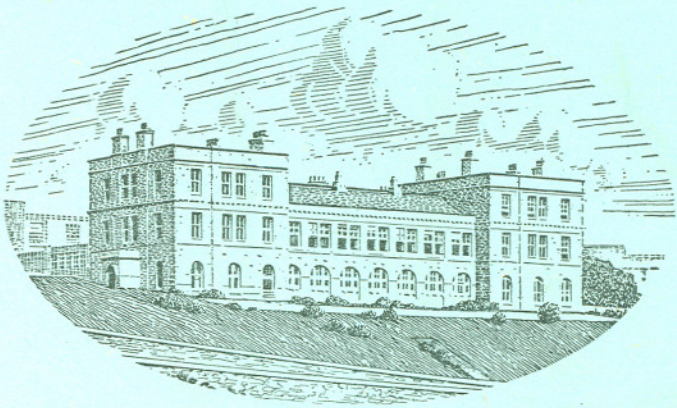
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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Dr Alec Sand, F.R.S.

In the sad death of Dr Alec Sand in July 1945, at the age of 43, we have lost one of the ablest comparative physiologists in the country.

Born in Warsaw, he was two years old when his parents brought him to London. As a youth he was determined to get a University training, but his funds would not permit him to do so in this country. So, with characteristic drive, he went to Canada and worked his way through College in British Columbia, taking a degree in Science and Agriculture. This enabled him to take a junior post in bacteriology in the Agricultural Faculty of McGill University. He took up research on soil micro-organisms and on this obtained his Ph.D. degree. This was the origin of his first published paper, on *Azotobacter*.

While at McGill, Sand came under the influence of Prof. Lancelot Hogben who had begun at that University to develop his school of comparative physiology. This was a turning point in Sand's career, and when Hogben went to the University of Cape Town, he soon joined him on his staff. It was here that Sand's work turned towards comparative physiology. The rich fauna which he now saw and the varied adaptations to the conditions of existence strongly appealed to him. His work on the respiratory mechanism of crabs, scorpions and Sabellid worms was done at this time. From Hogben he derived a great interest in colour response in animals and he did excellent work on the pigmentary effector system of the Chameleon.

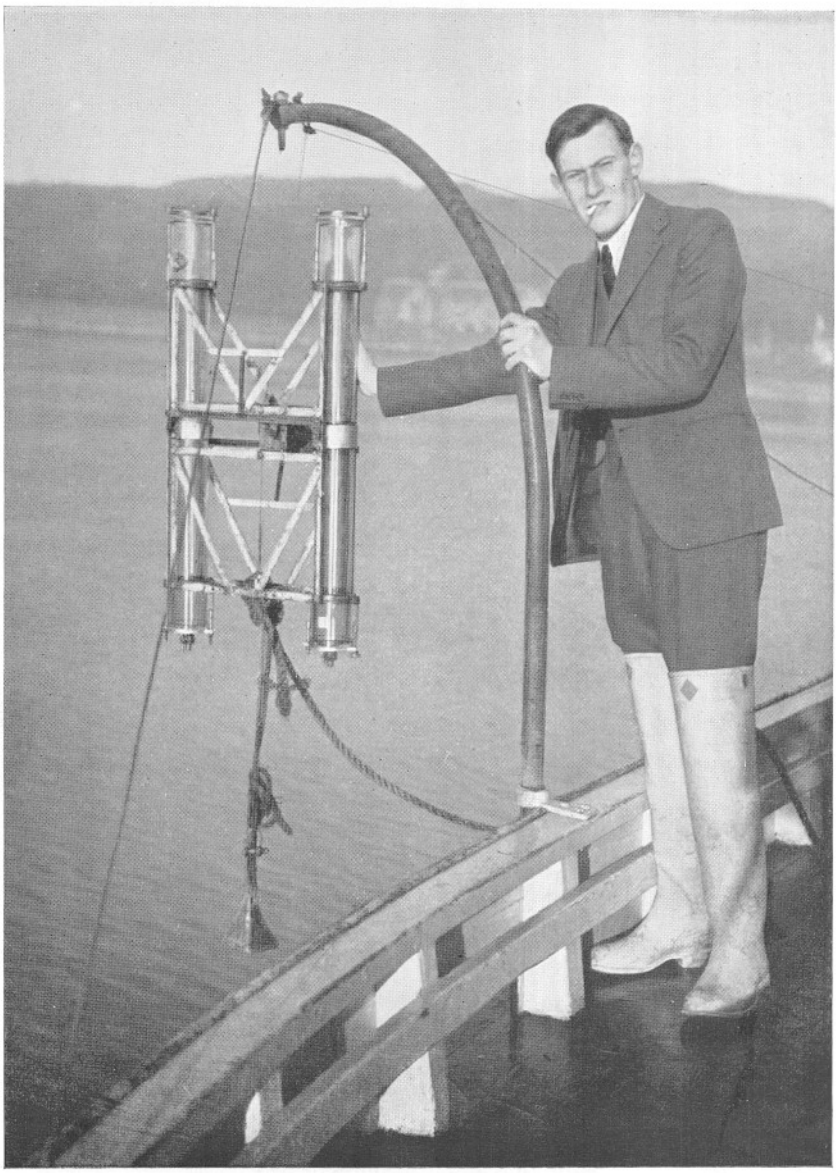
In 1933 Sand left South Africa and went to Cambridge to work with Prof. J. Gray in his studies of locomotion in Vertebrates. The ideas and techniques he then developed bore fruit when soon afterwards he was appointed Physiologist at the Marine Biological Laboratory, Plymouth. It was there that partly by himself and partly with the able co-operation of Dr O. Lowenstein he did his outstanding work on the sense organs of fishes. It is to this work more than to any other that we owe our knowledge of the excitatory mechanism of the lateral line system and labyrinth in fishes. His further unexpected demonstration that the ampullae of Lorenzini function as temperature receptors is a masterpiece of careful observation and experimental design combined with insight and shrewdness of interpretation. It was these characteristics, which come out so clearly in this work, that were the memorable features of the man himself. Visitors to the Plymouth Laboratory will remember not only his brilliance and ingenuity, but also his kindly and helpful criticism, qualities which are not always linked in the same personality as they were in his. His fine work in biology was recognized by his election to the Royal Society in 1945.

