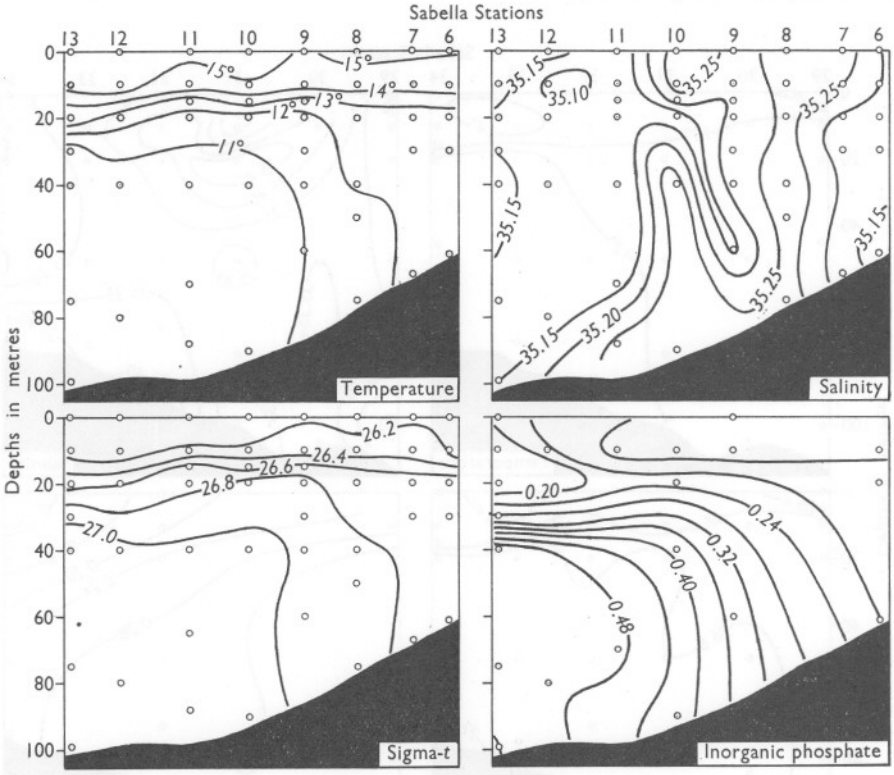

Fig. 10. A vertical section north of the Scillies along latitude 50° 41′ N. on 15 June. The doubts about the data where two currents adjoin at Stations 9 and 10 are discussed in the text.

based on the occurrence of biological indicators, of the water masses around Lands End in July 1935 is in quite remarkable agreement with this account derived entirely from physical and chemical observations.

An inflexion of geopotential (Figs. 10 and 11) at Station 10 represents clearly the western boundary of the warm and saline relatively well-mixed water emerging from the Lands End corner current (Stations 9–6) with the cold, less saline water of the Northern Celtic Sea (Stations 13–11). The June Stations 9 and 10 contain anomalous salinities, confirmed by the analyst, which it is quite impossible to contour according to accepted principles of

oceanographic presentation. The contouring in Fig. 10 is the least improbable if no data are rejected. I have not attempted to reconcile T, S and σ_t between Stations 9 and 10 in this drawing. Either we must reject at least two duplicated analyses or we have to accept strong eddying at the current boundary with some accompanying instability, amounting to σ_t 0·06. Stations 9–6 and 5 (Figs. 8 and 10) represent a water mass in the southern entrance to the Bristol Channel with a history comparable with stations 31 and 30 (Fig. 9) in the southern entrance to the English Channel at the same time (Cooper, 1960*b*). Both had been reformed around headlands. In June 1950, considered as a model, the Bristol Channel was much easier to study.

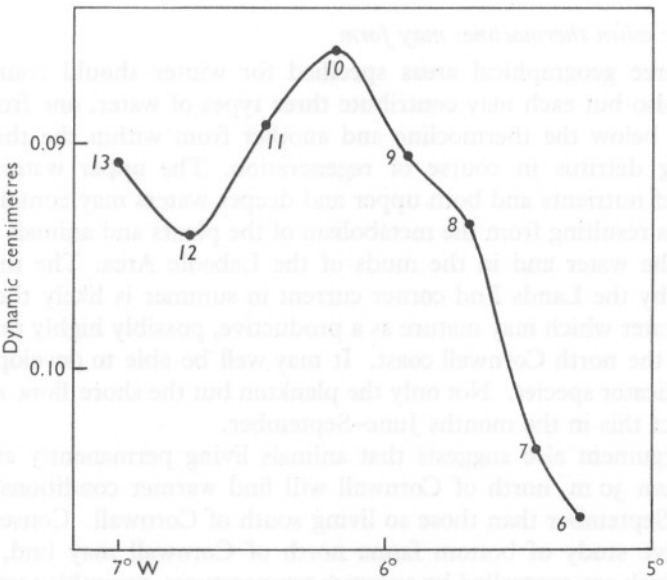

Fig. 11. Geopotential heights along latitude 50° 41′ N. (Stations 13–6 on 15 June); surface compared with 70 m.

The concept of narrow well-mixed corner currents running at depth round headlands and then fanning out under the influence of their momentum and the earth's rotation is a fruitful one from both a physical and biological point of view. It requires more proof than is given here, since cruises such as ours in 1950 were wrongly conceived. An understanding of corner currents requires intensive studies using a variety of techniques and spread over at least a fortnight.

Biological consequences of the Lands End corner current

Some biological consequences may also be deduced for both shore and planktonic flora and fauna of north Cornwall between Cape Cornwall and Hartland Point.

Under winter isothermal conditions

The Lands End corner current may incorporate three types of water, (i) south Cornwall coastal water containing run-off from the rivers of south Cornwall and south Devon, (ii) water from the western approaches south of Scilly, and (iii) water from north of Scilly which the current measurements of Carruthers *et al.* (1951) suggest often passes the Seven Stones Light Vessel proceeding south-east. Since mixed waters are often productive there may be a tendency, but in winter no more than a tendency, for the waters north of Cornwall to be somewhat more productive than those to the west and south.

In summer when thermoclines may form

The three geographical areas specified for winter should contribute in summer also but each may contribute three types of water, one from above, one from below the thermocline and another from within the thermocline containing detritus in course of regeneration. The upper waters may be stripped of nutrients and both upper and deeper waters may contain organic substances resulting from the metabolism of the plants and animals that have lived in the water and in the muds of the Labadie Area. The mixing pot provided by the Lands End corner current in summer is likely therefore to create a water which may mature as a productive, possibly highly productive, water off the north Cornwall coast. It may well be able to develop characteristic indicator species. Not only the plankton but the shore flora and fauna may reflect this in the months June–September.

This argument also suggests that animals living permanently at a depth greater than 30 m. north of Cornwall will find warmer conditions between July and September than those so living south of Cornwall. Consequently a comparative study of bottom fauna north of Cornwall may find, in those species which are controlled by summer temperatures, resemblances with the fauna north of Brittany rather than south of Cornwall. Setting off the two-degree difference in latitude against the secular rise in temperature in this region, comparison may prove closest between the north Cornwall bottom fauna of today with the north Brittany bottom fauna half a century or so ago.

The Bristol Channel as a site for experiment

The Bristol Channel offers a better site for experimental studies than the English Channel, because there is no eastern exit corresponding to the Straits of Dover, because it receives the largest river in England and Wales and much sewage and industrial waste, because the contrast in salinity and temperature on the north and south sides is usually greater than in the English Channel, and because the area requiring study is smaller.

A meteorological consequence of the Lands End corner current

West Cornwall, a narrow peninsula, is well known for differences in weather between its two coasts, the north coast in popular repute being the more bracing. Between 1 and 5 August 1945 I was engaged in a co-operative investigation involving boats working from Falmouth (Fig. 1) and aircraft based on Portreath. On the south coast the weather was superb throughout whereas the north was blanketed with fog. This fog was entered at the crest of the road between, while the aircraft had regularly to use Predannack, only 18 miles from Portreath but on the south coast, as an emergency base.

This very strong contrast evidently reflects differences in air and in sea temperatures on the two coasts. An intermittent corner current bringing variable amounts of well-mixed relatively saline water round to the north coast to replace Bristol Channel water is likely to control these local variations in weather.

The northern side of the Bristol Channel has a much more estuarine character than the northern side of the English Channel west of Start Point. The southern side of the Bristol Channel may be bathed in turn by either kind of water or by water from west of the Scillies or by mixtures of these. Waters from the south will also be subjected to vertical mixing whilst in the corner current. It is clear that an understanding of the local climate of north Cornwall, especially of fog formation, may be had only if the behaviour of the Lands End corner current is more fully understood.

I wish to acknowledge the cordial co-operation of Captain C. A. Hoodless then master of R.V. 'Sabella' and his crew, also of Mr P. G. Corbin, Mr G. A. Robinson and Mr G. R. Forster on the cruises in April and of Mr A. D. Mattacola on that in June. The salinities were determined by the Government Chemist and inorganic and total phosphorus by Mr F. A. J. Armstrong. I am also much indebted to the Lowestoft Laboratory for their assistance during the joint 1950 programme, in particular to Mr David Vaux who discussed many of the issues at the time and provided the clear-cut drift-bottle data. These have very severely restricted the possibilities that could be considered and in the end have given more confidence to the solution now presented. The paper has been illustrated by Mr G. A. Battin.

SUMMARY

Measurements of currents by meters and drift-bottles, of temperature, of salinity and of phosphate at the Seven Stones Light Vessel and in the encircling waters around Lands End and the Scilly Isles have led to conflicting conclusions on water movement. The conflict may be resolved if it is assumed that a narrow well-mixed corner current flows intermittently around Lands End

from the south to the north coast of Cornwall. Evidence obtained in 1950 is produced in support of this deduction and supported by a development of the current measurements at the light vessel in an accompanying paper with Lawford and Veley.

It is suggested that the Lands End corner current may create conditions north of Cornwall to encourage development in summer of a small but characteristic biological community on the shore and on the off-lying sea bed and to create a local climate rather different from that off the south coast.

The Bristol Channel is considered to offer a better site for experimental oceanography than the English Channel.

Information on the effect of tidal streaming on biological productivity in summer is presented.

Temperature of the water at the Seven Stones Light Vessel has increased on average by about 0·3° C in the spring months and by about 0·7° C in autumn.

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ON VARIATIONS IN THE CURRENT AT THE SEVEN STONES LIGHT VESSEL

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(Text-figs. 1–4)

Measurements of current at the Seven Stones Light Vessel, 50° 03·5′ N. lat., 6° 05·1′ W. long. (for position, see Cooper, 1960*b*, fig. 1) were first made with the Carruthers Drift Indicator between 17 August and 15 September 1933 (Carruthers, 1934). The much longer series with the Vertical Log between July 1939 and April 1941 showed average travel of the residual current at a rate of 2·5 miles per day towards east-south-east (110° true) (Carruthers, Lawford & Veley, 1951). It was shown clearly that there was a strong causal connexion between the direction and strength of the wind and direction and strength of current, but that there were evidently other factors concerned as well. These current measurements were not easy to reconcile with deductions from the observed distributions of temperature and salinity in the area (Matthews, 1914; Harvey, 1925, 1929; Cooper, 1960*b*). A rational explanation could be achieved if it is assumed that the passage of water from the English Channel to the Bristol Channel occurs intermittently and is confined to a narrow current close into Lands End. This 'corner current' rarely extends as far west as the Seven Stones Light Vessel.

During 1950 as a result of R.V. 'Sabella's' work on 20–24 April 1950 we deduced from a study of the observed winds the probable current at the Seven Stones for the 3 days when R.V. 'Sabella' was in the vicinity (Table 1). Around 21–23 April the predicted residual current was, no doubt, setting towards 120°. This is close to the direction 110° (true) computed for the average water movement over the whole period of 600 days in 1939–41. On 21 April 'Sabella' Stations 30 and 29 bracketed the position of the light vessel and Stations 27 and 28 were 8 and 12 miles to the westward and immediately north of the Scilly Islands; they were occupied by water of relatively low temperature and salinity. This is a consistent picture of a movement of water

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TABLE 1. PREDICTED RESIDUAL WATER MOVEMENTS AT SEVEN STONES LIGHT VESSEL

Date, April 1950 ...	21		23		30	
	Speed m.p.d.	Dir.	Speed m.p.d.	Dir.	Speed m.p.d.	Dir.
Intrinsic water movement irrespective of tides	2	50°	1·5	10°	3	100°
Water movement produced by winds	4·1	155°	4·3	145°	6·4	15°
Residual water movement	4	125°	3·5	120°	7·5	40°

from the north-west. The water at Stations 27 and 28 had much in common with that at Station 89, 14 miles to the north on 30 April. This distribution is also consistent with the eastern sector of an eddy or rising centre conditioned by the distribution of density during a period of warming up within and around Scilly (Cooper, 1960*a*).

Again (Cooper, 1960*b*) the distribution of temperature and salinity west and north of Cornwall in April 1950 (Cooper, 1960*a*, fig. 4) could be understood only if a very considerable transport of water had occurred during the preceding neap tides but had been suppressed by the spring tides occurring when the observations were made. Also in the observations of temperature and salinity at the Seven Stones in 1950 (Cooper, 1960*b*, fig. 2) there is a suggestion of lunar periodicity in summer.

We therefore further analysed the 1939–41 current observations for the effect of tide and season. There are three restrictions inherent in the analysis. (i) The current is much influenced by wind and by factors at a distance from the Seven Stones. Over the whole period, the strength of the mean residual local wind was only 3% of the maximum strength recorded. But when individual lunar months are considered, the strength of the mean residual local wind may be as much as 30% of the maximum and cannot then be neglected. (ii) The vertical log current meter used reads the direction of water movement only to within $\pm 22\frac{1}{2}°$. Summing and averaging may considerably reduce the error of the mean measurements. (iii) In these computations, the *magnitude* and *direction* of the residual water movement were treated independently, i.e. the directions (or magnitudes) were 'summed' algebraically and divided by the number of days involved.

The first step in the analysis was to determine the mean direction of the residual water movement during each of 22 consecutive lunar months (Fig. 1, lower). The direction varied between 90° and 150°, the mean for the whole period being 114°.

The variation in direction of the residual water movement about its over-all mean seems to be periodic, being to the north of the mean in winter and spring and to the south during summer and early autumn. Most of the 'peaks' on the plot coincide with periods when the residual wind was either very

strong or blew from directions at right angles to the mean direction of the residual water movement. Taking this into account, it is suggested that the intrinsic residual water movement is most northerly in December and most southerly in July.

The variation in flow (magnitude) of the residual water movement per lunar month (Fig. 1, upper) is not as clear as the variation in direction. However we suspect that at the time a long-term periodic factor was decaying,

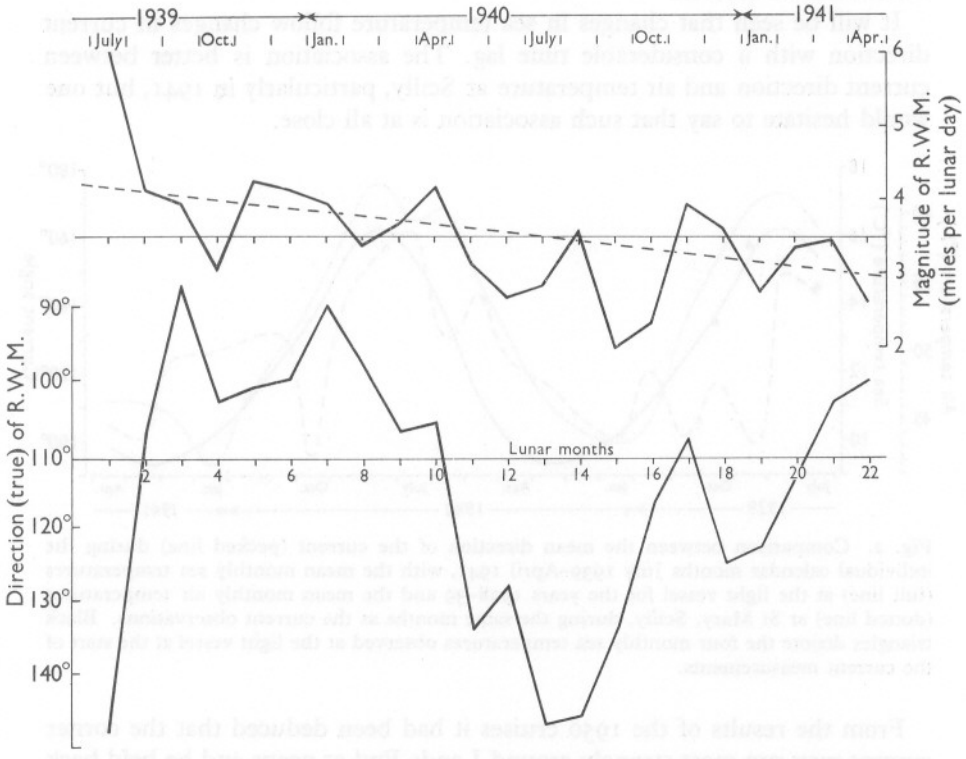

Fig. 1. Residual water movements at the Seven Stones Light Vessel during individual lunar months between July 1939 and April 1941. Upper panel, magnitude in miles per lunar day; lower panel, true direction.

so that the plot of mean values should be read about the pecked line tentatively drawn in. It would seem that the mean magnitude of the residual water movement may be higher in winter and spring and lower in summer and autumn.

The high magnitude for the residual water movement in July 1939 provides a problem; however, the mean wind during the lunar month favoured this residual water movement and may have accounted for about 2 miles per day of the 6 miles per day found.

The direction of the current is not closely tied to either sea or air temperatures. For this comparison calendar months are more convenient (Fig. 2).

It is most unfortunate that due to war conditions the temperature records were maintained only for the first 4 months of the Vertical Log measurements so that a direct comparison between sea temperature and current direction cannot be made. A comparison is here made between the monthly mean temperature over the years 1928–39 (Cooper, 1960*b*, table 1) and the monthly mean residual current.

It will be seen that changes in sea temperature follow changes in current direction with a considerable time lag. The association is better between current direction and air temperature at Scilly, particularly in 1941, but one would hesitate to say that such association is at all close.

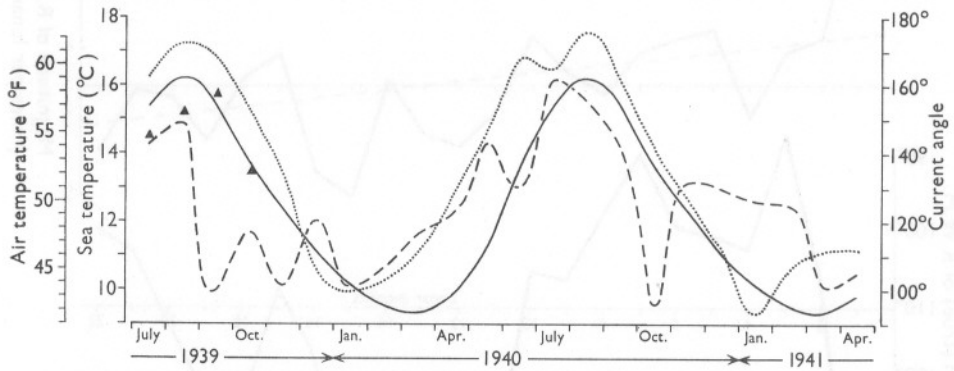

Fig. 2. Comparison between the mean direction of the current (pecked line) during the individual calendar months July 1939–April 1941, with the mean monthly sea temperatures (full line) at the light vessel for the years 1928–39 and the mean monthly air temperatures (dotted line) at St Mary, Scilly, during the same months as the current observations. Black triangles denote the four monthly sea temperatures observed at the light vessel at the start of the current measurements.

From the results of the 1950 cruises it had been deduced that the corner current may run most strongly around Lands End at neaps and be held back at springs. Consequently for each lunar month of the 1939–41 measurements we calculated the daily deviations from the mean direction of the water movement appropriate for that month. From these for each day of the generalized lunar month an average deviation of the direction of the residual water movement, clockwise or anti-clockwise, was obtained (Fig. 3, lower).

These deviations (maximum 27°) were of the same order as the error of single measurements. Nevertheless, it is reasonably certain that the residual water movement deviates to the northward of the mean in the vicinity of the springs and to the southward in the vicinity of the neaps. The deviation is greater at neaps than at springs but occurs for a shorter period. There are marked 'reactionary' deviations on either side of new moon, however, and

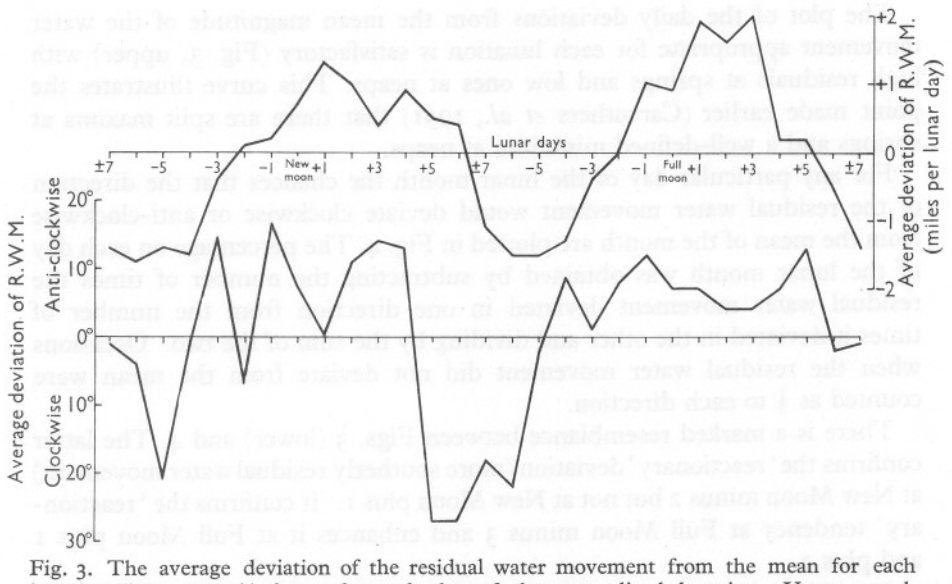

Fig. 3. The average deviation of the residual water movement from the mean for each lunation (lunar month) drawn for each day of the generalized lunation. Upper panel, magnitude in miles per lunar day; lower panel, direction.