Early in the war he volunteered for the Navy. He was selected for work on radiolocation, and commissioned as Lieutenant. He served in the north of

Scotland, in England and in a cruiser in the Indian Ocean. There his work scored some signal successes. He was later on a monitor at the invasion of Sicily, where his ship sustained heavy casualties from a bomb. After this he was seconded to the Medical Research Council's Laboratory for work on naval problems. With the conclusion of the war we all hoped soon to see him return to Plymouth. As it is, we have lost one of the ablest biologists at a time when he is most needed, and at a time when his full power of mind had just developed.

Alec Sand was married and during the war his wife and two boys went to South Africa. We can only give them our sympathy for their great loss.

C.F.A.P.



The late Lieut. W. Neil Paton, D.S.C., R.N.V.R., with Apparatus No 1 in the revised form.

EXPERIMENTS ON THE VERTICAL MIGRATION OF PLANKTON ANIMALS

By A. C. Hardy, D.Sc., F.R.S.

From the Department of Oceanography, University College of Hull

and the late Lieut. W. Neil Paton, D.S.C., B.A., R.N.V.R.

Formerly Assistant Naturalist at the Marine Station, Millport

(Plates VIII–XI and Text-figs. 1–20)

Preface by the first author. Soon after the outbreak of war Neil Paton volunteered for service with the R.N.V.R.; he received his commission in the spring of 1940 and later transferred to the Fleet Air Arm, being stationed at Malta. After many valiant aerial combats, which won him the Distinguished Service Cross and a mention in dispatches, he was reported missing in June 1942 and later officially presumed killed. Marine biology has lost a recruit of great promise and the country a very gallant officer. An appreciation of him and a brief account of his heroic battles based on Admiralty reports will be found in *Nature*, Vol. 151, p. 48, 1943. The present joint paper was almost complete before he left for service overseas; but there remained a few points still to be considered. Its completion has been delayed by my taking up new appointments and engaging in research in relation to the war.

CONTENTS

Introduction

It is well known that many plankton animals exhibit what is termed a diurnal vertical migration; they usually rise towards the surface in the evening and descend away from it in the daytime. That this behaviour should have been developed independently in so many different animal groups would seem to indicate that it is an activity of much importance in their lives; examples have been recorded among medusae, Ctenophora, Polychaeta (*Tomopteris*), Chaetognatha, Crustacea of many groups (Cladocera, Copepoda, Mysidacea, Amphipoda, Euphausiacea and Decapoda), Pteropoda, Cephalopoda, pelagic Tunicata (*Salpa*) and young fish. For a general account of its occurrence reference may be made to Murray & Hjort (1912) and to a special review of the subject and its earlier literature by Russell (1927); it has been shown to be as common in the southern hemisphere (Hardy & Gunther, 1935) as in the north.