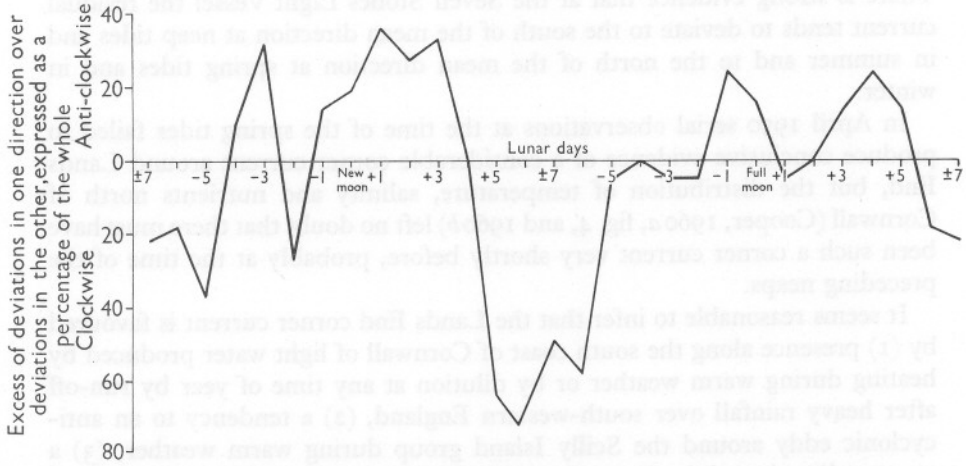

Fig. 4. Frequency of deviations of the residual water movement from the mean for each day of the lunar month.

less marked ones on either side of full moon. It is just possible that this may be due to the wind, on the majority of days involved, being unfavourable to the intrinsic direction of the residual water movements but, as the plot is for a mean of 22 lunar months it is more likely that there is in fact some reaction towards the opposite side of the mean direction for the month.

The plot of the daily deviations from the mean magnitude of the water movement appropriate for each lunation is satisfactory (Fig. 3, upper) with high residuals at springs and low ones at neaps. This curve illustrates the point made earlier (Carruthers *et al.*, 1951) that there are split maxima at springs and a well-defined minimum at neaps.

For any particular day of the lunar month the chances that the direction of the residual water movement would deviate clockwise or anti-clockwise from the mean of the month are plotted in Fig. 4. The percentage on each day of the lunar month was obtained by subtracting the number of times the residual water movement deviated in one direction from the number of times it deviated in the other and dividing by the sum of the two. Occasions when the residual water movement did not deviate from the mean were counted as $\frac{1}{2}$ to each direction.

There is a marked resemblance between Figs. 3 (lower) and 4. The latter confirms the 'reactionary' deviation (more southerly residual water movement) at New Moon minus 2 but not at New Moon plus 1. It confirms the 'reactionary' tendency at Full Moon minus 3 and enhances it at Full Moon plus 1 and plus 2.

DISCUSSION

There is strong evidence that at the Seven Stones Light Vessel the residual current tends to deviate to the south of the mean direction at neap tides and in summer and to the north of the mean direction at spring tides and in winter.

In April 1950 serial observations at the time of the spring tides failed to produce conclusive evidence of a considerable corner current around Lands End, but the distribution of temperature, salinity and nutrients north of Cornwall (Cooper, 1960*a*, fig. 4, and 1960*b*) left no doubt that there must have been such a corner current very shortly before, probably at the time of the preceding neaps.

It seems reasonable to infer that the Lands End corner current is favoured by (1) presence along the south coast of Cornwall of light water produced by heating during warm weather or by dilution at any time of year by run-off after heavy rainfall over south-western England, (2) a tendency to an anti-cyclonic eddy around the Scilly Island group during warm weather, (3) a current direction at the Seven Stones Light Vessel setting well to the south of the Runnelstone, (4) weak currents at the light vessel, (5) neap tides (i.e. that the Lands End corner current will be most evident during neap tides in very warm or very wet weather).

Conversely, the Lands End corner current may be hindered by (1) homogeneous water stretching south of Cornwall, as after a heavy south-westerly gale, (2) a tendency to a cyclonic eddy around the Scilly Island group during cold weather, (3) a current at the Seven Stones lightvessel setting east towards

the Lands End promontory, (4) spring tides, though these may mix waters ready to be carried around on the following neap tides.

Our argument has included neither what may happen when the current at the lightvessel sets towards a northerly or westerly direction, nor what may happen during severe gales which may override the forces acting during moderate winds.

SUMMARY

On a first appreciation, findings during the cruise of the Plymouth research vessel 'Sabella' around Lands End in April 1950 appeared to conflict with conclusions drawn from long-period measurements of current at the Seven Stones Light Vessel. The results could be harmonized if it is assumed that there may be a narrow intermittent current around Lands End, transporting water from the south to the north coast of Cornwall and rarely extending as far west as the Seven Stones Light Vessel.

A detailed examination gave strong support to this explanation but the desired direct confirmation has, unfortunately, not yet been attempted.

The conclusions are set out in the Discussion.

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THE INFLUENCE OF TEMPERATURE ON THE BREEDING AND THE MOULTING ACTIVITIES OF SOME WARM-WATER SPECIES OF OPERCULATE BARNACLES

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(Text-figs. 1 and 2)

Thorson (1946) considered in detail the earlier views of Appellöf (1912), Orton (1920) and Runnström (1928) that breeding activities of the majority of marine organisms were controlled by the temperature of the sea and referred to this as Orton's rule. Recently Crisp (1954) and Qasim (1956) also reviewed the existing literature on this subject in relation to barnacles and fish. By considering the seasonal availability of planktonic food in conjunction with Orton's rule, they explained why tropical species inhabiting cool temperate waters have a breeding season confined to the warmer months, whereas boreo-arctic species throughout their whole range breed only during colder months.

Loosanoff & Davis (1950) succeeded in bringing the bivalve mollusc *Venus mercenaria* into the spawning condition by gradually raising the water temperature and providing suitable food. Patel (1959) maintained specimens of *Lepas anatifera* L. under laboratory conditions, raised the temperature, and fed them on *Artemia* larvae and thereby induced the species to breed. On the other hand, Crisp (1957) reported moderate success in causing the breeding of certain boreo-arctic barnacles during the period when the natural population was not breeding by lowering the temperature.

It was considered desirable to have a liberal supply of fertilized egg masses, larvae and cyprids of the commoner fouling organisms, especially of cirripedes, at all the seasons of the year for conducting experimental work. The following experiments were carried out to induce these animals to breed outside the normal breeding period of the natural population. Simultaneously, consideration was given to the influence of temperature on moulting rhythm, cirral activity and egg size.

Tropical or subtropical species of operculate barnacles inhabiting British waters, namely *Chthamalus stellatus* (Poli), *Elminius modestus* Darwin, *Balanus perforatus* Bruguière and *B. amphitrite* var. *denticulata* (Broch), were selected for the investigation.

MATERIAL AND METHODS

Specimens of *Chthamalus stellatus* were collected on pieces of rock from Aberffraw, Anglesey; *Elminius modestus* on mussels attached to the piles of Bangor pier in the Menai Straits; *Balanus perforatus* on rock chippings from the coast of the Gower peninsula; and *B. amphitrite* on pieces of glass bottle from the warm docks at Swansea. All specimens were obtained during the winter.

Immediately after the sample had been collected, about 70 to 100 individuals of each species were examined for the presence of egg masses. Of the four species only *Elminius modestus* could not be obtained normally free of embryos in the cooler months of the year (Crisp & Davies, 1955). To obtain *E. modestus* without egg masses all the individuals settled on each *Mytilus* shell, except for one specimen of mature size, were removed. The isolated specimens so obtained were kept in separate dishes to prevent further fertilization and were fed for about a fortnight to encourage liberation (Crisp, 1956; Crisp & Spencer, 1958). Individuals which liberated nauplii during isolation were then certain to be empty, since self-fertilization does not occur in this species (Barnes & Crisp, 1956). They were then used to investigate the induction of further breeding. The other three species were found to be entirely free of egg masses at the season when the experiments were conducted.

About 20 to 30 individuals of each species were kept in 6 in. diameter glass crystallizing dishes and maintained at a series of different temperatures, each one varying by not more than $\pm 2^{\circ}$ C. The temperatures were recorded each day throughout the experiments and a mean value calculated at the end.

Two identical groups of animals belonging to the same species were selected for each experiment at each temperature, except for *E. modestus* which had to be given a preliminary feeding as described above. One group was fed liberally on *Artemia* larvae and the other group was kept without food. The large quantities of *Artemia* larvae required were hatched from commercially available *Artemia* eggs in a warmed $3 \times 1\frac{1}{2}$ ft. glass tank containing sea water and continuously aerated to keep the eggs circulating throughout the tank. Hatched larvae were strained off, and transferred daily to the dishes containing barnacles, when fresh sea water, brought to the required temperature was added. Throughout the experiment the water surrounding the barnacles was freely aerated both to oxygenate it, and to keep the food moving over the barnacles, which then fed by simply extending the cirri (Southward & Crisp, 1959).

Cast skins, expelled egg masses and any liberations of nauplii were carefully noted, a separate record for each dish being kept. After an interval of 8–10 days at each temperature a few animals from each dish were examined to see whether any had become fertilized. If so, the stages of development of the fertilized egg masses were determined, using the categories given by Crisp

(1954). The condition of the ovary of all unfertilized specimens was visually determined, the stage of ovarian development being divided into five categories and points assigned as shown in Table 1. A mean ovary index was obtained for the samples taken from each dish.

TABLE 1. STAGES OF OVARIAN DEVELOPMENT

Condition of ovary	Ovary index score
Fertilized egg masses	4
Well-developed ovary filling mantle space	3
Moderately developed ovary	2
Slightly developed ovary with minute eggs	1
No ovarian development observed	0

The lengths and breadths of the fertilized eggs were measured in microns. Since the fertilized egg was approximately a prolate spheroid, the volume was calculated as $4/3\pi ab^2$, where $a = \frac{1}{2}$ length and $b = \frac{1}{2}$ breadth.

To study the influence of temperature on the size of released nauplii (stage I), normally fertilized *E. modestus* were collected from the field. Egg masses produced by each parent were divided into three batches, each of which was then incubated *in vitro* at different temperatures following the methods described by Patel & Crisp (1960). Immediately after being released stage I nauplii were preserved in 5% sea water formaldehyde and their dimensions measured.

These experiments were conducted during December 1957 to February 1958 and during December 1958 to February 1959, when the natural population of all the species was dormant and generally had poorly developed gonads. The results of both the years were identical and were therefore combined in the tabulated results.

EFFECT OF TEMPERATURE ON BREEDING

The results on the influence of temperature on the breeding activities of animals maintained at a series of different temperatures (as described above) are shown in Table 2. Breeding activity may be judged from the percentage of individuals fertilized at the end of the experiments at each temperature. It will be evident from Table 2 that the fed specimens of all the four species, though having scarcely any development of the gonads at the outset, developed gonads within a short time and soon reached breeding condition. In most cases they were able to breed after being kept for only 2–3 weeks at their breeding temperature. Both the percentage of the individuals carrying embryos and also, in general, the ovary index increased as the temperature was raised above the critical minimum value for breeding. This minimum varied with each species, thus *B. amphitrite* started breeding activity at 17–18° C, *B. perforatus* and *C. stellatus* at 15–16° C and *E. modestus* was found

TABLE 2. THE EFFECT OF TEMPERATURE AND FEEDING ON THE MEAN INDEX OF DEVELOPMENT OF THE OVARY, ON THE PERCENTAGE OF FERTILIZED INDIVIDUALS AND ON THE NUMBER OF BROODS IN BARNACLES

	Fed				Starved			
Mean temperature (°C)	No. of days animals were kept at stated temperature	% fertilized	Mean ovary index	No. of broods	No. of days animals kept at stated temperature	% fertilized	Mean ovary index	No. of broods
			(*a*) *Chthamalus stellatus*					
32	15	10	2·1	1	25	0	1·0	0
30	15	36	2·7	1	—	—	—	—
28	15	30	3·1	1	25	0	1·2	0
25	25	20	3·6	1	35	0	1·0	0
20	25	60	3·4	1	35	0	1·0	0
15	25	12	2·7	1	35	0	1·0	0
9	35	0	1·6	0	—	—	—	—
6	40	0	1·2	0	40	0	0·5	0
			(*b*) *Balanus perforatus*					
31·5	10	0	—	*	10	0	—	*
28·0	20	53	3·5	1	25	0	1·0	0
23·5	20	77	3·8	1	25	0	1·5	0
19·0	20	60	3·5	1	25	0	1·5	0
15·0	35	5	2·4	1	40	0	1·0	0
13·0	40	0	2·0	0	40	0	0·8	0
10·0	40	0	1·2	0	—	—	—	—
6·0	40	0	0·9	0	40	0	0·5	0

* Indicates specimens died within 8–10 days.

			(*c*) *Balanus amphitrite*					
31·5	40	100	4·0	2	45	0	0·5	0
27·5	40	100	4·0	2	45	0	0·5	0
24·5	40	100	4·0	2	—	—	—	—
22·5	40	100	4·0	2	45	0	0·7	0
19·5	20	73	3·6	1	—	—	—	—
17·5	20	34	3·0	1	45	0	1·0	0
14·5	45	0	2·0	0	45	0	0·8	0
11·5	35	0	2·0	0	—	—	—	—
7·5	35	0	1·0	0	—	—	—	—

(*d*) *Elminius modestus*

(All animals fed throughout experiment.)

Mean temperature (°C)	No. of days animals were kept at stated temperature	% fertilized	Mean ovary index	No. of broods
30	30	35	2·9	1
25	19	93	3·9	1
20	19	90	3·9	1
15	20	70	3·7	1
9	32	54	3·3	1

fertilized at 8°–9° C. Above the optimum temperature for breeding, the percentage of fertilized individuals and the mean ovary index fell. Thus *B. perforatus* bred at an optimum rate between 22° and 23° C, and continued to breed up to 27°–28° C. At even higher temperatures (30°–32° C) animals survived for only 7–10 days and did not breed. *C. stellatus* did not reach its optimum until 24°–25° C, and continued producing broods up to 30° –32° C, though a lower percentage of the population was found to be carrying eggs at this temperature. In *B. amphitrite* all the experimental individuals bred readily between 22° and 32° C, and on one occasion when the thermostat failed they withstood temperatures of the order 38°–40° C for over 24 h. Individuals of *E. modestus* reached their optimum rate at 22°–25° C, and both the percentage of fertilized individuals and the mean ovary index fell considerably at 30°–31° C.

EFFECT OF NUTRITION ON BREEDING

It can be seen from Table 2 that, within the characteristic temperature range of breeding for any given species, only those groups of individuals which were given food developed gonads rapidly and bred readily. When barnacles were fed on *Artemia* larvae the newly developed ovary assumed an abnormal pinkish tint instead of its usual yellow colour. Similar colour changes, but more pronounced, were observed in artificially fed *Lepas anatifera* (Patel, 1959). The operculate barnacles, unlike *Lepas* however, could live without food for long periods. These starved individuals failed to develop the gonads, as is evident from the continuing low mean ovary index. It should be borne in mind that these animals were collected at the season when the feeding activity and reserves were already at a minimum. Had they been collected just before the normal breeding season, when the gonads would have been more fully developed, a proportion at least of the observed specimens would doubtless have bred on raising the temperature. This was later found to be so with *C. stellatus* and *B. perforatus* during May and June, respectively.

To confirm that nutrition played a major role in allowing breeding to commence, some of the starved individuals of the species *B. amphitrite*, *B. perforatus* and *C. stellatus*, which had not fertilized even after having been kept for 30–40 days above the critical breeding temperatures, were fed liberally on *Artemia* larvae. Within 18–20 days these specimens entered the breeding condition and fertilized readily. The mean ovary index was also accordingly increased.

The temperature above which breeding begins in each species agrees well with the natural breeding season and the geographical distribution. *E. modestus* which breeds throughout the year in south-west England (Crisp & Davies, 1955) and whose distribution extends to the colder east coast of Britain, has the lowest critical breeding temperature of 8°–9° C. *C. stellatus*, which breeds only from May to September (Crisp, 1950) and whose distribution

extends up the west and north coasts of Scotland but not to the east coast, has the next highest breeding temperature of 15°–16° C. *B. perforatus* has a breeding range whose lower limit is about equal to that of *C. stellatus*, but, since its habitat is lower on the shore, it does not benefit to the same degree as *C. stellatus* from the sun's heat and the increase in temperature that occurs in spring. This may explain its later onset of breeding (July) and its more restricted distribution, which extends only to St David's Head (Norris & Crisp, 1953). *B. amphitrite*, with a critical breeding point of 17°–18° C, is a more tropical form, found in Britain only in exceptionally warm areas, such as power station effluents, and does not occur on the open coast further north than the Charente area in the Bay of Biscay (Bishop, Crisp, Fischer-Piette & Prenant, 1957).

The upper temperature limits of breeding are not far removed from the upper limits of survival of each species. The most sensitive of the four was *B. perforatus* which could not survive temperatures in excess of 30° C for long, and ceased to breed in this range. *C. stellatus* survives at the level of high water springs where it may be exposed to temperatures of at least 38° C (Southward, 1955). This species continued to breed at 32° C but, as only 10% contained fertilized eggs at this temperature, it is unlikely that breeding would have continued at temperatures much in excess of this. *E. modestus*, which can survive at levels almost as high as those occupied by *C. stellatus*, was not tested above 30° C; the fall in the percentage fertilized at this temperature suggests, however, that its upper limit is close to that of *C. stellatus*. *B. amphitrite*, the species most tolerant of high water temperatures, showed no fall-off in breeding at 31·5° C, all individuals containing embryos.

INFLUENCE OF TEMPERATURE AND NUTRITION ON THE MOULTING RHYTHM

Crisp & Patel (1958, 1960) have reported that the frequency of moulting was dependent on the temperatures during and of nutrition prior to the experimental period. During the present series of experiments the frequency of moulting at different temperatures was measured for fed and starved individuals of all the four species. The results are illustrated in Fig. 1 in which the rate of moulting per barnacle per day is plotted against temperature, together with Southward's (1955, 1957) observations on their cirral activity.

The temperature optimum of moulting activity was generally slightly lower than that of cirral activity. The difference may well be explained by the difference in duration of the two types of experiments. Experiments on cirral beats could be completed in a much shorter time than those on moulting which required 10–15 days. At the upper limit of temperature tolerance, therefore, rates of cirral beat could be measured before the elevated temper-

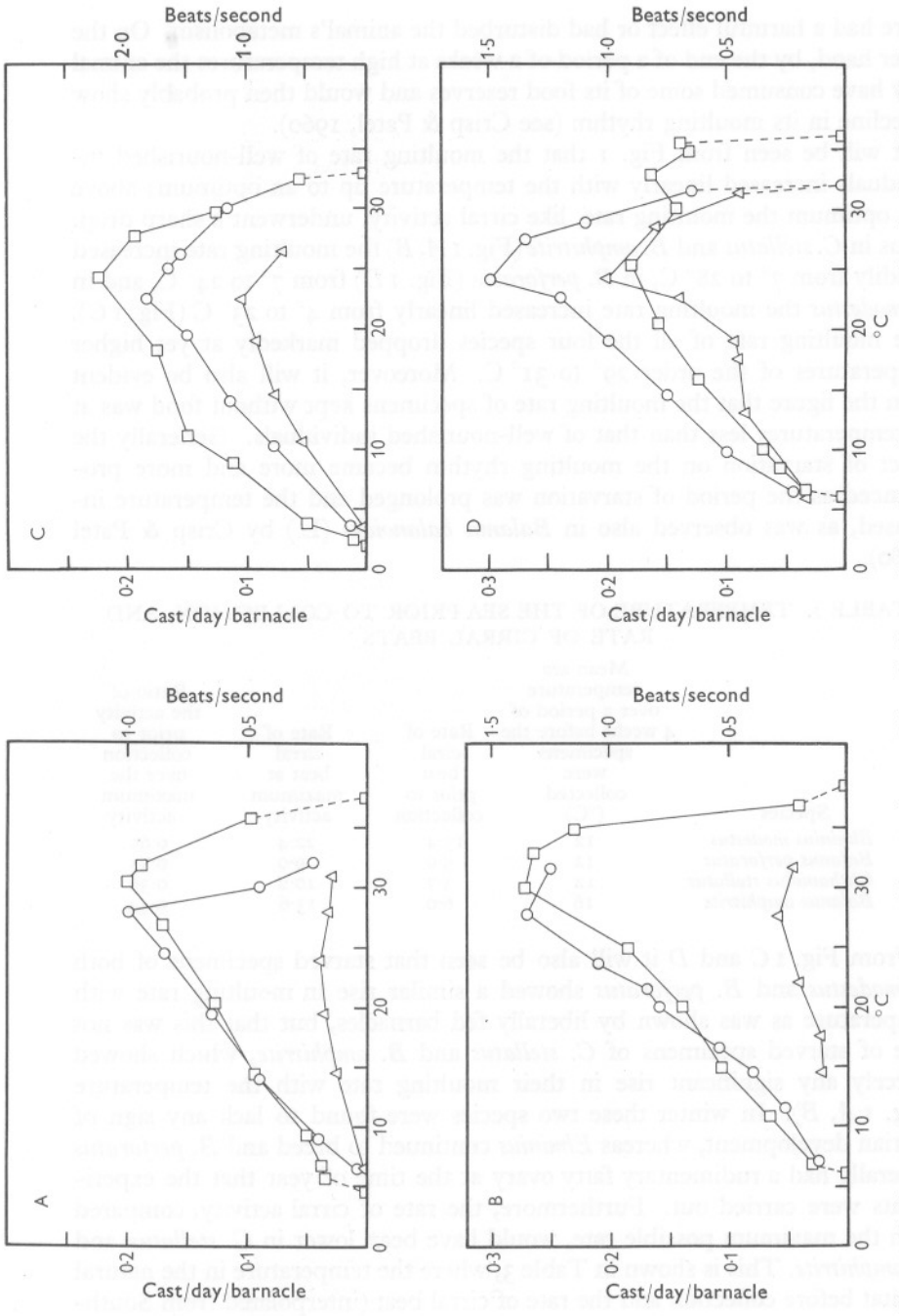

Fig. 1. Influence of temperature and nutrition on the moulting rhythm and the effect of temperature on the cirral activity (the latter is taken from Southward, 1955 and 1957) (*A*) *Chthamalus stellatus*, (*B*) *Balanus amphitrite* var. *denticulata*, (*C*) *Elminius modestus* and (*D*) *Balanus perforatus*. ○ Indicates moulting rate of fed specimens. △ Indicates moulting rate of starved specimens. □ Indicates the rate of cirral beating. (Note: In order to accommodate the high rate of beating in *Elminius modestus*, the scale on the ordinate of Fig. 1 *C* showing the rate of beat has been reduced in comparison with the scales in Fig. 1 *A*, *B* and *D*.)

ature had a harmful effect or had disturbed the animal's metabolism. On the other hand, by the end of a period of 2 weeks at high temperatures the animal may have consumed some of its food reserves and would then probably show a decline in its moulting rhythm (see Crisp & Patel, 1960).

It will be seen from Fig. 1 that the moulting rate of well-nourished individuals increased linearly with the temperature up to an optimum; above this optimum the moulting rate, like cirral activity, underwent a sharp drop. Thus in *C. stellatus* and *B. amphitrite* (Fig. 1 *A*, *B*) the moulting rate increased steadily from 7° to 28° C, in *B. perforatus* (Fig. 1 *D*) from 7° to 24° C, and in *E. modestus* the moulting rate increased linearly from 4° to 23° C (Fig. 1 *C*). The moulting rate of all the four species dropped markedly at yet higher temperatures of the order 29° to 31° C. Moreover, it will also be evident from the figure that the moulting rate of specimens kept without food was at all temperatures less than that of well-nourished individuals. Generally the effect of starvation on the moulting rhythm became more and more pronounced as the period of starvation was prolonged and the temperature increased, as was observed also in *Balanus balanoides* (L.) by Crisp & Patel (1960).

TABLE 3. TEMPERATURE OF THE SEA PRIOR TO COLLECTION, AND RATE OF CIRRAL BEATS

Species	Mean sea temperature over a period of 4 weeks before the specimens were collected (°C)	Rate of ciral beat prior to collection	Rate of cirral beat at maximum activity	Ratio of the activity prior to collection over the maximum activity
Elminius modestus	12	15·4	22·4	0·69
Balanus perforatus	12	5·0	9·0	0·55
Chthamalus stellatus	12	3·7	10·2	0·36
Balanus amphitrite	16	6·0	13·6	0·44

From Fig. 1 *C* and *D* it will also be seen that starved specimens of both *E. modestus* and *B. perforatus* showed a similar rise in moulting rate with temperature as was shown by liberally fed barnacles, but that this was not true of starved specimens of *C. stellatus* and *B. amphitrite*, which showed scarcely any significant rise in their moulting rate with the temperature (Fig. 1 *A*, *B*). In winter these two species were found to lack any sign of ovarian development, whereas *Elminius* continued to breed and *B. perforatus* generally had a rudimentary fatty ovary at the time of year that the experiments were carried out. Furthermore, the rate of cirral activity, compared with the maximum possible rate, would have been lower in *C. stellatus* and *B. amphitrite*. This is shown in Table 3, where the temperature in the natural habitat before collection and the rate of cirral beat (interpolated from Southward's results) is given. It seems likely therefore that, whereas *Elminius*

modestus and *B. perforatus* may have been feeding at a sufficient rate to maintain their reserves in some degree, *C. stellatus* and *B. amphitrite* had been feeding more sluggishly in relation to their optimum, and were in a more starved condition. In consequence starved individuals of these two species were probably unable to maintain a moulting rate in step with the rise in temperature.

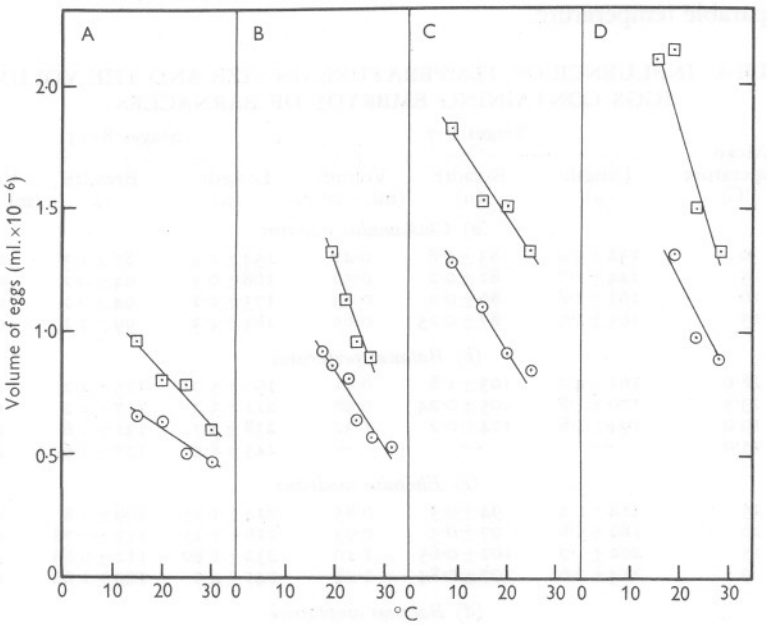

Fig. 2. Effect of temperature on the volume of eggs (*A*) *Chthamalus stellatus*, (*B*) *Balanus amphitrite* var. *denticulata*, (*C*) *Elminius modestus* and (*D*) *Balanus perforatus*. ⊙ indicates volumes of eggs containing early stage embryos. ⊡ Indicates volumes of eggs containing late stage embryos.

TEMPERATURE AND EGG SIZE

The dimensions of fertilized eggs from the adults kept and fed at a series of different temperatures during the period that the ovary and subsequent brood were developing, are given in Table 4. The mean lengths, breadths and deduced volumes are shown together with the corresponding standard errors. The egg volumes are plotted in Fig. 2, against the temperature of development. In all the four species at all temperatures the volume of the eggs increased as the embryos developed. Furthermore, the volumes of both early (stages 1 to 7) and late stages (stages 8 to 13) increased with the lowering of the temperature at which they had developed as ova. Generally, the breadth remained more or less constant but the length varied considerably. Identical results were reported by Patel (1959) in *Lepas anatifera*, and Crisp (1960)

found a significant change in volume of the fertilized eggs of the boreo-arctic species *B. balanoides* collected from different latitudes. The size of the eggs decreased from north to south, i.e. from colder to warmer water. Earlier Crisp (1954) had shown that the dimensions of fertilized eggs in boreo-arctic species of operculate cirripedes were in general larger than those of their relatives from the lower latitudes. The measurements given in Table 4 are approximately of the same value as given by Crisp (1954) at the nearest comparable temperature.

TABLE 4. INFLUENCE OF TEMPERATURE ON SIZE AND THE VOLUME OF EGGS CONTAINING EMBRYOS OF BARNACLES

Mean temperature (°C)	Stages 1–7			Stages 8–13		
	Length (μ)	Breadth (μ)	Volume (ml. $\times 10^{-6}$)	Length (μ)	Breadth (μ)	Volume (ml. $\times 10^{-6}$)
			(*a*) *Chthamalus stellatus*			
30	132 ± 5·4	83 ± 0·8	0·47	154 ± 2·4	87 ± 1·3	0·60
25	144 ± 1·7	82 ± 0·2	0·50	168 ± 0·3	94 ± 0·2	0·78
20	163 ± 1·8	86 ± 0·2	0·63	173 ± 1·2	94 ± 0·2	0·80
15	165 ± 1·6	87 ± 0·25	0·65	184 ± 4·3	99 ± 2·2	0·95
			(*b*) *Balanus perforatus*			
28·0	161 ± 4·2	103 ± 1·8	0·91	193 ± 5·0	115 ± 2·2	1·33
23·5	170 ± 1·8	105 ± 0·24	0·98	211 ± 3·2	117 ± 1·2	1·50
19·0	194 ± 1·8	114 ± 0·2	1·32	238 ± 3·7	131 ± 1·6	2·14
15·0	—	—	—	245 ± 8·5	127 ± 3·6	2·10
			(*c*) *Elminius modestus*			
25	184 ± 1·4	94 ± 0·5	0·85	214 ± 1·25	109 ± 0·8	1·33
20	189 ± 5·8	97 ± 0·5	0·93	226 ± 1·25	113 ± 0·78	1·51
15	202 ± 1·7	102 ± 0·65	1·10	232 ± 1·80	112 ± 0·86	1·53
9	214 ± 2·6	107 ± 0·84	1·28	241 ± 4·0	120 ± 2·60	1·82
			(*d*) *Balanus amphitrite*			
31·5	127 ± 6·0	88 ± 2·0	0·53	—	—	—
27·5	136 ± 3·7	89 ± 0·3	0·57	162 ± 5·0	103 ± 3·0	0·90
24·5	145 ± 3·5	92 ± 0·4	0·64	173 ± 2·0	103 ± 1·4	0·96
22·5	159 ± 2·8	99 ± 0·2	0·81	178 ± 2·8	110 ± 1·2	1·13
19·5	165 ± 1·5	100 ± 1·2	0·86	184 ± 3·0	117 ± 1·4	1·32
17·5	167 ± 2·4	102 ± 0·8	0·92	—	—	—

It will be seen that in three of the four species the influence of temperature on egg size is accentuated in the later embryonic stages, though the curve for *E. modestus* (Fig. 2*C*) has a similar slope for both early and late stages. If egg size was related to the size of the developing embryo these changes in slope suggest that temperature influences not only the initial size of the ova but also the amount of embryonic growth, both effects determining the ultimate size which the developing embryo can attain. In order to test the influence of temperature during development on the ultimate size of the embryo, fertilized eggs of *E. modestus*, which had been oviposited by the same parent in July at the prevailing sea temperature, were incubated *in vitro* at a series of different temperatures. The first stage nauplii formed showed a variation

in size (Table 5). That those which developed at the highest temperature were the smallest in size confirms that in barnacles the embryos are reduced in size if they undergo embryonic development at a higher temperature.

Our results agree with those obtained by Gray (1928*a*, *b*) who, in an essentially similar experiment reported that the eggs of *Salmo fario* from the same female, when incubated at a series of different temperatures hatched into fry of different size. Those reared at a higher temperature were smaller than those incubated towards the lower limit of normal development. However, both our findings and Gray's differ from those of Loosanoff (1959) who used

TABLE 5. INFLUENCE OF TEMPERATURE ON LENGTHS AND BREADTHS OF STAGE I NAUPLII OF *ELMINIUS MODESTUS*. EGG MASSES REMOVED FROM ONE PARENT WERE INCUBATED *IN VITRO* AT THE FOLLOWING DIFFERENT TEMPERATURES

Parent no.	Stage of development of embryos at beginning of experiment	11° C		16° C		23° C	
		Length (μ)	Breadth (μ)	Length (μ)	Breadth (μ)	Length (μ)	Breadth (μ)
1	3–4	$268 \pm 1{\cdot}5$	$116 \pm 0{\cdot}5$	$252 \pm 2{\cdot}5$	$115 \pm 0{\cdot}6$	$229 \pm 3{\cdot}9$	$108 \pm 1{\cdot}3$
2	6–7	$259 \pm 1{\cdot}1$	$118 \pm 0{\cdot}9$	$247 \pm 2{\cdot}6$	$114 \pm 0{\cdot}8$	$232 \pm 5{\cdot}6$	$112 \pm 1{\cdot}4$
3	8–9	$260 \pm 1{\cdot}1$	$118 \pm 1{\cdot}2$	$252 \pm 2{\cdot}0$	$119 \pm 2{\cdot}4$	$246 \pm 0{\cdot}5$	$114 \pm 0{\cdot}7$

eggs of *Venus* (*Mercenaria*) *mercenaria* which had been artificially induced to spawn during winter. The spawn was maintained at a series of different temperatures. Loosanoff found no significant difference in the final size of the larvae at the time of settlement. However, the results in Fig. 2 of his paper show a drop in size as the temperature was raised above 20° C and the failure to observe any size difference may have been due to the great variation in the larval size at each temperature.

The effect of temperature on egg size is common to many other groups of animals. Moore (1942) found eggs of graded diameter in different species of frogs belonging to the genus *Rana*, the northern forms laying larger eggs than the southern forms. Later the same author reported similar differences in the diameter of fertilized eggs of *Rana pipiens* inhabiting different latitudes (Moore, 1949). Colder conditions not only increase the size attained by the embryos but in many animals lead also to a larger size in the adults. Many observers have noticed that marine organisms belonging to the same species but inhabiting different latitudes grow more slowly but attain a significantly larger size in higher latitudes (for literature see Gunter, 1950, 1957).

Although the amount of growth is less at higher temperatures, the rate at which the final condition of maturity is reached is greater, whether the system be a developing oocyte, an embryo, or an adult poikilotherm. Gray's simple and direct explanation for embryos was based on the fact that in this system only a limited amount of nutrient was available as yolk. If the growing tissue

requires proportionately more energy for maintenance at a higher temperature, less material would inevitably be left over for growth. An exactly analogous explanation for developing oocytes or for adult animals cannot be sustained because in these systems the amount of living matter could, if necessary, be augmented during development to allow for increased metabolic activity. Moreover, even in embryos, there is no obvious reason why rapid development over a shorter time interval should be less efficient and so use more reserve food than slow development over a longer time. In barnacles the size of developing ova does not appear to depend to any significant extent on the nutrition of the parent, for animals which are poorly fed produce fewer, but not necessarily smaller, eggs.

It seems possible that in all three systems development may be controlled by similar basic processes in which the temperature coefficient of differentiation, leading to maturity, is greater than the temperature coefficient of tissue multiplication or growth. These two processes, differentiation and growth, do not therefore keep exactly in step at all temperatures; at low temperatures differentiation is relatively slower leading to a larger mature size, while at high temperatures growth is rapid leading to a smaller size at maturity.

We are grateful to Prof. E. W. Knight-Jones of the Department of Zoology, Swansea, for obtaining for us specimens of *B. perforatus* and *B. amphitrite*, and to Dr E. Naylor for supplying us with temperature records of Queen's Dock and other places around the Gower peninsula.

SUMMARY

Tropical species of operculate cirripedes, including *Elminius modestus* Darwin, *Chthamalus stellatus* (Poli), *Balanus perforatus* Bruguière and *B. amphitrite* var. *denticulata* (Broch), collected during the winters of 1957 to 1959, were induced to breed by raising the temperature and feeding liberally on *Artemia* larvae. Well-nourished specimens of *B. perforatus* and *C. stellatus* commenced to breed after being kept for 2–3 weeks at 15° –16° C; *B. amphitrite* required a temperature of 17°–18° C, whereas *E. modestus* bred at 8°–9° C. The percentage of the specimens bearing embryos increased with the temperature and reached optima lying in all four species between 22° and 25° C. The animals continued to breed, though less efficiently, up to temperatures of the order 28°–30° C, the limits varying a little for each species. Only fed individuals produced gonads and broods; those kept without food showed no breeding activity at any temperature even after 4–5 weeks, but after being fed for 2–3 weeks bred readily. The moulting rate of all four species was dependent both on temperature and on their prior nutrition. The moulting rate of well-fed specimens increased linearly to an optimum and subsequently dropped sharply. The moulting rhythm followed a pattern in relation to temperature

like that of cirral activity, but generally with a lower optimum temperature. The volume of the fertilized eggs increased during development and was greater the lower the breeding temperature.

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RED BLOOD VALUES IN THE PLAICE (*PLEURONECTES PLATESSA* L.)

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(Text-fig. 1)

The work reported in this paper forms part of a programme of investigation into the normal parameters of radiosensitive tissues in the plaice. The work was conducted prior to investigations into the effects of ionizing radiations on these tissues, in order to form a background to examinations of fish from areas of radioactive pollution resulting from the controlled disposal of radioactive effluent. Tissues were selected on the basis of known radiosensitive tissues in mammals and the work on red blood values reported here arose from these preliminary investigations.

In the first instance it was realized from the work of Schaefer (1925), Kawamoto (1929), Yokoyama*, Dombrowski (1953), Antipova (1954) and Kaplan & Crouse (1956), that the value of such indices of the red blood picture as packed cell volume (PCV), red cell count (RBC) and haemoglobin (Hb) might vary both with the size of the animal and with season. A preliminary investigation was therefore carried out in April 1956, using PCV as the index, to determine at what size asymptotic values for red blood were reached. This was followed in 1957 by measurement throughout the year of PCV, RBC, Hb and sedimentation rate (SR) in order to determine the existence and extent of seasonal variation, among fish that were large enough to have reached asymptotic values for red blood.

MATERIALS AND METHODS

The relationship between PCV and size was determined in April 1956 from a sample of 108 freshly caught live plaice. Seasonal variation was determined from samples of twenty to thirty freshly caught live plaice, obtained off Lowestoft at approximately 2-month intervals from the end of February to the beginning of September, together with a final sample examined at the beginning of December. A sample of 0·5 ml. of blood was removed from each fish, by cardiac puncture (Yoffey 1929), using a heparinized 1 c.c. glass syringe with No. 19 needle, and sufficient quantities of blood were transferred

* Yokoyama, H. O. Studies on the origin, development and seasonal variation in the blood cells of the perch (*Perca flavescens*). Ph.D. Thesis, Univ. Wisconsin, 150 pp., 1947.

to a clean paraffin waxed watch glass for each measurement. Using standard techniques (Kolmer, Spaulding & Robinson, 1938), packed cell volumes were measured with Wintrobe microhaematocrit tubes. Red-cell counts were carried out using standard red-cell pipettes and a Hawksley improved Neubauer crystallite counting chamber. Fifty per cent filtered sea water is isotonic with plaice erythrocytes and was used as diluting fluid. It was just coloured with gentian violet to provide sufficient coloration of the cells to facilitate counting. The fluid was freshly filtered prior to each dilution, to remove precipitated stain.

Haemoglobin estimations were made by the alkaline haematin method (Gibson & Harrison, 1945), using the B.D.H. artificial standard and a photoelectric absorptiometer. Sedimentation rates were measured by standard techniques, using microsedimentation tubes. During the early determinations of sedimentation rate measurements were made every fifteen minutes for 1 h, but in later determinations only the hourly rate was recorded.

PACKED CELL VOLUME AND WEIGHT

The data obtained on the relationship between PCV and weight are set out in Table 1. There is an increase in mean PCV with increase in weight of the fish up to a weight of approximately 120 g, when the PCV value stabilizes.

TABLE 1. RELATION BETWEEN PACKED CELL VOLUME AND WEIGHT. DATA FROM A SAMPLE OF FRESHLY CAUGHT LIVE PLAICE, APRIL 1956

No. of fish in sample	Weight range (g)	Mean weight of sample (g)	Mean PCV (%)	Range PCV % in sample	Standard deviation PCV
11	1– 20	14·1	17·2	14·1–20·6	2·2
16	21– 40	32·9	19·5	15·3–23·8	2·8
15	41– 60	52·0	21·9	19·2–24·6	1·7
12	61– 80	72·3	22·9	19·2–26·7	2·4
14	81–120	97·5	25·8	20·1–30·2	3·0
9	121–150	136·0	25·7	15·3–31·5	6·0
8	151–200	174·6	25·0	20·5–32·2	4·3
13	201–300	247·9	25·6	18·0–32·1	4·5
10	301–500	374·2	24·7	20·4–27·7	2·4

Inspection of the data in Table 1 shows that there is a considerable variation about the mean value for PCV, percentage variation ranging from 24 to 62%, which is not uncommon in the determination of PCV in fish blood. Field, Elvehjem & Juday (1943) give percentage variations of 61% for carp blood and 50% for trout blood, and Young (1949), measuring the PCV of individual fish at time intervals of from 10 to 14 days, remarks that the variation in PCV of individual fish at different times is comparable to that between different fishes of the same species at the same time. He gives percentage variation figures of from 15 to 67% of the mean PCV.