Many investigators have made a special study of this diurnal vertical migration, for example, Esterly (1911, 1912, 1917 and 1919), Michael (1911, 1913), Rose (1925), Russell (1925–34), Clarke (1930–4), Gardiner (1933), Southern & Gardiner (1932), Worthington (1931), Nicholls (1933) and others. The concensus of opinion holds that light is a very important, if not the most important, factor controlling these changes in the vertical distribution of the animals. The work in the past has for the most part involved the analysis of many tow-net hauls taken at a series of different depths at different times of the day and night, and to a less extent laboratory experiment. Hitherto attempts do not appear to have been made to perform experiments with the animals in their natural habitat.

It was with this last idea in mind that the senior author designed a special apparatus (to be described in the next section) to study the vertical movements of plankton animals under as natural conditions as possible at various depths below the surface of the sea. It was his intention that the apparatus should provide a means of testing by experiment his hypothesis of animal exclusion (Hardy & Gunther, 1935; Hardy, 1936, 1938). In this he has suggested that the distribution of animals as seen in a plankton survey might in part be the result of changes in their more normal vertical migrations brought about by dense phytoplankton concentrations in the upper layers. He pointed out that, since the two water layers, between which they migrate, are nearly always travelling at different speeds, any change in the animals' vertical migrational behaviour would usually alter their distribution as seen in plan. Before proceeding, however, to perform experiments designed to reveal the effects of various unusual conditions, such as excessive phytoplankton, it was clear that work must first be done to elucidate the factors governing the animals' more normal vertical migrations. The investigations described in this paper are mainly of this character. The animal chosen for experiment was the copepod

Calanus finmarchicus (Gunner.), upon the vertical migration of which much analytical work has already been done (Esterly, 1911; Russell, 1925, 1926, 1928 *b*, 1934; Gardiner, 1933; Nicholls, 1933; Clarke, 1934 *a*).

Through the generosity of the Leverhulme Trust a grant was provided to start the research which was later continued at Millport. We express our great indebtedness to the Leverhulme Trustees who, in addition, made a contribution towards the cost of constructing the apparatus. We are also most grateful to Mr Richard Elmhirst, Director of the Millport Laboratory, for his interest in the experiments and the excellent facilities he gave for them, and to the two boatmen Mr R. Kerr and Mr D. Burnie who throughout, on the motor research boat *Nautilus*, helped in the manipulation of the apparatus with so much care and devotion to the work.

Because the research has been suspended on account of the war, and since it is not known when it may be continued, we have thought it desirable to publish the results as far as they have gone.[1] It must be understood that the experiments are preliminary in character, and consequently no attempt is made at present to elaborate a theory to cover the results; a number of hypotheses suggested by the work must be tested by further experiment. It is hoped, however, that the publication of the results as far as they go may invite comment and criticism which will be helpful in planning the future development of the investigations. The results of all the experiments are given, but many are indicative rather than conclusive.