The increase of RBC values with increase in size of the fish has been noted before by Dombrowski during a study of the blood of the carp. He found that the erythrocyte counts increased from $1{\cdot}1 \times 10^6$ per mm^3 at hatching to $1{\cdot}5$–$1{\cdot}8 \times 10^6$ per mm^3 at the end of the fourth season, a mean increase of 50%, and that this was accompanied by an increase in haemoglobin from values of 7·3 g/100 ml. to 10·8 g/100 ml. over the same period, an increase of 48%. The increase in mean PCV in the plaice over the weight range 14–120 g (a 3–4 year period) is comparable, i.e. 17·2–25·6, an increase of 49%.

From the preceding plaice data it was decided to confine the study on seasonal variation to fish of not less than 140 g, so as to obviate the fluctuations due to differences in size of the fish. The data that follow are accordingly only applicable to plaice of weights in excess of 140 g.

SEASONAL VARIATION IN RED BLOOD VALUES

The data on seasonal variation of PCV, RBC, Hb and SR given in Table 2 and Fig. 1 show clearly that a process of haemoconcentration occurs throughout the late spring and summer, and that this is followed in the late summer and autumn by haemodilution.

TABLE 2. SEASONAL VARIATION IN RED BLOOD VALUES: PACKED CELL VOLUME (PCV), RED BLOOD CELL COUNT (RBC), HAEMOGLOBIN (Hb) AND SEDIMENTATION RATE (SR), DURING 1957

	Date of sample				
Parameter	28 February	23 April	21 June	29 August	1 December
No. observations	28	26	22	26	24
PCV Range (%)	16·7–27·5	16·2–27·2	22·2–32·2	20·6–32·4	17·4–27·0
Mean (%)	21·4	21·8	27·0	25·6	21·3
Standard deviation	2·9	3·0	3·1	3·3	2·7
No. observations	29	25	22	26	20
RBC Range (10^6/mm^3)	1·52–2·81	1·53–2·54	1·86–2·62	1·79–3·01	1·72–2·42
Mean (10^6/mm^3)	2·05	2·02	2·28	2·38	2·03
Standard deviation	0·35	0·28	0·22	0·29	0·20
No. observations	29	26	22	26	21
Hb Range (g/100 ml.)	5·52–11·06	4·55–7·87	6·70–10·42	4·38–8·51	4·22–6·85
Mean (g/100 ml.)	8·12	5·66	8·75	6·37	5·93
Standard deviation	1·38	0·88	1·03	1·03	0·66
No. observations	26	25	20	20	20
SR Range (mm/hr)	1·0–2·75	0·7–2·05	0·5–1·8	0·3–1·65	0·7–1·75
Mean (mm/hr)	1·65	1·37	1·01	0·96	1·14
Standard deviation	0·49	0·35	0·37	0·34	0·28

The values for PCV and RBC reach their lowest points, in the period examined, at the end of the winter and then increase fairly rapidly during the early summer. The increase in PCV from April to June is rather more rapid than the increase in RBC, and the plasma volume is thus decreasing slightly over the period, i.e. the blood is becoming more concentrated. SR—which is some measure of the concentration of the blood, the rate slowing as the

RBC increases—is consistent with these changes by its significant decline over the same period. It can be calculated from Table 2 that there is no significant difference between PCV values in June and August, nor in RBC over the same period. These values are therefore probably steady during the

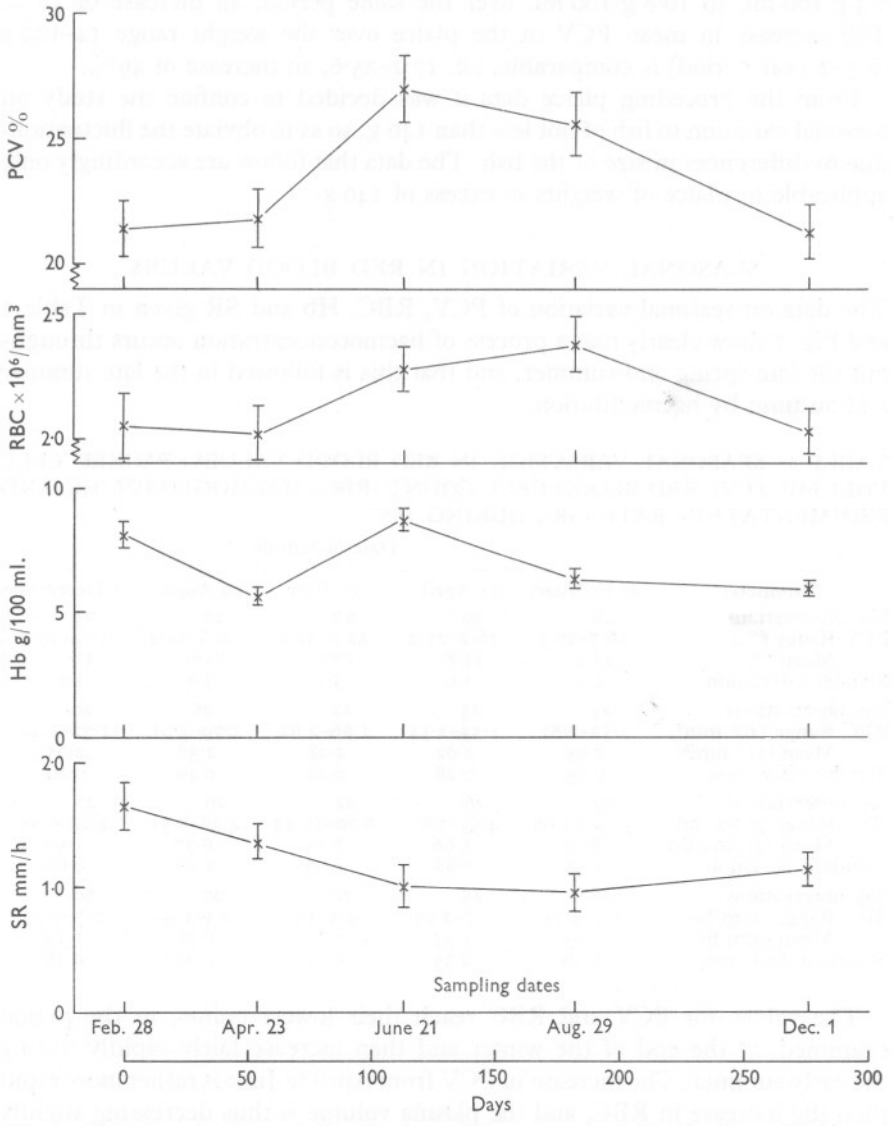

Fig. 1. Variation of plaice red blood values with season; packed cell volume (PCV), red blood cell count (RBC), haemoglobin (Hb), and sedimentation rate (SR), during 1957. The vertical lines show ± twice the standard error of the mean.

summer months, as is the SR, which halts its rapid fall and levels out over this period. From August to December both PCV and RBC fall steadily and the SR increases as the blood becomes more dilute.

It is interesting to note that the concentration of the blood revealed by the relative changes in PCV and RBC from April to June, is foreshadowed by a significant decrease in mean SR over the period February to April.

The values for Hb afford a less clear picture of events, in that they are already high at the end of the winter, falling to their lowest value of the whole period during the early spring. From then on they follow the same general trend as PCV and RBC, though their decline, which commences in June, is somewhat earlier than the decline in RBC.

A similar picture of haemoconcentration is described for another poikilotherm, the frog, by Kaplan & Crouse, though the time and magnitude of events are somewhat different, and the spring spawning obviously interrupts the rhythm.

It seems unlikely that the haemodilution which occurs in the plaice throughout the autumn and winter is a direct result of the decreased food intake occurring at this time. Schaefer, using pumpkin seed fish (*Eupomotis gibbosus* L. Cuvier and Valenciennes), found that these fish exhibited haemodilution during the late autumn and winter, but that the blood was able to concentrate again during the spring in spite of starvation throughout the whole period under investigation.

From the work of Musacchia & Sievers (1956), on cold torpor in the turtle (*Chrysemys picta*), it seems that the mechanism behind these changes is basically one of temperature. They found that turtles subjected to a low environmental temperature, $2 \pm 4^{\circ}$ C, exhibited haemodilution and that this was particularly well shown by the rapid fall in PCV and whole blood specific gravity. Thus the concentration of the blood of the plaice in late spring and summer may be a response to an increase in water temperature, and the subsequent haemodilution later in the year, the result of a falling water temperature.

ABNORMAL SEDIMENTATION RATES

It is well known that in mammals some disease conditions are accompanied by an accelerated SR; this has also been reported by Schumacher, Hamilton & Longtin (1956) for brook trout with furunculosis. These authors commented on the future of the method as a diagnostic tool in fish hatcheries and stressed the necessity for further information with respect to additional species and disease conditions.

During the early months, February and April, of the 1957 sampling programme some plaice were obtained exhibiting necrosis of the caudal fins and the posterior margins of the dorsal and ventral fins. When sedimentation rates were determined for these fish they proved to be abnormally fast (see Table 3).

TABLE 3. ABNORMAL SEDIMENTATION RATES, OF FISH WITH FIN NECROSIS, COMPARED WITH NORMAL FISH, FROM FEBRUARY AND APRIL 1957 SAMPLES

Time of observations (min)	Sedimentation rate: Healthy fish Range (mm)	Healthy fish Average (mm)	Fish with fin necrosis Range (mm)	Fish with fin necrosis Average (mm)
15	0·1–0·8	0·3	1·0–1·2	1·1
30	0·4–1·6	0·8	2·0–2·9	2·5
45	0·8–2·5	1·4	2·9–5·8	4·6
60	0·8–3·5	1·7	4·0–7·8	6·2

It is a pleasure to record my thanks to Mr F. Morgan who initiated and guided this work and to Mr C. Barker for his help throughout.

SUMMARY

The present study was undertaken as part of a programme designed to measure various parameters of normal fish tissues, prior to an investigation into the effects of ionizing radiation upon these tissues. The tissues were selected on the basis of known radiosensitive tissues in mammals. It was found that red blood values for the plaice, as indicated by packed cell volume, increased with the weight of the fish, up to a weight of approximately 120 g. Seasonal variations in packed cell volume, red blood cell count, haemoglobin and sedimentation rate among fish of not less than 140 g in weight were examined. A process of haemoconcentration during the spring and summer and one of haemodilution during the autumn and winter occurred. Data on accelerated sedimentation rates among diseased plaice are recorded.

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ON THE TOLERATION OF ANAEROBIC CONDITIONS BY *CALIGUS DIAPHANUS* NORDMANN

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Many free-living and parasitic invertebrates have been known to tolerate low oxygen tensions and anaerobic conditions. Von Brand (1946) who reviewed the extensive literature on anaerobiosis in invertebrates listed species of *Cyclops* which under experimental conditions could tolerate 2–18 h of anaerobiosis. Apart from this, few experimental studies have been made on anaerobiosis in copepods, especially the parasitic species. Availability of a number of live *Caligus diaphanus* at Plymouth made it possible to make a few preliminary observations on the behaviour of this copepod parasite under anaerobic conditions.

MATERIAL AND METHODS

Gurnards (*Trigla* sp.) examined at Plymouth, were found to be infected by *Caligus diaphanus* Nordmann, the parasite being usually found on the inner side of the operculum. Although over a hundred gurnards were examined it was possible to obtain only ten parasites.

Experimental anaerobic conditions were produced by bubbling oxygen-free nitrogen from a cylinder into sea water. The nitrogen was first passed through a wash-bottle containing alkaline-pyrogallol to remove any traces of oxygen. Estimations of dissolved oxygen using Winkler's method usually gave a value which was equivalent only to that found dissolved in the reagents. Bubbling nitrogen for 40 min usually produced very low oxygen tensions. Four parasites were transferred to a small glass-stoppered bottle (30 ml. capacity) and flushed with oxygen-free sea water under liquid paraffin. The glass stopper was inserted and smeared with stop-cock grease to prevent air leaking into the bottle. The bottles were immersed in a trough of water kept at room temperature (18° C). A similar number of animals in identical bottles with fresh sea water served as control.

C. diaphanus when left in fresh sea water usually attaches itself to the sides or to the bottom of the container. The urosome of the animal is usually slightly tilted at an angle and shows periodic movement. The thigmotactic behaviour of the parasite in remaining attached to the surface of the container was used as a measure of behaviour under low oxygen tensions. *Caligus* is

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also slightly transparent and the anal peristalsis could be easily observed in live animals. This was used as an indication of the recovery of these animals after transferring to fresh sea water from anaerobic conditions.

When exposed to anaerobic conditions, the animals usually become detached and lie inactive at the bottom of the container although anal peristalsis continues. Under anaerobic conditions the time taken by the animal to become detached varied from 10 min to 4 h. The results are tabulated in Table 1.

TABLE 1. TOLERATION OF ANAEROBIC CONDITIONS BY *CALIGUS DIAPHANUS*

Time of exposure of anaerobiosis	No. of animals		
	Active and attached	Moribund	Dead
10 min	4	—	—
10 min	4	—	—
20 min	4	—	—
30 min	2	—	—
30 min	4	—	—
45 min	—	4	—
1 h	—	2	2
1 h	4	—	—
1½ h	4	—	—
2 h	4	—	—
2 h	2	—	2
3 h	2	—	1
3 h	—	2	2
4 h	1	3	—
4 h	1	3	—
8 h	—	—	4
9 h	—	—	4

Note: Three types of reaction were used as arbitrary criteria in these experiments. (1) active and attached; (2) moribund, i.e. lying inert on the bottom but showing anal peristalsis. (3) dead, i.e. not reacting to mechanical stimuli. Four animals were used in each experiment; four animals in fresh sea water served as control.

TABLE 2. THE TIME TAKEN FOR RECOVERY OF *CALIGUS DIAPHANUS* AFTER A PERIOD OF ANAEROBIOSIS

No. of animals	Duration of anaerobiosis (h)	Time taken for complete recovery (min)
2*	3	2
1	3	4
1	3	2
2*	3	2
2	3	3
2	4	No recovery
1	4	15
2	4	15
2	4	10
2	8	20
1	9	30

Note. In a few instances owing to shortage of material, the same animals had to be used in more than one experiment. (These experiments are shown with an asterisk.) The use of the same animals did not cause any variation.

On transferring to fresh sea water over 60% of the parasites recovered. The time taken for complete recovery, i.e. for the animal which lies moribund to be attached again varied from 2 to 30 min, depending on the time of exposure to anaerobic conditions (Table 2). The animals under anaerobic conditions for 3 h recovered in 2–3 min, while animals exposed to similar conditions for 4 h recovered in 4–15 min. Prolonged exposure of 8 and 9 h duration (in two experiments) resulted in the animal recovering after a period of 20–30 min.

The results would tend to show that *C. diaphanus* is capable of enduring anaerobic conditions without apparent ill effects.

I wish to thank Prof. J. E. G. Raymont, Professor of Zoology, University of Southampton, for several valuable suggestions and the Director and Staff of the Marine Biological Laboratory, Plymouth, for all the facilities given while working there.

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ON THE PIGMENTS OF THE CHRYSOPHYCEAE

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(Text-figs. 1–3)

The colour of the chromoplasts in the Chrysophyceae varies from a greenish yellow to a golden brown. Klebs (1892) described this colour as being due to a special pigment which he called 'chrysochrom'. Gaidukov (1900) made an acetone extract of a dense bloom of *Chromulina rosanoffii* (Woronin, 1880) Bütschli, filtered from the tanks in the cold glasshouses of the Botanic Gardens in St Petersburg. He found a water soluble pigment which he called 'phycochrysin' together with 'chrysochlorophyll' and 'chrysoxanthophyll'. Most authors have since questioned the existence of special pigments in the Chrysophyceae (Fritsch, 1937; Smith, 1938). Carter, Heilbron & Lythgoe (1939) analysed extracts of an incrustation of *Apistonema carteri*, *Thallochrysis litoralis* and *Gleochrysis maritima* (identified by F. E. Fritsch) found on the chalk cliffs at Folkestone, and identified β-carotene, fucoxanthin and lutein, using calcium carbonate as adsorbent in their analysis. Heilbron (1942) later drew attention to the fact that these pigments are present in the Bacillariophyceae but not in the Xanthophyceae, throwing doubt on Pascher's view of the close relationship of all three groups. We now know that it is not lutein but diadinoxanthin that is present in the Bacillariophyceae (Strain, Manning & Hardin, 1944). Seybold, Egle & Hülsbruch (1941) then showed that the chlorophyll present in *Hydrurus foetidus* and *Chromulina rosanoffii* was chlorophyll *a*, apparently without other chlorophylls. Seybold (1941) has commented further on the singular occurrence and implications of chlorophyll *a* alone, and this has been recently discussed by Allen (1958). In recent years our knowledge of the pigments of the algae has been greatly advanced by Strain and his colleagues (Strain, 1958) but, while the pigments of the Xanthophyceae and Bacillariophyceae have been examined with the improved techniques now available (Pace, 1941; Strain, Manning & Hardin, 1943, 1944; Strain, 1958), those of the Chrysophyceae have not.

This paper does not represent a complete account of the pigments occurring in these organisms, but results presented here are of interest in view of the relationship of the Chrysophyceae with other algae.

METHOD AND MATERIAL

The pigments of eight species have been analysed. Unialgal cultures were grown for some weeks until a density sufficient to give good extracts was obtained. In most instances about 4–6 l. of culture after 6 weeks of (winter) growth was adequate. The organisms were centrifuged, treated with distilled water to extract any water-soluble pigments, recentrifuged and then extracted with acetone. The acetone extract was taken into light petroleum (B.P. 40–60°) and separated into epiphasic and hypophasic fractions with 90% methanol, the methanolic layer being twice extracted with light petroleum, and the petrol layer similarly extracted with 90% methanol. The hypophasic pigments were driven into diethyl ether by addition of water. Both phases were evaporated to dryness and redissolved in light petroleum. The epiphase was chromatographed on activated alumina or magnesium oxide, the column being developed by addition of acetone to the light petroleum. The hypophase was chromatographed on sugar (Tate and Lyle icing sugar containing 1½% calcium phosphate) and the column developed by dropwise addition of *n*-propanol to the light petroleum. The bands in each case were eluted and portions evaporated and redissolved in hexane and carbon disulphide (epiphasic) or ethanol and carbon disulphide (hypophasic) for examination in a Unicam S.P. 500 spectrophotometer. The chlorophylls were examined in light petroleum.

The following species from the Plymouth cultures have been examined:

	Plymouth no.
Pseudopedinella sp.	167
Phaeaster-type with haptonema	168
Pavlova gyrans Butcher	93
Isochrysis galbana Parke	I
Phaeocystis pouchetii-motile *Prymnesium* stage	147
Chrysochromulina ericina P. & M.	25
Dicrateria inornata Parke	B
Hymenomonas sp.	156

In addition, extracts of the diatom *Phaeodactylum tricornutum* Bohlin and of *Dunaliella tertiolecta* Butcher, a chlorophycean, were also analysed in the same manner to provide specimens of other xanthophylls for running mixed chromatograms with those of the Chrysophyceae.

RESULTS

Cultures of *Isochrysis galbana* were analysed on five or six different occasions and this species has been studied in more detail than the others.

In every species all the pigment was extractable by acetone and was soluble in light petroleum; no water-soluble pigments were found either on the preliminary treatment with distilled water, or when the hypophase was re-extracted with diethyl ether.

ISOCHRYSIS GALBANA

Epiphase

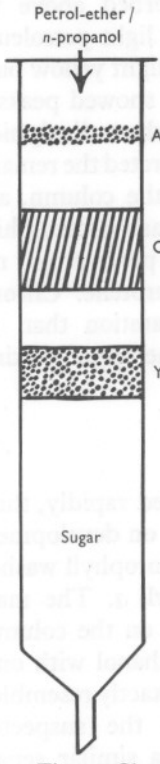
Careful development and slow elution of the bands formed on alumina or magnesium oxide showed that α-, β- and γ-carotenes were present. All the chlorophyll appeared to be chlorophyll *a*, strongly adsorbed above the carotenes and showing maxima at 430, 612 and 660 mμ in light petroleum. The addition of a trace of acetone to the developer caused a light yellow band to separate and move rapidly down the column. This band showed peaks at 445 and 474 mμ in hexane and 477 and 504 mμ in carbon disulphide, characteristic of α-carotene. Further addition of acetone separated the remaining carotene into a main orange band slowly passing down the column, and showing peaks at 451 and 478 mμ in hexane, 485 mμ in carbon disulphide (β-carotene), and a narrower red band above with the main peaks at 461 mμ in hexane and 496 mμ in carbon disluphide, resembling γ-carotene. Chromatography using magnesium oxide effected a better separation than on alumina, when both β-carotene and γ-carotene exhibited the upper maxima characteristic of these compounds.

Hypophase

If extraction and chromatographic analysis were performed rapidly, three yellow or orange bands were obtained on the sugar column on development with *n*-propanol: light petroleum mixtures (Fig. 1). Any chlorophyll washed through first; it always showed the spectrum of chlorophyll *a*. The main orange band resembled fucoxanthin in colour and position on the column, and in having a single absorption maximum (446 mμ) in ethanol with only a slight inflexion near 470 mμ. The suspected fucoxanthin exactly resembled that of *Phaeodactylum*, and a mixed chromatogram of the suspected fucoxanthin from *Isochrysis* and a specimen prepared by a similar separation on icing sugar of the xanthophylls of *Phaeodactylum* did not separate. The spectrum of each was similar (Fig. 2). The lower, yellow band could, from its spectrum, be either lutein or diadinoxanthin. A mixed chromatogram was run with a specimen of lutein prepared from *Dunaliella*, when the two pigments separated again on the column, indicating that the pigment was not lutein. When mixed with diadinoxanthin prepared from *Phaeodactylum*, however, no separation occurred when washed down a sugar column with the appropriate *n*-propanol:light petroleum mixture. The *Isochrysis* pigment also separated when run against violaxanthin from *Dunaliella*.

The two main xanthophylls of *Isochrysis* are, therefore, fucoxanthin (the main pigment) and diadinoxanthin (Fig. 3). The amber band above the fucoxanthin also exhibited a single broad peak in ethanol and was presumably an isomer (neofucoxanthin). If extraction and analysis extended over

a long period, an additional yellow band was sometimes obtained below the diadinoxanthin. This could, from its position on the column, be diatoxanthin, but its absorption spectrum and colour resembled diadinoxanthin and it probably represented an artifact.



	Absorption maxima (mμ)						Pigment
	In ethanol			In carbon disulphide			
Amber-yellow		445			475	504	neofucoxanthin
Orange		446			475	506	fucoxanthin
Yellow	425	445	476	442	474	506	diadinoxanthin

Fig. 1. Chromatographic separation of the hypophasic pigments of *Isochrysis*.

OTHER SPECIES

A similar analysis of the other species produced substantially the same chromatographic picture, though mixed chromatograms have not been run in every case. Chlorophyll *c* was not detected and chlorophyll *a* appeared to be the only chlorophyll present. In the hypophasic fraction of each the two main pigments were fucoxanthin and diadinoxanthin, the fucoxanthin showing maxima in ethanol:

448 mμ	from culture no. 167, 168
447 mμ	25, B
449 mμ	156

These maxima are lower than that found by Strain *et al.* (1944)—453 mμ—but the mixed chromatograms with *Phaeodactylum* fucoxanthin (447 mμ) suggest

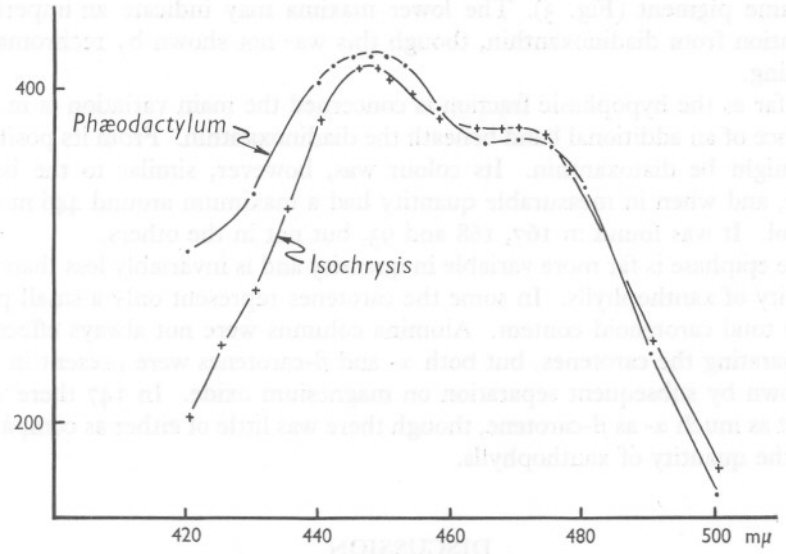


Fig. 2. Absorption spectra of fucoxanthin from *Phaeodactylum* and *Isochrysis* in ethanol.

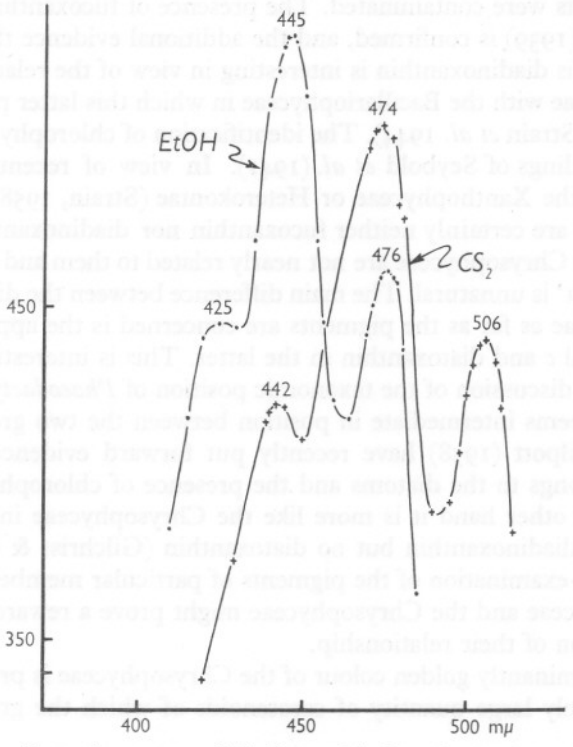


Fig. 3. Absorption spectra of diadinoxanthin from *Isochrysis* in ethanol and carbon disulphide.

the same pigment (Fig. 3). The lower maxima may indicate an imperfect separation from diadinoxanthin, though this was not shown by rechromatographing.

As far as the hypophasic fraction is concerned the main variation is in the presence of an additional band beneath the diadinoxanthin. From its position this might be diatoxanthin. Its colour was, however, similar to the band above, and when in measurable quantity had a maximum around 446 mμ in ethanol. It was found in 167, 168 and 93, but not in the others.

The epiphase is far more variable in quantity and is invariably less than the quantity of xanthophylls. In some the carotenes represent only a small part of the total carotenoid content. Alumina columns were not always effective in separating the carotenes, but both α- and β-carotenes were present in all, as shown by subsequent separation on magnesium oxide. In 147 there was almost as much α- as β-carotene, though there was little of either as compared with the quantity of xanthophylls.

DISCUSSION

No water-soluble pigments have been found and presumably Gaidukov's (1900) extracts were contaminated. The presence of fucoxanthin reported by Carter *et al.* (1939) is confirmed, and the additional evidence that the lutein-like pigment is diadinoxanthin is interesting in view of the relationship of the Chrysophyceae with the Bacillariophyceae in which this latter pigment is also to be found (Strain *et al.* 1944). The identification of chlorophyll *a* alone confirms the findings of Seybold *et al.* (1941). In view of recent work on the pigments of the Xanthophyceae or Heterokontae (Strain, 1958) in which the xanthophylls are certainly neither fucoxanthin nor diadinoxanthin, it would seem that the Chrysophyceae are not nearly related to them and that Pascher's 'Chrysophyta' is unnatural. The main difference between the diatoms and the Chrysophyceae as far as the pigments are concerned is the apparent absence of chlorophyll *c* and diatoxanthin in the latter. This is interesting in relation to the recent discussion of the taxonomic position of *Phaeodactylum* which in some ways seems intermediate in position between the two groups. Lewin, Lewin & Philpott (1958) have recently put forward evidence that *Phaeodactylum* belongs to the diatoms and the presence of chlorophyll *c* confirms this. On the other hand it is more like the Chrysophyceae in having fucoxanthin and diadinoxanthin but no diatoxanthin (Gilchrist & Green, 1960). A detailed re-examination of the pigments of particular members of both the Bacillariophyceae and the Chrysophyceae might prove a rewarding study for the elucidation of their relationship.

The predominantly golden colour of the Chrysophyceae is presumably due to the relatively large quantity of carotenoids of which the greater part are xanthophylls.

I am most grateful to Dr M. Parke for culturing the algae for me at the Plymouth Laboratory, and I also wish to thank Dr B. M. Gilchrist of Bedford College for kindly providing the cultures of *Phaeodactylum* and *Dunaliella*.

SUMMARY

No special pigments have been found in any of the marine Chrysophyceae examined. In all species the only chlorophyll identified was chlorophyll *a*. The carotenes represent a much smaller part of the total carotenoids than the xanthophylls, and the amount varies greatly from one species to another, perhaps accounting for their variable colour. α-Carotene represents a large proportion of the carotenes; γ-carotene was identified only in *Isochrysis galbana*. Fucoxanthin and diadinoxanthin represent the main xanthophylls.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ATKINS, D., 1959. The growth stages of the lophophore and loop of the brachiopod *Terebratalia transversa* (Sowerby). *J. Morph.*, Vol. 105, pp. 401–26.

The growth stages of the lophophore and loop from the early schizolophe to the adult plectolophe are described for the first time. The descending branches of the loop grow from both crura and septum to meet and fuse; the bearing of this on the taxonomic position of the species is discussed. Characteristic of the early growth stages is the presence of conspicuous flanges on the hood: these gradually become reduced in size and disappear about the time the ascending branches become free from the septum. The flanges are compared with accessory brachial structures in other terebratellaceans. The structure of the adult lophophore is described. The ciliary feeding mechanism is essentially similar to that already described by the author in other brachiopods with plectolophous lophophores.

D. A.

BONE, Q., 1959. The central nervous system in larval acraniates. *Quart. J. micr. Sci.*, Vol. 100, pp. 509–27.

A part of the organization of the spinal cord of acraniate larvae is described, chief attention being directed toward those tracts and cell groups which are probably concerned with the control of the swimming pattern. The first section deals with the arrangement of the fibre tracts in the cord, and of the cell bodies giving rise to these fibres. The form and connexions of the giant Rohde cells are then described, it is shown that these cells possess peripheral processes passing out of the dorsal root nerves, and are thus similar to the Rohon-Beard cells of craniate embryos. It is concluded that at present, it is not safe to homologize these two cell types, for the acraniate Rohde cells differ in several respects from the craniate Rohon-Beard cells. The innervation of the gill musculature is described, it is shown that it is asymmetrical, and that this asymmetry is not related to changes in symmetry at metamorphosis.

Finally, the arrangement of the whole system is discussed in relation to the systems found in the larval stages of primitive craniates.

Q. B.

CARLISLE, D. B., 1960. Sexual differentiation in Crustacea Malacostraca. *Mem. Soc. Endocrin.*, Vol. 7, pp. 9–15.

A summary of the present state of our knowledge of the endocrine control of sexual differentiation in the higher Crustacea, drawing attention to the role of the vas deferens gland and the X organ–sinus gland complex. The paper includes a classification and terminology of the various types of successive hermaphroditism.

D. B. C.

JEWELL, B. R., 1959. The nature of the phasic and the tonic responses of the anterior byssal retractor muscle of *Mytilus*. *J. Physiol.*, Vol. 149, pp. 154–77.

In this paper a further attempt has been made to elucidate the nature of the phasic and the tonic responses that are produced by many lamellibranch muscles. Experiments involving release techniques have shown that two quite distinct states of contraction are possible in the anterior byssal retractor muscle of *Mytilus*: there is an

'active' state which bears a strong qualitative resemblance to that found in vertebrate skeletal muscle, and a 'fused' state which appears to be peculiar to lamellibranch muscle in that it allows considerable tensions to be maintained with a very low expenditure of energy. A theory has been put forward in which it is postulated that all types of excitatory stimuli produce an 'active' state which gives way to a 'fused' state when stimulation ceases, and it is supposed that inhibitory stimuli act by abolishing the 'fused' state. By means of this hypothesis it is possible to explain many of the curious properties that are characteristic of lamellibranch muscle. B. R. J.

JONES, W. C., 1959. Spicule growth rates in *Leucosolenia variabilis*. *Quart. J. micr. Sci.*, Vol. 100, pp. 557–70.

The growth of triradiate spicules was investigated by photographing at intervals three pieces of the wall of the oscular tubes. The basal rays grew faster than the paired rays at first, but for both types of ray the growth rate increased to a steady level as the rays lengthened. When their length exceeded 25 μ, the basal and paired rays grew at similar rates, regardless of the different relationships between the axis of the rays and the orientation of the optic axis of the mineral constituent. The average rates for rays exceeding 25 μ on the three pieces were respectively 2·50 (18–21° C), 1·64 (18° C) and 1·29 (17° C) μ per hour. W. C. J.

NICHOLS, D., 1959. The histology and activities of the tube-feet of *Echinocyamus pusillus*. *Quart. J. micr. Sci.*, Vol. 100, pp. 539–55.

The histological structure of the tube-feet of this clypeasteroid sea-urchin is interpreted functionally. Each suckered tube-foot possesses a special set of levator muscles within its lumen to raise the centre of the disk for attachment. The disk is probably raised further by contraction of a ring of short muscles embedded in the disk itself; these muscles are also active in detachment, pulling the edge of the disk away from the substratum relative to the disk centre. There are four columns of retractor muscles in the tube-foot stem for postural movement. The buccal sensory tube-feet have a ring of cilia, probably tactile, round the edge of the disc and a nervous pad, probably chemoreceptive, in its centre. Circulation of oxygenated water round the respiratory tube-feet is maintained by patches of external cilia and the tall thin shape is maintained by cross-connexion internally. D. N.

WELLS, G. P., 1960. The genera of Arenicolidae (Polychaeta). *Proc. zool. Soc. Lond.*, Vol. 133, pp. 301–14.

It is argued that the species currently grouped as *Arenicola* Lamarck should be distributed between *Arenicola*, *Arenicolides* Mesnil and *Abarenicola* gen.nov. Formal diagnoses of the family and its constituent genera are given and suggestions are made as to the most convenient characters for referring arenicolid worms to their genera. The forms found at Plymouth are *Arenicola marina*, *Arenicolides ecaudata* and *Arenicolides branchialis*. G. P. W.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1959–60

The Association was greatly honoured on 18 March 1960 by a visit to the Plymouth laboratory of our Patron, H.R.H. The Duke of Edinburgh. His Royal Highness spent over an hour in the laboratory and aquarium, and met members of the staff and visiting research workers. The President and Honorary Treasurer were present for the occasion.

The Council have to report with regret the death of Dr W. R. G. Atkins, C.B.E., F.R.S., who was Head of the Department of General Physiology at the Plymouth laboratory from 1921 to 1955. During these years Dr Atkins laid the foundations of much of our present knowledge of the chemistry and physics of the sea and brought international renown to the Plymouth laboratory.

The Council and Officers

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

The Plymouth Laboratory

During the year a small wooden building was erected on the reservoir roof in the space between the lavatories and the porch of the door into the north building. This is to house subaqua diving equipment, which is now much in use. Two windows have been enlarged and a new window built in the lavatories.

The internal decoration of the south building has been completed, and the outside woodwork and chuting of the north wall repaired and repainted.

Laboratory Extension

The Council are pleased to report that H.M. Treasury have sanctioned a grant to meet the cost of an extension to the Plymouth laboratory. The north building will be extended and consist of cellars for experimental work, physiological laboratories on the ground floor, and chemical laboratories on the first floor. The north and south buildings will be joined by an extension having a lecture hall on the ground floor and botanical laboratories on the first floor. It is hoped that building will begin at the end of April 1960.

Aquarium

The new aquarium was officially opened on 30 June 1959 by the Lord Mayor of Plymouth, Councillor P. N. Washbourn, who cut a strand of sea-weed with a pair of silver grape scissors presented by the Architects.

The aquarium was designed by our architect, Mr F. L. Preston, F.R.I.B.A., of Messrs Easton & Robertson, Cusdin, Preston and Smith, London, from original plans and ideas supplied by Dr D. P. Wilson. It was built by Messrs John Garrett & Son, Ltd., Builders, of Plymouth, and the rockwork was designed and carried out by Mr H. R. Allen, A.R.C.A., of Westerham. The whole construction has been most successful and is much appreciated by the public.

The new aquarium differs radically from the old, is pleasingly proportioned and much better lit. Quietness is ensured by an acoustically tiled ceiling. Tanks extend part-way along both north and south walls, somewhat as before, but they are of equal depth from back to front so that the row of pillars supporting the floor above is now centrally placed. A very large tank at the east end occupies the whole width of the room, with alcoves between it and the eastern ends of the north and south rows of tanks. The north alcove contains one small tank and the south alcove a small tank and an emergency exit. As viewed from the public entrance the three windows of the big tank complete an attractive vista.

The new tanks, of which there are eighteen, vary in size from very large to very small. With the exception of the three smallest none is rectangular, side walls being set at 45° so that tanks wider behind than in front alternate with triangular tanks. This is the arrangement first suggested by J. Garnaud in 1952 and subsequently carried out in the aquarium of the Institute of Oceanography at Monaco. The tanks are of reinforced concrete with slate inserts framing the window openings, which are mostly a foot wider than in the old aquarium. Lintel walk-ways and catwalks above the tanks hidden from public view greatly facilitate servicing. The sea water mains are of black polythene and the flow is regulated with 'Saunders' diaphragm valves with polythene bodies. Inflowing water enters the tanks at concealed positions and emerges at the bottom. Overflow pipes of asbestos are cast in the thickness of the walls and drain off surface water. Compressed air is used to increase water movement within the larger tanks and to give a rippled surface with resulting pleasing play of light and shadow over the bottom. Removable partitions between the largest tanks will allow fish to be diverted from one tank to another during major cleaning operations. Electric lighting is used, and almost all daylight is excluded. There are special arrangements for ventilating the public hall. These are but few of the new features which will be described in detail in a future number of the *Journal*.

The Council wish to record their appreciation of the very valuable assistance given by Dr D. P. Wilson who spent so much time and thought in seeing the work through to completion from his original ideas. The Council also wish to thank those members of the Plymouth laboratory staff who gave special technical assistance, especially Mr A. N. Bennett, Mr F. G. C. Ryder and Mr F. J. Warren.

Research Ships

Apart from normal overhauls the three research vessels R.V. 'Sarsia', R.V. 'Sula' and M.V. 'Gammarus' have operated regularly throughout the year.

Ray Lankester Investigator

The Council have pleasure in reporting that Prof. J. E. Smith, F.R.S., has been appointed Ray Lankester Investigator to work at the Plymouth laboratory in 1960.

Grant for Flagellate Research

The Council are pleased to report that H.M. Treasury have sanctioned a grant to the Association to enable a cytologist to assist in the research on marine flagellates with the electron microscope which is being done in Prof. Irene Manton's department at Leeds University in collaboration with Dr Mary Parke. Dr G. F. Leedale has been appointed for this purpose as from 1 October 1959 and seconded to work at Leeds.

Staff

Mr J. V. Howarth joined the staff of the Plymouth laboratory as Senior Scientific Officer on 1 April 1959.

Dr L. H. N. Cooper attended the International Oceanographic Congress in New York in September 1959 and the meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1959.

Dr Mary Parke attended the Ninth International Congress of Botany in Montreal in August 1959 and the International Oceanographic Congress in New York in September 1959.

Dr E. J. Denton attended the International Oceanographic Congress in New York in September 1959.

Dr D. B. Carlisle worked during September 1959 at the Kristinebergs Zoologisk Station in Sweden and attended the meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1959.

Dr T. I. Shaw and Dr G. W. Bryan attended the Meeting of the International Atomic Energy Agency and U.N.E.S.C.O. Conference on the Disposal of Radioactive Wastes held in Monaco in November 1959.

Occupation of Tables

The following one hundred and forty-one workers have occupied tables at the Plymouth Laboratory during the year.

Miss M. N. E. Adams, Kingston-upon-Thames (Library).
E. Adams, Plymouth (Library).
Dr J. S. Alexandrowicz, Plymouth (Nervous system of invertebrates).
S. R. Armstrong, Bryanston (Molluscs).
D. C. Arnold, Swansea (Library).
Dr Daphne Atkins, Plymouth (Brachiopods).
W. J. Ballantine, D.S.I.R., London (Ecology of limpets).
Dr P. R. O. Barnett, Southampton and Millport (Bottom copepods).
Prof. E. J. W. Barrington, Nottingham (Histochemistry of *Amphioxus* and tunicates).
E. R. B. Bernabe, Manila (Plankton).
Dr Anna M. Bidder, Cambridge (Cranchid histology).
Dr G. T. Boalch, International Paints Research Fellow (Effects of toxic substances on algae).
Dr A. D. Boney, Plymouth (Ecology of red algae).
J. Bracken, Dublin (S. Ireland herring fishery).
M. C. Brown, London (Library).
Dr Eleanor M. Brown, London (Plankton).
Dr P. C. J. Brunet, Oxford (Biochemistry of dogfish egg-capsule).
Prof. W. D. Burbanck, Woods Hole (Ecology of *Cyathura*).
A. C. Burd, Lowestoft (S. Ireland herring fishery).
B. M. H. Bush, Cambridge (Crustacean neuro-muscular physiology).
Miss J. G. Caldwell, Yale (Crustacea).
Dr P. C. Caldwell, Alan Johnston, Lawrence and Mosely Research Fellow of the Royal Society (Muscle and nerve physiology).
Dr Phoebe Caldwell, Plymouth (Library).
Dr M. R. Clarke, N.I.O. Wormley (Testing otter boards).
Miss E. Clay, Brixham (Library).
J. W. Coles, London (Shore collecting).
D. A. Conroy, Berkhamsted (Library).
C. A. Cosway, Torquay (Library).
Miss A. C. Coupland, Birmingham (Trematode parasites).
Dr C. B. Cowey, Shinfield (Vitamin B_{12} in sea water).
J. W. Cowie, Bristol (Submarine geology).
W. D. G. Cox, Chichester (Library).
Dr A. B. Cribb, Brisbane (Algal taxonomy and ecology).
Dr D. J. Crisp, Anglesey (General).
D. Curry, Bristol (Submarine geology).
Dr K. W. Daisley, Shinfield (Vitamin B_{12} in sea water).
Dr R. Phillips Dales, London (*Spirographis*).
Mrs M. Phillips Dales, London (*Spirographis*).
F. W. Darwin, Cambridge (Gastropod osphradia).
Dr G. B. David, Cardiff (Library).
J. B. Davies, Oxford (General).
Dr Elizabeth J. Dimelow, New Brunswick (Biology of *Antedon*).
L. A. W. Downer, Tavistock (Library).
J. H. Elgood, Rustington (Library).