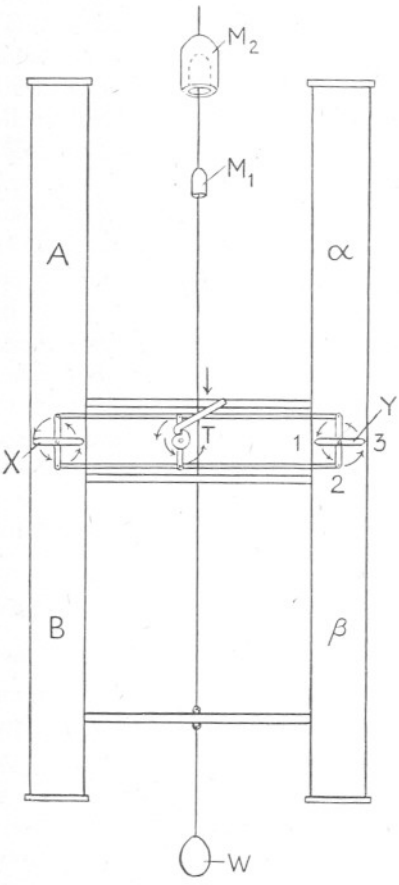
Apparatus No. 1

General description

The essential nature of the apparatus will be understood with the aid of the diagram in Text-fig. 1. It consists of two glass cylinders, AB and $\alpha\beta$, each 1 m. tall and with an internal diameter of 3 in., mounted in a frame so that they may be suspended vertically in the water and lowered by a wire rope to any desired depth. The frame is so made that it cuts off as little light as possible from the cylinders. A weight, W, hanging below, provides stability. The ends of the cylinders are closed at the top and bottom by glass and metal plates respectively; these are removable and interchangeable. Swivelling disks, which will be called trapdoors, are placed half-way down each cylinder at X and Y and fixed to spindles passing through watertight bearings in the cylinder walls. They are arranged so that they may be turned through 180° to take up any one of three positions. At 'position 1' they are each at right angles to the axis of their cylinders, so that, fitting closely, they form partitions dividing their respective cylinders into two compartments, A and B in one cylinder, and α and β in the other. At 'position 2' the trapdoors have been

[1] This was written before Lieut. Paton was killed on active service: see my prefatory note. A. C. H.

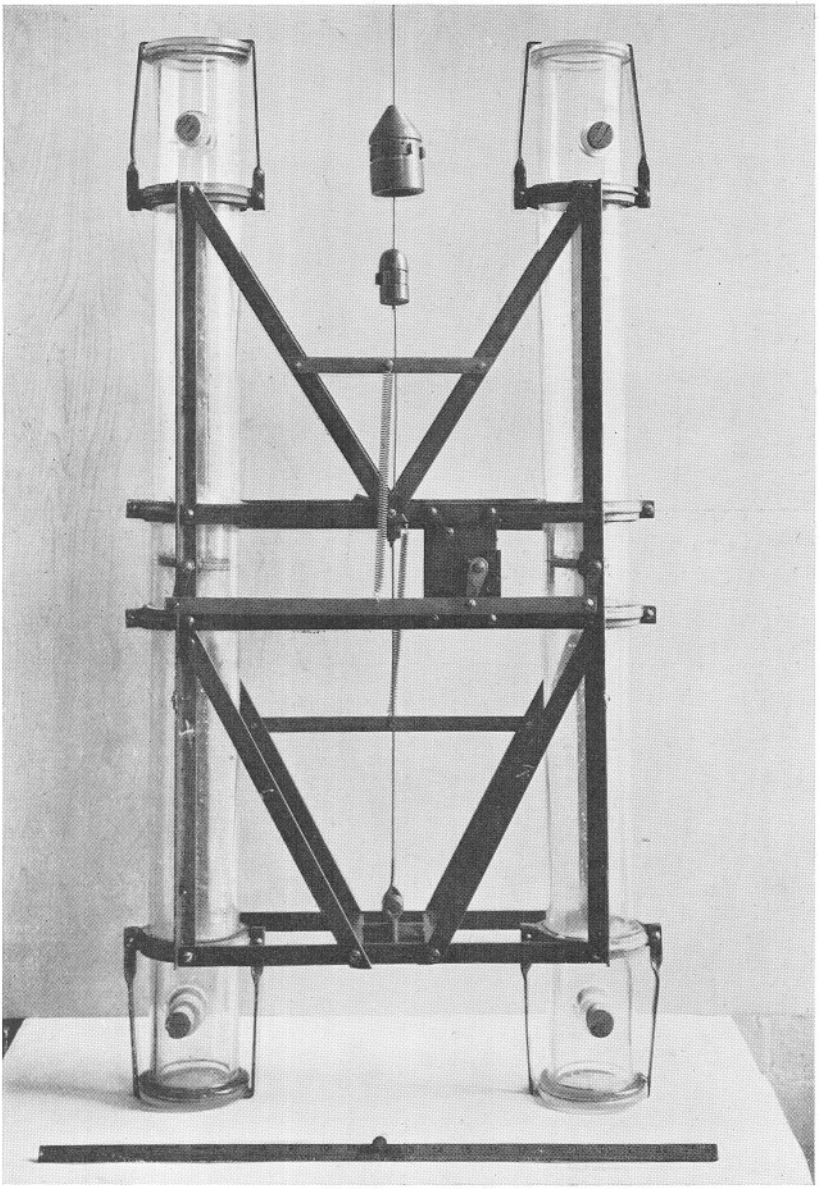
turned through 90° so that they now allow free communication between A and B, and α and β. A further turn of 90° brings them into 'position 3', so that they again form a partition between the two compartments as in 'position 1'. The spindles of the two trapdoors, being linked together by cranks and connecting rods, are turned by a spring and trigger mechanism T which may be operated at any depth below the surface by messenger weights M_1 and M_2 slid down the supporting wire from above.