D. J. ELLETT, Lowestoft (S. Ireland herring fishery).
Mrs JOY ETHERINGTON, London (*Ectocarpus*).
D. ETHERINGTON, London (*Phascolion*).
Dr L. R. FISHER, Shinfield (Pigments of invertebrate eyes).
I. H. FORD, Bristol (Submarine geology).
Mrs J. D. FREEMAN, London (Digenetic trematodes).
R. F. H. FREEMAN, London (Metabolism of *Scrobicularia*).
DR VERA FRETTER, Reading (Prosobranch molluscs).
Dr I. FRIEDMANN, Leeds (Ecology of *Prasicola stipitata*).
Prof. A. C. GIESE, U.S.A. (Constituents of tissues of echinoderms).
K. R. GILL, Cambridge (Magnetic survey of W. Approaches).
Dr J. B. GILPIN-BROWN, Plymouth (Biology of nereids; cuttlefish).
D. R. GLASSON, Cambridge (Magnetic survey of W. Approaches).
Dr I. M. GOODBODY, Jamaica (Digestion in ascidians).
Prof. A. GRAHAM, Reading (Prosobranch molluscs).
P. J. M. GREENDALE, Exeter (Library).
D. N. F. HALL, Colonial Office (Indo-west Pacific Penaeidae).
Dr Y. HANEDA, Yokosuka (Bioluminescence).
EIJI HARADA, Kyoto (Crustacean larvae).
M. G. HARDY, Reading (Histology of lamellibranchs).
Prof. J. E. HARRIS, F.R.S., Bristol (Vertical migration of plankton).
J. W. HARRISON, Cambridge (Magnetic survey of W. Approaches).
Dr H. W. HARVEY, F.R.S., Plymouth (Productivity of sea water).
B. T. HEPPER, Conway (Lobster marking).
Dr M. N. HILL, Cambridge (Magnetic survey of W. Approaches).
Dr J. A. HINKE, London (Squid axons).
Prof. A. L. HODGKIN, F.R.S., Cambridge (Physiology of squid giant axons).
Dr G. M. HUGHES, Cambridge (Gill structure of fishes).
D. J. HUME, Teignmouth (Library).
O. D. HUNT, Newton Ferrers (Library).
B. L. JAMES, Aberystwyth (Trematode parasites of gastropods).
Dr C. H. JELLARD, Plymouth (Library).
Dr PENELOPE M. JENKIN, Bristol (Library).
Dr N. G. JERLOV, Göteborg (Light penetration in sea).
Dr G. Y. KENNEDY, Sheffield (Chlorophyll pigments).
Dr A. K. KENT, London (Teleost colour changes).
Mrs R. S. M. KENT, London (Uptake of 'thoroplast').
Dr R. D. KEYNES, F.R.S., Cambridge (Physiology of squid giant axons).
Dr H. G. KLEMPERER, London (Iodine metabolism of algae).
Sir FRANCIS G. W. KNOWLES, Birmingham (Crustacean endocrinology).
Dr S. K. KON, Shinfield (Pigment of invertebrate eyes).
Dr S. KRISHNASWAMY, Southampton (Fat content of plankton).
Dr MARIE V. LEBOUR, Plymouth (Decapod larvae).
J. G. E. LEWIS, London (Distribution and reproduction of *Scolioplanes*).
Dr J. LLEWELLYN, Birmingham (Trematode parasites of fishes).
Miss R. D. LONG, Plymouth (Library).
Prof. O. E. LOWENSTEIN, F.R.S., Birmingham (Central nervous responses in elasmobranchs).
M. J. MANN, Lagos (Library).
Prof. IRENE MANTON, Leeds (Library).
Dr SHEINA M. MARSHALL, Millport (Respiration of *Calanus*).

A. L. MARTIN, London (Library).
M. H. MARTIN, Looe (Library).
Miss H. F. MAUNSELL, D.S.I.R., Oxford (Crustacean endocrines).
R. MAYNE, Plymouth (Library).
Dr FRANCES M. MOLLOY, Rothamsted (Digestion in mysids).
Dr J. E. MORTON, London (Molluscs).
Dr R. W. MURRAY, Birmingham (Neurophysiology and body fluids of elasmobranchs).
H. MUTVEI, Stockholm (Molluscs).
Prof. G. E. NEWELL, London (Library).
Dr D. NICHOLS, Oxford (Histology of holothurians).
A. M. OLSEN, Hobart (Library).
Dr A. P. ORR, Millport (Respiration of *Calanus*).
K. H. PALMORK, Bergen (Chemistry of sea water).
Dr K. PAMPAPATHI-RAO, India (Sensory physiology of rays).
Prof. C. F. A. PANTIN, F.R.S., Cambridge (*Hydratuba*).
C. J. PENNYCUICK, Cambridge (Physiology of dogfish locomotion).
Dr W. T. W. POTTS, Birmingham (Body fluids of elasmobranchs).
B. L. POWELL, Swansea (*Carcinus* endocrine organs).
Cdr. C. F. B. POWELL, R.N. (Rtd.), Plymouth (Library).
M. QUICK, Bristol (Submarine geology).
A. M. QURESHY, London (Haemogregarines of fishes).
Prof. J. E. G. RAYMONT, Southampton (Fat content in marine plankton).
Dr W. J. REES, British Museum (*Stygiomedusa*).
D. J. ROWLANDS, London (General).
D. J. SCARRATT, D.S.I.R. (Fauna of *Laminaria* holdfasts).
Miss J. M. SHEPHARD, London (Polyzoa).
J. SHIELDS, Southampton (Effects of metals upon marine organisms).
Prof. J. E. SMITH, F.R.S., Ray Lankester Investigator, London (Nervous system of *Echinus*).
Dr EVE C. SOUTHWARD, Plymouth (Pogonophora; polychaetes).
B. W. P. SPARROW, Newton Ferrers (Library).
Miss F. A. STANBURY, Plymouth (*Cladophora*).
O. SUDDABY, Plymouth (Library).
Dr MURIEL F. SUTTON, London (Ascidians).
M. E. U. TAYLOR, Lowestoft (S. Ireland herring fishery).
Dr K. K. TIWARI, Calcutta (General).
R. VAISSIÈRE, Algiers (Deep-water copepods).
Dr H. G. VEVERS, London (General).
Miss J. D. WADDLE, London (General).
G. E. WALSTER, Plymouth (Glycolysis in *Maia*).
Miss B. V. WARNE, Stafford (General).
Prof. T. H. WATERMAN, Yale (Crustacean physiology).
Dr J. O. WERSÄLL, Stockholm (Innervation of hair cells of elasmobranchs).
Prof. W. F. WHITTARD, F.R.S., Bristol (Submarine geology).
J. H. WICKSTEAD, Colonial Office (Tropical plankton).
Dr H. H. WILLIAMS, Aberystwyth (Helminth parasites of elasmobranchs).
Dr S. E. WILSON, London (Feeding habits of *Teredo*).
R. C. WOLEDGE, London (Muscle physiology).

Among the many other scientists who have visited Plymouth during the year to see the general work of the laboratory and to discuss problems with

members of the scientific staff, the following have come from overseas: Prof. S. D. Gerking (U.S.A.), D. E. Kurth (Australia), Miss B. A. Lewis (Pakistan), Dr Howard S. Mason (U.S.A.), Dr M. J. Cohen (U.S.A.), J. Hamre (Bergen), Dr I. D. Hiscock (Queensland), Dr Chas. C. Davis (U.S.A.), Dr Mary A. Pocock (S. Africa), Dr M. M. Vaskesaeger (Belgium), Dr L. P. Sayles (U.S.A.), Dr D. S. Rawson (Canada), Prof. F. Crescitelli (U.S.A.), Dr S. Uyeda (Japan), J. Phipps (Sierra Leone), Prof. A. von Muralt (Switzerland), Dr A. M. Shanes (U.S.A.), Prof. F. A. Brown (U.S.A.), Prof. M. Uda (Japan), Dr W. Wieser (Austria), Dr A. J. Kohn (U.S.A.), Miss P. McDonald (Sydney), Dr G. M. Moore (U.S.A.), Dr D. Davenport (U.S.A.), Prof. A. Barash (Israel), Nezihe Öztan (Turkey), P. de Wolf (Holland), Prof. A. Fleckenstein (Germany), B. Carlburg (Sweden), M. Waldichuk (Canada), Prof. E. R. Noble (U.S.A.), Prof. G. A. Knox (New Zealand), A. A. Mills (Canada), Dr G. F. Humphrey (Australia).

On 8 and 9 May a meeting of members of the Photobiology Group was held at the Plymouth laboratory. Papers were given by members of the staff and fourteen members of the group came to the laboratory for the meeting.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin and were attended by thirty-nine students from the following Universities: Oxford, Cambridge, Reading, Exeter, Aberystwyth, Southampton, London, Sheffield, Glasgow, Swansea, Leicester, Durham, Newcastle, Cambridge Technical College and Regent Street Polytechnic.

Also during the Easter Vacation Mr J. Peirson brought a party of three boys from Rugby School and during the Summer Vacation Miss M. Christianson brought a party of six girls from Harrow County Girls' School.

Scientific Work of the Plymouth Laboratory Staff

Sea Water and Plankton

The I.G.Y. cruise in November 1958, to the Gulf of Gibraltar by R.R.S. 'Discovery II', was staffed by an international team of nine scientists including Dr L. H. N. Cooper and Mr E. I. Butler from the Plymouth Laboratory. The purpose was to study in detail the manner of the outflow of the Mediterranean water and of its admixture with North Atlantic water. In addition to temperature measurements, more than 5000 chemical analyses on samples drawn from a grid of over 100 stations were made, followed at once by dynamic calculations. With this knowledge and with a chart of the echo-soundings obtained it was possible to place neutral buoyancy floats in positions where they could yield information of maximum value. Four laboratories are involved and working up is not complete. The most striking feature was a large eddy at 1250 m in the mixed Mediterranean–Atlantic water. The deep phosphate measurements combined with those of U.S.S. 'Crawford' promise evidence about the deep circulation. The cruise provided an opportunity to

compare equipment and methods, particularly for oxygen determinations. Three standards on board for standardising thiosulphate did not give similar results. The issue was referred to Mr F. A. J. Armstrong who was able to show that dichromate, as used in one of the methods, is an unsatisfactory standard.

At the International Oceanographic Congress in New York Dr Cooper presented a paper based on work on R.V. 'Sarsia' and R.R.S. 'Discovery II' in 1958 in the northern Bay of Biscay in association with the I.G.Y. The main, but tentative, conclusion was that the deep ocean is filled not by water of steadily increasing density but by a series of strata, each of which is in neutral adiabatic equilibrium. Separating these 'resident water masses', there seem to be thin discontinuity layers within which density increases rapidly. These discontinuity layers, thin though they are, seem to have a strongly laminated structure, attributed to their possible origin as extension plates derived from boluses which have descended along the eastern face of the Reykjanes Ridge from the Iceland–Faeroe Ridge. Some consequences of this structure were presented.

He has also worked up the hydrographical observations made in the Celtic Sea in 1950 by R.V. 'Sir Lancelot', R.V. 'Sabella' and R.R.S. 'Discovery II'. Once the summer thermocline has been strongly developed, it seems that recruitment of new water into the English Channel comes only from thermocline level (25–45 m) west of Ushant. The waters from above and below the thermocline did not enter the Channel, neither in high summer did water from the westward. This agrees with Dr F. S. Russell's earlier deductions from biological indicators. This mechanism explains about one-half the loss in phosphate which water undergoes on passage from the Bay of Biscay into the English Channel. A more detailed understanding of the movement and nature of the waters in the Northern Celtic Sea and Bristol Channel has also been achieved.

Dr T. I. Shaw has started some experimental studies upon the state of iodine in sea water in order to examine the hypothesis put forward by him and Dr L. H. N. Cooper (*Nature, Lond.*, Vol. 180, p. 250) that the oxidized form of iodine in sea water is hypoiodous acid rather than iodate. Preliminary results show that only a part of any carrier-free ^{131}I, added as iodide to sea water, is precipitable by silver ions; the addition of inactive iodate does not affect the amount of precipitable activity but the addition of either inactive iodide or a reducing agent such as sulphite render almost all the activity precipitable. These observations confirm that part of the iodine in sea water is in an oxidized form and indicate that this form, unlike iodate, is capable of rapidly exchanging its iodine atom with iodide.

Mr F. A. J. Armstrong and Mr E. I. Butler have continued the monthly cruises to the International Hydrographic Station E 1. The results of analyses in 1958 have been prepared for publication in the *Journal*. In 1959 the

monthly observations have been supplemented by two surveys (in January and in June) of the area surrounding the station, in an attempt to discover the immediate causes of the rather sudden changes which occur from time to time at E 1. In January some quite marked boundaries were found, near E 1, which was seen to be in the narrow part of a tongue of low salinity water of high phosphate and silicate content, which projected from Plymouth in a south-east direction for at least 50 miles into the Channel. In June, no such tongue was seen, but there was an interesting gradation from west to east with falling surface temperature and rising thermocline as vertical mixing increased. On neither occasion could it be said that conditions at E 1 were typical of the area off Plymouth.

In association with Dr G. T. Boalch, International Paints Research Fellow, Mr Armstrong has made measurements of the ultra-violet absorption of sea water samples. Small but significant increases in the 200–250 mμ region have been found in the spring, but the large absorption of the inorganic salts in this region makes the work difficult. During attempts to accentuate small differences by concentrating the water it was found that when sea water is distilled the distillate has a higher ultra violet absorption than has pure distilled water. The first 10% may have an absorbancy of 0·1–0·4 in a 10 cm cuvette at 200 mμ, and has a marked 'weedy' smell. There appears to be a seasonal variation with maximum values in late summer. The nature of this volatile material is not yet known. The weedy odour suggested the presence of dimethyl sulphide (which is known to be evolved by *Polysiphonia* and *Enteromorpha*) and in fact organic sulphides have been detected in those distillates from sea water, in quantities equivalent to about 1 μg S per litre. There is reason to associate these sulphides with the phytoplankton and indeed they have been found in considerably larger amount in a culture of *Phaeodactylum*. However, they can account for only a very small fraction of the volatile material.

With the co-operation of Mr E. I. Butler monthly samples of sea water have been taken again this year at stations L 2–L 6 and E 1 (surface to 70 m) for the examination of the nanoplankton by Dr Mary Parke and Miss I. M. Adams. The records of the organisms developing in temporary cultures set up from these samples now cover a period of 2 years and they are being tabulated to assess the information obtained by this study. A number of new interesting forms have been isolated during the year from these samples including an organism which so far cannot be placed with certainty in any algal class. Prof. I. Manton (electron microscopy), Dr G. Y. Kennedy (pigments), Dr M. R. Droop (growth requirements) and Mr J. Dodge (cytology) are co-operating in the study of this organism.

Valuable information is also being accumulated by Dr Parke and Miss Adams on the life histories of a number of organisms in the Plymouth collection. It is now known that the recently described coccolithophorid

Crystallolithus hyalinus, two strains of which were successfully isolated last year and which is similar to the genus *Chrysochromulina*, except that it has a deposit of calcite crystals on its scales, is the motile stage in the life history of the well-known non-motile coccolithophorid *Coccolithus pelagicus*. This finding is of extreme importance from the point of view of the classification of the Coccolithophoridaceae. The system of classification developed recently in which two main series are separated, i.e. organisms bearing holococcoliths and organisms bearing heterococcoliths, will have to be abandoned, since both types (holococcoliths on *Crystallolithus hyalinus* and heterococcoliths on *Coccolithus pelagicus*) can be found on different stages in the life history of one organism. Another organism of the *Crystallolithus* type, probably the motile stage of another well-known coccolithophorid, has just been isolated for the study of its non-motile phases.

It has also been found that the organism *Pleurochrysis scherffelii* must be placed in the Coccolithophoridaceae since both motile and non-motile stages become covered by coccoliths and the motile stage bears, in addition to two acronematic flagella, a very short haptonema.

Knowledge concerning the problematic genus *Ochrosphaera* has also been considerably increased during the past year. Previously it was considered to have an *Ochromonas*-type motile stage, but it has now been shown that the motile stage of the type species, *O. neapolitana*, is covered by scales and has two acronematic flagella as do other motile coccolithophorid stages. Interesting cyst stages of this organism have also developed in culture, the structure of which may help in the understanding of some recent and fossil cyst forms placed in the families Thoracosphaeridae and Discoasteridae as the organisms which produced them were unknown. Recently Mr W. J. Ballantine of Queen Mary College, London, drew our attention to a brown symbiont in the ciliate *Urceolaria patellae* (Cuénot) living on the pallial gills of *Patella aspera*. By culturing the symbiont it has been shown to be a stage in the life history of an *Ochrosphaera* species, probably *O. neapolitana*.

Work has also continued on the isolation and culturing of *Phaeocystis* type colonies and it has now been proved that the commonly occurring *P. pouchetii* has two types of motile phase, structurally different, in its life history. Cultures of *Phaeocystis* colonies have also been sent to Prof. J. McN. Sieburth of the Department of Veterinary Science, Virginia Polytechnic Institute, U.S.A., to be used in connexion with his work on antibacterial activity in the gastro-intestinal tract of penguins, since the activity is thought to be caused by *Phaeocystis*.

Dr F. S. Russell has continued the preparation of a monograph on British scyphomedusae. He has now completed the Coronatae, of which seven species are known to occur in deep water west of the British Isles. On a cruise in October 1959 to the Bay of Biscay R.V. 'Sarsia' collected a very large deep-sea scyphomedusa in a deep-water haul off Santander. This has proved to

be a new genus and species and Dr Russell has published a preliminary note in *Nature* giving the medusa the name *Stygiomedusa fabulosa*. The most striking feature is that it is viviparous. The medusa, which is about 50 cm in diameter, has attached capsules from which perfectly developed young hatch which are already about 10 cm in diameter. A detailed description is being prepared in collaboration with Dr W. J. Rees of the British Museum (Nat. Hist.).

Dr E. D. S. Corner has begun an investigation of the nutrition of the copepod *Calanus helgolandicus*. An apparatus has been constructed in which up to 300 animals can be kept for several days under a continuous flow of 'outside' sea water; and the quantities of food which they remove has been estimated from analyses of the changing amounts of suspended organic matter in the medium. Initial experiments have shown that the quantities of carbohydrates, protein and fat assimilated daily by the animals from 'outside' sea water are more than enough to account for their respiration rate. However, *Calanus* kept under these conditions showed no increase in weight, nor were they able to survive for more than 5–6 days. Accordingly, further experiments are planned in which the animals will be allowed to feed in sea water to which varying amounts of different species of diatoms have been added.

Dr A. J. Southward has continued investigations on the distribution of zooplankton 'indicator' species in the western Channel by means of high-speed samplers. The area surveyed has been extended to include parts of the Bristol Channel and north Celtic Sea in order to study macroplankton resembling that found off Plymouth before 1930. Samples taken by the research vessels 'Sir Lancelot' and 'Anton Dohrn' have been examined as well as standard ring trawl hauls taken in earlier years by R.V. 'Sarsia'. A preliminary account of the work is being prepared and it is hoped to present an explanation of the faunistic and other changes that have taken place in the area since the 1900's.

Macro-fauna and Flora

Dr Parke has published 'Corrections and Additions III' to the 'Check-list of British Marine Algae' in the *British Phycological Bulletin*, No. 7.

The fine spring, summer and autumn of 1959, following a mild winter, has had marked effects on the abundance of intertidal barnacles. Dr A. J. Southward has found that the northern species, *Balanus balanoides*, has declined, the new generation having failed to settle or survive. In contrast, extensive early settlements of the southern form, *Chthamalus stellatus*, occurred at all stations examined, and the young specimens showed a high rate of growth. Work on cirral activity of barnacles has been continued: valuable ciné records of the large species, *Balanus hameri*, were obtained during a visit to the Marine Biological Station, Port Erin. In collaboration with Dr D. J. Crisp, Dr Southward has published a note, in Vol. 38, No. 3 of the *Journal*, on the further spread of the immigrant Australasian barnacle,

Elminius modestus, in the British Isles, based on surveys made up to the spring of 1959. A joint account of recent changes in the distribution of marine organisms in north-west Europe was prepared for the International Oceanographic Congress in New York, where it was read by Dr Crisp.

Dr D. P. Wilson has prepared for publication in Vol. 38, No. 3, of the *Journal* an account of another new species of the polychaete genus *Magelona* and has named the new worm *filiformis*. It was first found in 1939 at Mill Bay, Salcombe, in silty sand near low-water mark associated with *M. papillicornis*. Although still fairly common it appears to be now less abundant than when first found. Fragile and extremely slender, it reaches a length of about 10 cm and is distinguishable from all other known species of the genus by the shape of its prostomium and by its parapodial characters. In its typical form it has been obtained only at Salcombe, but a markedly dwarf variety exists off shore off the east coast of Scotland. This dwarf form had been recorded by Mr A. D. McIntyre as *M. rosea* Moore. Dr Wilson has found, after examining specimens kindly sent by Mr McIntyre, that it is not only not *rosea* but that it is structurally identical with *filiformis* from Salcombe, although very much smaller when adult. After seeing Salcombe specimens Mr McIntyre is in agreement with this. In his paper Dr Wilson compares *filiformis* with other species of *Magelona*, especially *longicornis* Johnson which is shown to be imperfectly established, and with *cornuta* Wesenberg-Lund the original account of which he has amended and expanded from a re-examination of the type specimen.

Mr G. M. Spooner has continued the study of the fauna of the Eddystone shell-gravel and comparable deposits, and is attempting to distinguish between the members living close to the surface and those distributed through the bulk of the deposit. The Forster anchor-dredge is proving useful for this purpose.

Among additional small malacostracans found in the Eddystone gravel are two further representatives of phreatic genera of special interest. One is a new species of *Ingolfiella* itself, an isolated amphipod genus which, though very seldom observed, is already noted for its remarkable cosmopolitan distribution. Twenty specimens have now been isolated from the only two hauls made with the anchor-dredge. The other is a new species of the genus *Bogidiella*, the first truly marine species to be discovered. The genus, to date, is known from southern Europe and Asia and South America; six of the previously known species occur in terrestrial ground water, and three interstitially in intertidal deposits. In addition, further examples of a species (found first last year) belonging to a new genus of the Bogidiellidae have been found.

In a letter to *Nature* published in June 1959, certain other little-known animals are recorded, some of which had not previously been noticed in British waters. For example, three species of acochlideacean gastropods,

representing three separate families, appeared in a bucket of gravel collected by Mr G. R. Forster near the entrance to the Sound. With these three species a new suborder can now be added to the list of British Mollusca. One of these species appears also in the Eddystone gravel, together with another that is probably identical with one quite recently described from the Kiel area.

The same letter also briefly points out the significance of the occurrence of species of phreatic genera in marine gravels. These animals may be considered as having invaded the gravels *from below* rather than from the water above—that is to say, the species, genera, or even families to which they belong have slowly spread and evolved in ground-water held by the rocks of the earth's crust, and have penetrated under continent and ocean alike.

A single specimen of another blind colourless crustacean, *Microjaera anisopoda*, originally described from two specimens taken off Roscoff, was found in the Eddystone gravel. Now about twenty specimens have been got from clean coarse sand in the Isles of Scilly—in the famous 'silver strand' of Tresco—in company with a subterrestrial fauna. This genus, therefore, may well be represented in fresh water.

The fauna of the Eddystone Rock is being studied and is showing features of interest. The fauna of arthropods and worms that seek shelter in the various tufted weeds, clumps of barnacle shells and cracks in the rock itself, is notably denser than on rocks along the coast of the mainland. Among amphipods *Parajassa pelagica* is abundant, while the genus *Hyale* is represented by three species which show overlapping ranges—*H. perieri* from the splash zone to near mid-tide level, *H. stebbingi* between low H.W.N. and high L.W.N., and *H. pontica* from somewhat below mid-tide to E.L.W.S. Insects are represented by at least three species—*Thalassomyia frauenfeldi* (larvae in the upper *Enteromorpha*), *Aphrosylus celtiber* (adults on wing and larvae in *Corallina*), and *Clunio marinus* (larvae in *Corallina*). The *Enteromorpha* carries a heavy population of marine mites of the genus *Metarhombognathus*.

Mr P. G. Corbin has continued to collect data on the Lucernarians and certain of the smaller fishes. An interesting record from the Scilly Isles was the find, in April 1959, of a single specimen of *Lucernaria quadricornis* by Mr J. M. Lock of Charterhouse School. This is a species not uncommon apparently in Norway, but the certain British records are only very few. Further notes have been made on the ventral melanophore patterns of small specimens of the three Dragonets, *Callionymus* spp. The Connemara Sucker, *Lepadogaster candollei*, recorded as rare in the second edition of the Plymouth Marine Fauna (1931) and not found in the area in the last 10 years although looked for intensively, has been found by the I.C.I. Marine Paints Division Laboratory, Brixham, to occur regularly at one beach in the neighbourhood. With a locality now known for the species, it is hoped to make further notes on its natural history.

Following the discovery of a form of the lamellibranch *Lutraria* corresponding to *L. elliptica* var. *angustior* Philippi, Mr N. A. Holme has made a study of the British species of this genus. In a paper published in Vol. 38, No. 3 of the *Journal* it is shown that this form differs sufficiently from *L. lutraria* (= *elliptica*), both in shell characters and in the form of the siphons, to merit specific rank. It has accordingly been called *L. angustior* Philippi, and the differences between it and the other two species described. Shells and siphons of *L. angustior* are regularly taken in dredgings from the Eddystone shell-gravel, and this species appears to be widely distributed in similar deposits elsewhere in the English Channel.

In Volume 38, No. 3 of the *Journal*, Mr N. A. Holme has described a hopper used at sea for washing bottom deposits into suspension, so facilitating sieving of dredge and grab hauls. This apparatus has been in use for a number of years, and has considerably reduced the labour involved in sieving large samples.

During the year Mr N. A. Holme has made a detailed qualitative survey of the bottom fauna of the English Channel. Samples have been taken with a heavy version of Forster's anchor-dredge at 147 stations off the south coast of England, mainly in depths of less than 25 fathoms. Study has centred on the distribution of lamellibranchs and echinoderms, and account has also been taken of empty shells as additional evidence of the absence of species from a particular area. While not directly comparable with the shore survey of D. J. Crisp and A. J. Southward published in Vol. 32, No. 1 of the *Journal*, the results agree in showing the absence of many species from the eastern basin, the most distinct boundary being in the region of Portland Bill, while other species reach their limit at the Isle of Wight. Comparison with data from the North Sea shows that certain species absent in the eastern basin occur in lower temperatures in the central and southern North Sea. This, and the absence of marked temperature gradients at the critical region between the east and west basins of the Channel, indicate that for some species temperature is not a direct limiting factor in the Channel.

Another, less well-defined, boundary lies somewhat to the west of Plymouth, and marks the eastward limit of certain species which may be associated with 'western' water. It is noticeable that some of these extend round the north of Scotland into the north-west North Sea, where, again, temperatures are lower than in the Channel. The results of the Channel Survey have still to be worked up in detail, but meanwhile a joint paper with Mr G. M. Spooner incorporating data from off the Dorset coast has been submitted for publication in the *Proceedings of the Dorset Natural History and Archaeological Society*.

Mr G. R. Forster has completed his notes on the underwater studies on *Echinus esculentus*, which were published in Vol. 38, No. 2 of the *Journal*. A further note in Vol. 38, No. 3 of the *Journal* has resulted from a re-examina-

tion of length measurements made on the common prawn in the light of Dr H. A. Cole's recent study of the species in North Wales. The length reached by the young prawns after 3 months' growth varies considerably from year to year and can be correlated with variations in sea temperature. A further sample of prawns was collected during the spring tides in September but has not yet been worked up.

Mr Forster has also assisted Dr G. Y. Kennedy of the Cancer Research Unit, Sheffield University, in experiments with various chemical effects on the regeneration of the sponge *Microciona atrasanguinea*. A small closed-circuit circulation is being set up in which most of the micro-organisms in the water will be killed by ultra-violet irradiation. It is hoped, in this way, to provide a certain amount of nutriment for the developing sponges and at the same time, prevent the cultures from being overgrown by Protozoa.

Aqualung diving work has been continued during the summer. Various delicate specimens were collected for the new aquarium tanks. The light cages used for feeding experiments with *Echinus* were recovered intact, though considerably distorted after 8 months on the sea floor at a depth of 9 fathoms. A few more spotted gobies have been collected. These gobies can best be coaxed out of their rocky retreats by using a garden syringe to project a jet of chlorine solution ('Domestos') into the rock crevices. The gobies are forced out of hiding, making it much easier to capture them. The method has long been used on coral reefs.

Survey work on the sessile rock fauna has been held up by the delay in delivery of some equipment, but an interesting area near the coastguard station on Hilsea Point has been examined. In this area there are a number of deep narrow gullies in the rock from which algal growth is largely excluded. Several particularly fine specimens of the sponge *Stelletta grubei* were observed; from rock scrapings Dr Eve Southward identified many small serpulids of the unusual species *Josephella maranzelleri*. This area should be well worth a more detailed survey.

Mr Q. Bone has worked upon the histology of the Acrania, and has completed two papers upon aspects of the nervous system. A study of the central nervous system in larval acraniates (*Quart. J. micr. Sci.*, Vol. 100, p. 509) has provided the first opportunity for comparison of the central nervous system of the larva with that known for the larvae of craniates, and allows some inferences as to the ancestral condition of the chordate nervous system. A detailed study of the peripheral atrial nervous system of adult amphioxus has shown that the system is predominantly sensory (it contains several rather different categories of peripheral sensory neurones), and that it is unlike the autonomic nervous systems of craniates, with which it has previously been homologized. The central nervous system of the adult amphioxus is being studied at present; preliminary results indicate that several of the components of the system have been misinterpreted, whilst others have not

been noticed; it is hoped to provide a functional analysis of the components of the system which will allow comparison with the spinal cord of craniates.

In collaboration with Mr J. H. Wickstead, a paper has been published in *Nature* upon the ecology of the various types of acraniate larvae collected by Mr Wickstead from the Indo-Malayan plankton; these larvae show interesting differences in their metamorphoses which will be described at a later date.

Experiments have been carried out upon the artificial fertilization of amphioxus, and larvae successfully reared to the stage at which feeding begins; this work will be continued next season.

Physiology of Marine Organisms

Micro-anatomical investigations of light-organs often provide valuable information about the functioning of these structures. This line of approach is especially valuable when applied to deep-sea animals, in many of which the luminous response has not been observed. Dr J. A. C. Nicol has re-examined the light-organs of the piddock, *Pholas dactylus*, one of the first animals in which the luciferin-lucerase reaction was demonstrated. The light-organs contain three kinds of glandular cells: one mucus, two photogenic. It is in the latter that the luminous substrate and enzyme are elaborated. His results have been published in Vol. 39, No. 1 of the *Journal*. Dr Nicol is now examining some pelagic animals secured on cruises of R.V. 'Sarsia' and R.R.S. 'Discovery II', especially *Gnathophausia* and stomiatoid fishes. The former discharges a blue luminous secretion. The stomiatoids have conspicuous suborbital light-organs of a common pattern. These contain photocytes, the animal generating its own light, and they are provided with a mechanism for occlusion by rotating the light-emitting surface downwards. Amplifying earlier work on light emission and vision, Dr Nicol has tested the attractiveness to various animals of weak lights resembling luminescence. Some inshore crustaceans are attracted by such lights. In a simple multiple choice apparatus, the minimal intensity for attracting *Praunus neglectus* was 3×10^{-5} μW falling on 1 cm^2 at the level of the animals' eyes. The results of this work are being published in Vol. 38, No. 3 of the *Journal*. A survey of recent work on luminescence has been prepared by Dr Nicol for publication in *Biological Reviews*, Vol. 35.

Dr Nicol has also investigated the course of digestion in sea anemones, especially *Calliactis parasitica*. The process of digestion in these animals turns out to be very similar to that in *Physalia* and corals. Mesenteric filaments closely adhere to the food mass, and digest it by secreting proteases over it. Various proteins and protein degradation-products were found to stimulate digestive secretion, and the time-course of digestion of a standard meal was followed. An account of this work has been published in Vol. 38, No. 3 of the *Journal*.

The results of the joint research done by Dr Nicol and Dr G. Y. Kennedy on the pigments of *Chaetopterus* have now been published in the *Proceedings of the Royal Society*, B. The green pigment, first named 'chaetopterin' over 60 years ago by Ray Lankester, has finally been shown to be a mixture of phaeophorbides *a* and *b*. These pigments are probably derived from the breakdown of chlorophyll present in the food of the worm.

Dr E. J. Denton, in collaboration with Dr J. Gilpin-Brown, is studying the buoyancy of the cuttlefish *Sepia officinalis*. They have shown that the lamellae of the cuttlebone form independent chambers within any one of which the gases and liquid which it contains can move. When a freshly dissected cuttlebone is placed under reduced pressure liquid can readily be extracted through the posterior margins of the lamellae. The yellowish membrane which is closely applied to the bone in this region has been shown not only to have a copious blood supply, but to contain numerous ampullae close to the bone which are connected by small ducts to the veins. Cuttlefish exhibit a wide range of cuttlebone densities 0·48–0·71 and differ not in weight of dry matter but in amount of liquid which they contain. Thus a cuttlebone of density 0·7 contains about 30% (by volume) liquid, whereas a cuttlebone of density 0·5 contains about 10% liquid. The remainder of the cuttlebone contains gas, but this gas is always at less than atmospheric pressure. Cuttlefish vary in density and this variation is given entirely by changes in the density of the cuttlebone. When the cuttlebone changes in density the *mass* of gas per unit volume remains almost constant whatever the density of the cuttlebone. In a bone of reduced density the pressure of gas is therefore even lower than usual. The gas within the cuttlebone plays a completely passive role in the density changes and the pressure of gas in the cuttlebone is in no way balanced against the external hydrostatic pressure as in the swimbladder of a fish. The cuttlebone is not, however, an impermeable structure and there must be a mechanism capable of pumping salts out of the bone. The liquid inside the cuttlebone is principally a solution of sodium chloride and hypotonic to the blood and sea water, simple osmotic forces playing a major role in holding water out of the cuttlebone. The cuttlebone is very strong and only implodes at depths appreciably greater than those at which *Sepia* lives. A short note describing this work has been published in *Nature* and demonstrations 'On three ways of achieving buoyancy equilibrium in marine animals' were given at the Royal Society Conversaziones in May and June by Dr Denton, Dr Shaw and Dr Gilpin-Brown, together with Mr N. B. Marshall of the British Museum (Nat. Hist.).

Mr J. V. Howarth is collaborating with Dr Denton and Dr Gilpin-Brown in studies of the pumping mechanism of the cuttlebone.

Dr Denton found that the purple colour characteristic of the retina of freshwater fish is present in the salmon parr and smolt in fresh water, in smolt caught in the estuary and kept in sea water for several months and in

estuarine salmon just returning from the sea. The two latter animals he obtained through the kindness of Dr P. F. Elson of the St Andrews Biological Station of New Brunswick. There is therefore no metamorphosis of pigments similar to that which Dr Carlisle and Dr Denton found in the freshwater eel on its return to the sea. This suggests that the salmon remains in the surface waters during its life in the ocean.

Investigations begun 2 years ago by Dr D. B. Carlisle in collaboration with Dr P. Carlson of Munich, into the comparative endocrinology of Crustacea and insects, have been widened in scope and now involve the active co-operation of Dr Peggy Ellis of the Anti-locust Research Centre, London. So far the only publication resulting from this work has been a brief communication on the ventral glands of locusts in *C.R. Acad. Sci., Paris*, T. 249, pp. 1059–60. Dr Carlisle is now devoting the major part of his attention to problems of comparative endocrinology, and with the aid of a gift of purified sheep follicle stimulating hormone donated by the United States Department of Health, Education and Welfare, he is endeavouring to determine whether this vertebrate hormone has any effect on crustacean sexual development.

He has continued his investigations into the endocrine basis of sex reversal in *Pandalus* and has begun a study of this phenomenon in the blind, burrowing reptantian *Calocaris*. An account of the anatomy and histology of those endocrine organs which are now known to be implicated in this phenomenon in *Pandalus* has appeared in Vol. 38, No. 2 of the *Journal*. Two further papers on endocrinological aspects have been published in Vol. 38, No. 3. These describe experiments and observations on the events associated with the termination of the male phase of the life history and with the beginning of the female phase, respectively. The former event is shown to be controlled mainly by the vas deferens gland and the latter by the endocrine complex of the eyestalk. *Calocaris* appears to differ from *Pandalus* in that although the testis and ovary develop successively, sperm is stored in the vas deferens till far into the female phase and probably throughout life, while the male copulatory appendages are also retained. It seems probable that although from the developmental aspect *Calocaris* is protandric, functionally it may well be a simultaneous hermaphrodite. It has no abrupt sex reversal.

The publication in Vol. 38, No. 2 of the *Journal* of Dr Carlisle's observations of the differences in the endocrinology of moulting in different populations of *Palaemon* goes far to explain the contradictory results obtained by previous workers when using different populations. The rate of moulting depends upon a fine balance between the moult-accelerating and moult-inhibiting hormones. This state of balance differs in different populations, so that the normal rate of moulting varies from one population to another, while the effect of extirpating the endocrine complex of the eyestalks may lead to either an increase or a decrease in the moult rate according to population.

Dr Carlisle has continued to work upon the Gephyrean *Priapulus* and is endeavouring to study the histology of neurosecretion in this form. His account of the neurosecretory system in another Gephyrean, *Sipunculus*, has been published in the *Gunma J. med. Sci.* in a memorial volume dedicated to the memory of the late Prof. Enami of Gunma University, Japan, with whom Dr Carlisle worked for a brief period in 1953. The neurosecretory system of *Sipunculus* shows a striking resemblance to the primitive condition of the hypothalamo-hypophysial system of vertebrates, the eyestalk complex of endocrine organs of crustaceans and the brain corpus cardium complex of insects.

Dr Carlisle has continued to employ diving equipment to study the biology of crustaceans and ascidians in their natural habitat.

In collaboration with Miss Andrée Leon and Dr R. D. Bulbrook of the Imperial Cancer Research Fund Laboratories (Royal College of Surgeons), Dr E. D. S. Corner has been studying the distribution of aryl sulphatase, β-glucuronidase and 'steroid sulphatase' among various marine invertebrates. Of the nine phyla so far examined only certain gastropod molluscs, subclass Prosobranchia, have been found to possess a 'steroid sulphatase'. Two species, *Buccinum undatum* and *Nassarius reticulatus* provide an enzyme of specificity similar to that of the 'steroid sulphatase' prepared from the land snail, *Helix pomatia*, in that it assists the hydrolysis of both aetiocholanolone and dehydro*epi*androsterone sulphates. However, the enzyme prepared from three other species, *Patella vulgata*, *Patina pellucida* and *Littorina littorea*, has a higher specificity, assisting the hydrolysis of only the latter substrate. No 'steroid sulphatase' has yet been found which will affect the hydrolysis of androsterone sulphate, but the enzyme obtained from *Nassarius* has a very high activity and should be of use in steroid analysis. Further experiments with molluscs have shown that the β-glucuronidase and aryl sulphatase activities of herbivores are, in general, greater than those of carnivores. Moreover, additional experiments using members of all the phyla examined have shown that, compared with herbivorous and carnivorous species, animals that feed on detritus are more often lacking in β-glucuronidase activity. By contrast, no correlation has been found between diet and 'steroid sulphatase' activity; and the results of studies of the behaviour of this enzyme under different experimental conditions indicate that it does not perform any physiological function related to the hydrolysis of steroid sulphates in the few species in which it has been found. An account dealing with the biochemical aspects of this work has been accepted for publication in the *Biochemical Journal*; and a second paper, concerned with the ecological aspects, has been published in Vol. 39, No. 1 of the *Journal*.

Dr Corner has continued his collaboration with Dr A. D. Boney of Plymouth Technical College in which heavy metal poisons have been used in studies of the ecological resistance of certain marine red algae. An account of this work has already appeared in Vol. 38, No. 2 of the *Journal* and the

investigation is now being extended to include experiments with various fluorescent dyes and carcinogens, several of which have been found to stimulate the growth of red algae sporelings.

Dr T. I. Shaw has submitted for publication in the *Proceedings of the Royal Society* an account of his experiments relating oxygen consumption and iodine uptake by the sea weed *Laminaria digitata*. Further studies upon ^{131}I uptake by the weed have been directed towards the discovery of inhibitors which interfere with iodine uptake other than by preventing the formation of elementary iodine. Perchlorate appears to be such an inhibitor. At concentrations of a few millimolar perchlorate does not prevent the ready conversion of iodide to iodine outside the plant although it blocks the uptake of ^{131}I by freshly collected weed. However, radio-iodine uptake by plants stored overnight in the laboratory is but little affected by perchlorate. Attempts made to demonstrate that perchlorate acts by interfering with the reduction of elementary iodine in the tissues have, so far, been inconclusive.

In conjunction with Prof. A. L. Hodgkin, F.R.S., and Dr R. D. Keynes, F.R.S., both of Cambridge, and Dr P. C. Caldwell, Alan Johnston, Lawrence and Mosely Research Fellow of the Royal Society, Dr Shaw has been further investigating the effects of injection of various phosphate esters upon the active transport of sodium and potassium across the membrane of the giant nerve fibres of *Loligo*. In particular it has been shown that the injection of relatively large amounts of arginine phosphate into a nerve fibre heavily poisoned with cyanide in large measure restores to its unpoisoned level the outward movement of sodium. Moreover, the efflux is dependent upon the presence of external potassium, a characteristic feature of the efflux from unpoisoned axons. A preliminary report of these findings has been published in the *Journal of Physiology*. Currently the fate of those phosphate esters shown to affect sodium transport when injected into poisoned axons is being studied. After injection of the phosphate into a poisoned fibre the axoplasm is extruded and the water soluble components separated by chromatography. While quantitative results are not yet available, it seems clear that injection of arginine phosphate causes rapid disappearance of a compound resembling adenosine monophosphate and rapid regeneration of a compound having many of the properties of adenosine triphosphate.

Mr J. V. Howarth joined the staff as a physiologist in April. He has made an apparatus based on the Hill-Baldes thermoelectric method for the measurement of the osmotic activity of very small samples of liquid.

He has also constructed an apparatus for measuring the metabolic rate of thin strips of tissue by observing their rate of heat production. At the time of writing this apparatus has only recently been completed. A few measurements have been made on the heat production of the anterior byssus retractor muscle of *Mytilus edulis*. The preliminary results indicate that it will be possible to record the heat production of this muscle in the interesting 'fused'

state which follows chemical stimulation and in which the muscle can resist great tension with apparently a minimum expenditure of energy.

Dr G. W. Bryan has been studying the uptake of radioactive caesium by marine invertebrates with a view to finding to what extent the accumulation of this ion is dependent on potassium balance. Among the decapod crustacea *Galathea squamifera*, *Carcinus maenas*, *Cancer pagurus* and *Palaemon serratus* have been used. Most of the experiments were carried out using ^{134}Cs, but in the prawn *Palaemon serratus* comparative experiments with the fission product ^{137}Cs were performed during a 2-week visit to the Windscale Works of the United Kingdom Atomic Energy Authority at the kind invitation of Mr W. L. Templeton. Rates of uptake of radioactive Cs from sea water by whole animals, their blood and principal tissues have been determined and the radioactive levels reached at equilibrium have been related to K concentration.

At 20° C equilibrium with radioactive sea water is substantially reached by *Galathea* after 200 hr. when the activity of the animal is about seven times that of an equal weight of sea water. Only 15 min. is required for the activity of the blood to reach 50% of the equilibrium level. Uptake in the other species is a slower process. The rate of uptake of ^{134}Cs by the muscles and digestive gland of *Galathea* at 20° C is more than double the rate at 8° C. At equilibrium the blood/sea-water ratio for ^{134}Cs is about the same as that for K in *Galathea*, *Carcinus* and *Cancer*. In *Palaemon* the ratio is less than unity for K and greater for Cs, while the urine/blood ratio is also less than unity for K and greater for Cs. In other respects all four species are rather similar. The muscle/blood Cs ratios at equilibrium are about the same as those for K, but Cs ratios for digestive gland and the gills usually markedly exceed those for K. This is particularly noticeable in *Galathea* where the digestive gland/blood Cs ratio is up to six times that for K. Reasons for this are being investigated at the present time. The effect of reduced sea-water K concentrations on the accumulation of Cs is also being studied in these animals.

Members of other phyla which have been used are the anemone *Tealia felina*, the polychaete *Perinereis cultrifera* and the nudibranch *Archidoris pseudoargus*. The whole animal/sea-water ratio for Cs at equilibrium exceeds that for K in *Tealia*. A similar result is found in *Archidoris* where the tissue/blood Cs ratio exceeds that for K in all tissues except the reproductive system. In *Perinereis* the distribution of ^{134}Cs at equilibrium is almost exactly governed by tissue/sea-water K ratios. Further species are being examined with a view to finding an animal which might concentrate Cs to such an extent as to be useful as an indicator of contamination of sea water with ^{137}Cs.

Dr G. T. Boalch, International Paints Research Fellow, has been investigating the toxicity of copper to the common fouling weed *Ectocarpus*. For this work a culture tank in which over 200 cultures can be grown at constant temperature and continuous illumination has been constructed. The growth of bacteria-free cultures of *Ectocarpus confervoides* treated with copper salts

at varying concentrations has been investigated with this apparatus. The results so far indicate that this weed is most sensitive to copper poisoning at the early stages of growth and that as growth proceeds the extracellular products released into the culture medium give some protection against the copper.

Cultures started from 'brown felt weed' collected from the test plates of the International Paints Research Laboratory, Newton Ferrers, have shown this growth to be a stunted form of *Ectocarpus*, and laboratory cultures in which *Ectocarpus* was grown in media containing high, but not lethal, levels of copper sulphate have produced similar growth forms.

Attempts have also been made to obtain pure cultures of green and red fouling weeds, but although a green alga has been obtained in a bacteria-free condition a suitable culture medium has not yet been devised.

Library

During the year the collections of reprints and books belonging to the late Sir Sidney Harmer and to the late Dr G. P. Bidder have been arranged, catalogued and incorporated in the general index. Thanks are due to Dr Anna M. Bidder and Mrs Barclay Russell for their generosity in paying for the binding of the latter collection.

The thanks of the Association are once more due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association.

Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

Published Memoirs

Vol. 38, No. 2, of the *Journal* was published in June, and Vol. 38, No. 3 in December 1959.

The following papers, the outcome of work done at the Plymouth laboratory, have been published elsewhere than in the *Journal* of the Association:

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Membership of the Association

The total number of members on 31 March 1960 was 1096, being 61 more than on 31 March 1959; of these the number of life members was 125 and of annual members 971. The number of associate members is five.

Grant for Aquarium Reconstruction

The Council wish to record their grateful thanks for the following donation towards the cost of reconstructing the Aquarium:

Shell International Petroleum Co. Ltd. £105.

Donations

The Council wish to record their appreciation for the following donations to the Plymouth laboratory: Water colour paintings made by Dr E. A. Wilson on the 1910–13 British Antarctic ('Terra Nova') Expedition which had belonged to the late Mrs E. W. Sexton, and have been presented by her son, Col. F. B. W. Sexton; a cathetometer for use in the Plymouth laboratory presented by Dr J. H. Oliver.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledge the following generous grants received during the year:

Fishmongers' Company (£400), The Royal Society (£100), British Association (£50), Physiological Society (£50), The Cornwall Sea Fisheries Committee (£10), The Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£25), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Sheffield (£10. 10*s*.), Southampton (£15. 15*s*.), Reading (£10. 10*s*.), Nottingham (£10. 10*s*.), Hull (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), The Imperial College of Science and Technology (£10), Gonville and Caius College, Cambridge (£5), and The Zoological Society of London (£10. 10*s*.).

PRESIDENT, VICE-PRESIDENTS, OFFICERS AND COUNCIL:

The following is the list of those proposed by the Council for election for the year 1960–61:

President

Prof. C. F. A. PANTIN, Sc.D., F.R.S.

Vice-Presidents

THE EARL OF IVEAGH, K.G., C.B., C.M.G.
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., LL.D., F.R.S.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., F.R.S.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.
Major E. G. CHRISTIE-MILLER
MORLEY H. NEALE, C.B.E.
THE EARL OF VERULAM
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S.
G. M. GRAHAM, C.M.G., O.B.E.

COUNCIL

To retire in 1961

H. A. COLE, D.Sc.
Prof. J. E. HARRIS, Ph.D., F.R.S.
Prof. C. M. YONGE, C.B.E., D.Sc., F.R.S.
G. E. FOGG, Ph.D.
C. E. LUCAS, C.M.G., D.Sc.

To retire in 1962

J. N. CARRUTHERS, D.Sc., F.Inst.P.
Prof. A. L. HODGKIN, F.R.S.
Prof. O. E. LOWENSTEIN, D.Sc., F.R.S.
Prof. G. E. NEWELL, T.D., D.Sc.
Prof. W. F. WHITTARD, D.Sc., F.R.S.

To retire in 1963

G. E. R. DEACON, C.B.E., D.Sc., F.R.S.
F. C. FRASER, D.Sc.
M. N. HILL, Ph.D.
O. D. HUNT, F.R.S.E.
Prof. G. P. WELLS, Sc.D., F.R.S.

Hon. Treasurer

HARRISON S. EDWARDS, Westhumble Lacey, near Dorking, Surrey

Secretary

F. S. RUSSELL, C.B.E., D.S.C., D.F.C., LL.D., F.R.S.

The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

B. C. ENGHOLM (Ministry of Agriculture, Fisheries and Food)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
HARRISON S. EDWARDS
Prof. Sir ALISTER HARDY, Kt., D.Sc., F.R.S. (Oxford University)
Prof. C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
EDWARD HINDLE, Sc.D., F.R.S. (British Association)
N. B. MARSHALL (Zoological Society)
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S. (Royal Society)

BALANCE SHEET 1959–60

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET

31 MARCH 1960

	£	£
CAPITAL RESERVE ACCOUNT:		
As at 31 March 1959	171,005	
Add: Expenditure on fixed assets recovered	490	
	171,495	
Less: Transfer to surplus account being an amount equivalent to the depreciation provided on assets acquired out of Development Fund grants	3,674	167,821
SURPLUS ACCOUNT:		
As at 31 March 1959	9,478	
Add: Transfer from Capital Reserve Account	3,674	
	13,152	
Deduct:		
Increase in provision for diminution in value of General Fund investments 65		
Excess of expenditure over income for the year ... 826		
	891	
		12,261
		180,082
BALANCES ON SPECIAL FUNDS (see annexed statement)		5,365
CURRENT LIABILITIES:		
Sundry creditors and accrued expenses	3,468	
Subscriptions and grants received in advance	327	
		3,795

Note: Capital commitments outstanding amount to approximately £2,730 (1959 £8,695) of which £1,500 (1959 £7,550) is recoverable

O. E. LOWENSTEIN
W. F. WHITTARD } *Members of the Council*

£189,242

FIXED ASSETS:	Cost or Valuation £	Depreciation £	£
Boats and equipment:			
At cost:			
R.V. 'Sarsia'	137,761	9,808	127,953
M.F.V. 'Sula'	12,500	1,210	11,290
R.L. 'Gammarus'	200	30	170
	150,461	11,048	139,413
Laboratory apparatus, equipment and machinery:			
At cost	17,669	6,554	11,115
Library at valuation in 1941 plus additions as valued by the Director	24,440	—	24,440
	£192,570	£17,602	
			174,968
INVESTMENTS AT MARKET VALUE:			
General Fund (including Composition Fees) at book amount (Market value £1,368; last year £1,370)			1,814
E. T. Browne Bequest Funds at cost (Market value £3,400; last year £3,431)			4,817
			6,631
Less: Provision for diminution in value of investments			1,863
			4,768
CURRENT ASSETS:			
Stocks on hand as valued by the Director			4,515
Sundry debtors and prepayments			2,112
Balances at bankers and cash in hand			2,879
			9,506
			£189,242

AUDITORS' REPORT TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31 March 1960 and of its excess of expenditure over income for the year ended on that date.

We have obtained all the information and explanations which we considered necessary. In our opinion the Association has kept proper books and the said accounts which are in agreement with them and with the said information and explanations, give in the prescribed manner the information required by the Companies Act 1948.

Norwich Union House
2 St Andrew's Cross
Plymouth
12 May 1960

PRICE WATERHOUSE & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT

FOR THE YEAR ENDED 31 MARCH 1960

	£	£
SALARIES (including additional for previous year) NATIONAL INSURANCE, SUPERANNUATION SCHEME CONTRIBUTIONS AND SUPPLEMENTARY PENSIONS		42,028
LABORATORY'S AND BOATS' CREWS' WAGES (including additional for previous years), NATIONAL INSURANCE, SUPERANNUATION SCHEME CONTRIBUTIONS, PENSIONS AND EMPLOYERS' LIABILITY INSURANCE		37,784
UPKEEP OF LIBRARY		980
SCIENTIFIC PUBLICATIONS, *less* SALES		1,985
UPKEEP OF LABORATORIES:		
Buildings and machinery	1,145	
Electricity, gas, coal and water	1,470	
Chemicals and apparatus	3,188	
Depreciation of laboratory apparatus, equipment and machinery	1,234	
Rents and insurance	437	
Travelling expenses	1,237	
Audit fee	175	
Stationery, postage, telephone and sundries	1,585	
Specimens	139	
Collecting expenses and upkeep of truck	237	
		10,847
MAINTENANCE AND OPERATION OF BOATS:		
Petrol, oil, paraffin, etc.	1,782	
Maintenance and repairs	7,364	
Depreciation	3,674	
Insurances	2,303	
Hire of Decca Navigator—R.V. 'Sarsia'	395	
		15,518
ENTERTAINMENT EXPENSES		79
BANK CHARGES, *less* INTEREST ON BANK DEPOSITS		15
		£109,236

	£	£
GRANTS AND TABLE RENTS:		
Ministry of Agriculture, Fisheries and Food—Grant from Development Fund	99,477	
Fishmongers' Company	400	
Miscellaneous (including Royal Society £100, British Association £50, Physiological Society £50, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10s., Leeds £25, Southampton £15. 15s., Durham £10. 10s., Exeter £10. 10s., Leicester £10. 10s., Manchester £10. 10s., Nottingham £10s. 10s., Hull £10. 10s., Reading £10. 10s., and Sheffield £10. 10s., Imperial College £10, Zoological Society of London £10. 10s., Ministry of Works £112, Imperial Chemical Industries Ltd., £52. 10s., International Paints Ltd. £52. 10s., Gonville and Caius College, Cambridge £5)	1,481	
		101,358
SUBSCRIPTIONS		1,092
SALES:		
Specimens	3,306	
Fish	341	
	£	
Nets, gear and hydrographical equipment	916	
Less: Cost of materials	709	
	207	
		3,854
INCOME FROM INVESTMENTS		62
AQUARIUM:		
Admission fees	2,425	
Sale of guides	38	
	2,463	
Less: Maintenance, printing and advertising	419	
		2,044
BALANCE being excess of expenditure over income for the year		826
		£109,236

MOVEMENTS ON SPECIAL FUNDS DURING THE YEAR TO 31 MARCH 1960

	E. T. Browne Bequest									
	Library £	Special Apparatus £	Scientific Publications £	Aquarium Reconstruction Fund £	Rockefeller Foundation Fund £	Library Extension and Dogfish House Fund £	Reservoir and Sea Water Tanks Fund £	Library Reserve Fund £	Research Funds* £	TOTAL £
BALANCES AT 31 MARCH 1959 (after providing £1,258 for diminution in value of investments)	1,058	2,070	656	1,141	501	697	(905)	—	243	5,461
Add: Income during year										
Grants (including amounts paid direct to the contractors by the Nuffield Foundation)	—	—	—	7,075	—	—	—	—	4,376	11,451
Income from investments	41	84	30	—	—	—	—	—	—	155
Bank deposit interest	—	—	—	26	—	15	—	—	—	41
Other income	—	—	102	—	—	—	—	325	—	427
Transfer from Library Extension and Dogfish House Fund	—	—	—	—	—	—	712	—	—	712
	1,099	2,154	788	8,242	501	712	(193)	325	4,619	18,247
Deduct: Expenditure during year	—	134	—	7,002	501	—	—	93	4,281	12,011
Increase in provision for diminution in value of investments	40	84	35	—	—	—	—	—	—	159
Transfer to Reservoir and Sea Water Tanks Fund	—	—	—	—	—	712	—	—	—	712
BALANCES AT 31 MARCH 1960	£1,059	£1,936	£753	£1,240	—	—	£(193)	£232	£338	£5,365

* Including International Paints Limited Research Fellowship.

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LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1960

GOVERNORS

THE BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE, 18 Adam Street, London, W.C. 2
THE UNIVERSITY OF OXFORD
THE UNIVERSITY OF CAMBRIDGE
THE WORSHIPFUL COMPANY OF CLOTHWORKERS, 48 Fenchurch Street, London, E.C. 3
THE WORSHIPFUL COMPANY OF FISHMONGERS, Fishmongers Hall, London, E.C. 4
THE PRIME WARDEN. (**Council,** 1886→)
EDWARDS, HARRISON S., Westhumble Lacey, near Dorking, Surrey. (**Council,** 1950→; **Hon. Treasurer,** 1956→)
CHRISTIE-MILLER, Major E. G., 38 Hyde Park Street, London, W. 2. (**Council,** 1941→; **Hon. Treasurer,** 1941→56; **Vice-President,** 1951→)
THE ZOOLOGICAL SOCIETY OF LONDON, Regent's Park, London, N.W. 1
THE ROYAL SOCIETY, Burlington House, Piccadilly, London, W. 1
MINISTRY OF AGRICULTURE, FISHERIES & FOOD, 3 Whitehall Place, London, S.W. 1
BAYLY, ROBERT (the late). (**Council,** 1896–1901)
BAYLY, JOHN (the late)
BROWNE, E. T. (the late). (**Council,** 1913–19; 1920–37)
THOMASSON, J. P. (the late). (**Council,** 1896–1903)
BIDDER, G. P., Sc.D. (the late). (**Council,** 1899–1953; **President,** 1939–45; **Vice-President,** 1948–53)
THE LORD MOYNE, P.C., D.S.O. (the late). (**Vice-President,** 1929; 1939–45; **President,** 1930–39)
ALLEN, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary). (**Council,** 1895–1942; **Secretary,** 1895–1936; **Hon. Governor,** 1937–42)

FOUNDERS

1884 THE CORPORATION OF THE CITY OF LONDON, The Guildhall, London, E.C. 3
1884 THE WORSHIPFUL COMPANY OF MERCERS, Mercers' Hall, 4 Ironmonger Lane London, E.C. 2
1884 THE WORSHIPFUL COMPANY OF GOLDSMITHS, Goldsmiths' Hall, Foster Lane, London, E.C. 2
1884 THE ROYAL MICROSCOPICAL SOCIETY, B.M.A. House, Tavistock Square, London, W.C. 1
1884 BULTEEL, THOS. (the late)
1884 BURDETT-COUTTS, W. L. A. BARTLETT (the late)
1884 CRISP, Sir FRANK, Bart. (the late). (**Council,** 1884–92; **Hon. Treasurer,** 1884–88)
1884 DAUBENY, Captain GILES A. (the late)
1884 EDDY, J. RAY (the late)
1884 GASSIOT, JOHN P. (the late)

1884 LANKESTER, Sir E. RAY, K.C.B., F.R.S. (the late). (**Hon. Secretary,** 1884–90; **President,** 1891–1929)
1884 Lord MASHAM (the late)
1884 MOSELEY, Prof. H. N., F.R.S. (the late). (**Chairman of Council,** 1884–88)
1884 Lord AVEBURY, F.R.S. (the late). (**Vice-President,** 1884–1913)
1884 POULTON, Prof. Sir EDWARD B., F.R.S. (the late). (**Council,** 1888–94)
1884 ROMANES, Prof. G. J., LL.D., F.R.S. (the late). (**Council,** 1884–91)
1884 WORTHINGTON, JAMES (the late)
1885 The 15th EARL OF DERBY (the late)
1887 WELDON, Prof. W. F. R., F.R.S. (the late). (**Council,** 1890–1901; representing British Association, 1901–5)
1888 BURY, HENRY, (the late)
1888 THE WORSHIPFUL COMPANY OF DRAPERS, Drapers' Hall, London, E.C. 2
1889 THE WORSHIPFUL COMPANY OF GROCERS, Grocers' Hall, Princes Street, London, E.C. 2
1889 THOMPSON, Sir HENRY, Bart. (the late). (**Vice-President,** 1890–1903)
1889 Lord REVELSTOKE (the late)
1890 RICHES, T. H. (the late). (**Council,** 1920–25)
1892 BROWNE, Mrs E. T. (the late)
1898 WORTH, R. HANSFORD, M.Inst.C.E. (the late)
1899 The EARL OF IVEAGH, K.G., C.B., C.M.G., 11 St James's Square, London, S.W. 1 (**Vice-President,** 1929→)
1902 GURNEY, ROBERT, D.Sc. (the late). (**Council,** 1932–5)
1904 SHAW, JOSEPH, K.C. (the late)
1909 HARDING, Colonel W. (the late)
1910 MURRAY, Sir JOHN, K.C.B., F.R.S. (the late). (**Council,** 1896–99; **Vice-President,** 1900–13)
1912 SWITHINBANK, H. (the late)
1913 SHEARER, Dr CRESSWELL, F.R.S. (the late)
1913 HERON-ALLEN, E., F.R.S. (the late)
1918 EVANS, GEORGE (the late). (**Hon. Treasurer,** 1915–31; **Vice-President,** 1925–33)
1920 MCCLEAN, Capt. W. N., 39 Phillimore Gardens, London, W. 8
1920 Lord BUCKLAND OF BWLCH (the late)
1920 LLEWELLYN, Sir D. R. (the late)
1921 HARMER, F. W. (the late)
1924 THE MACFISHERIES, LTD., Ocean House, Pudding Lane, London, E.C. 3
1924 Lady MURRAY (the late)
1925 THE INSTITUTION OF CIVIL ENGINEERS, Great George Street, Westminster, London, S.W. 1
1925 DISCOVERY COMMITTEE
1927 BIDDER, Miss ANNA M., Ph.D., 2A Cavendish Avenue, Hills Road, Cambridge. (**Council,** 1948–51, 1954–57)
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Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth, where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888, and, since that date, a new library, and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. 27 (p. 761) and Vol. 31 (p. 193) of this *Journal*.

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