Text-fig. 1. Diagram of Apparatus No. 1; for explanation see text.

At the beginning of an experiment the cylinders are filled with sea water and the trapdoors are set in 'position 1': plankton animals are then introduced into one only of the two compartments in each cylinder. When the machine has been lowered to the required depth, the first messenger weight M_1 is sent down to turn the trapdoors to 'position 2'. The plankton animals are now free to move up or down the whole length of the cylinders. After a certain time has elapsed the second messenger weight M_2 is dispatched to close the trapdoors again, to 'position 3', and so divide each cylinder once more into its two compartments; now the machine may be brought to the surface and the contents of each compartment extracted and preserved separately for laboratory examination and counting. If, for example, the plankton had been placed at the start in A, but not in B, and yet at the end of the experiment we find some animals in B, we can then estimate the percentage of those which have moved downward in AB, and similarly in $\alpha\beta$. *Vice versa* starting with the animals in B but not in A we can estimate the percentage of those which have moved upwards in AB and similarly in $\alpha\beta$. A sketch and photographs showing the details of the structure of the apparatus are given in Text-fig. 2, Pl. IX, and Pl. X, fig. 3.

It will be seen that the apparatus can be used for a number of different purposes. The animals may be introduced into the corresponding compartments of each side to give comparative dual experiments. At other times they may be introduced into the top compartment of one side and into the bottom



Apparatus No. 1 in its original form.

Fig. 1.

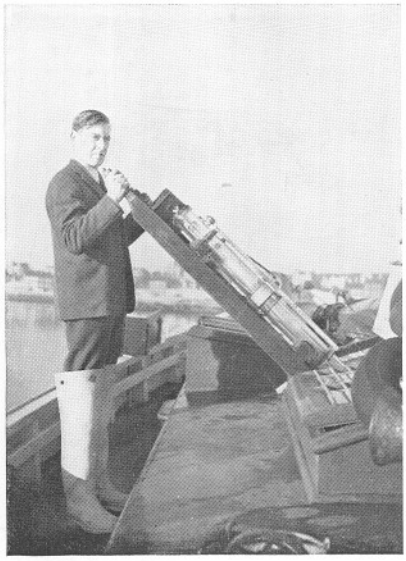


Fig. 2.

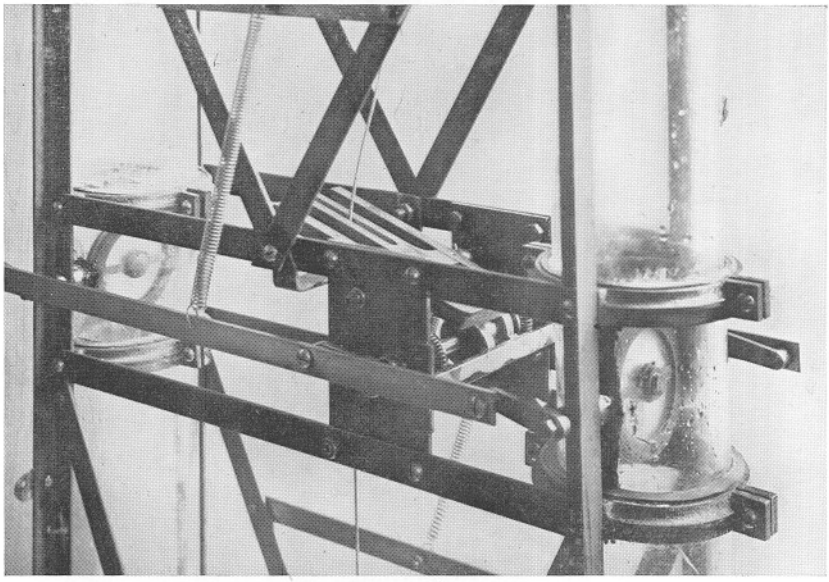
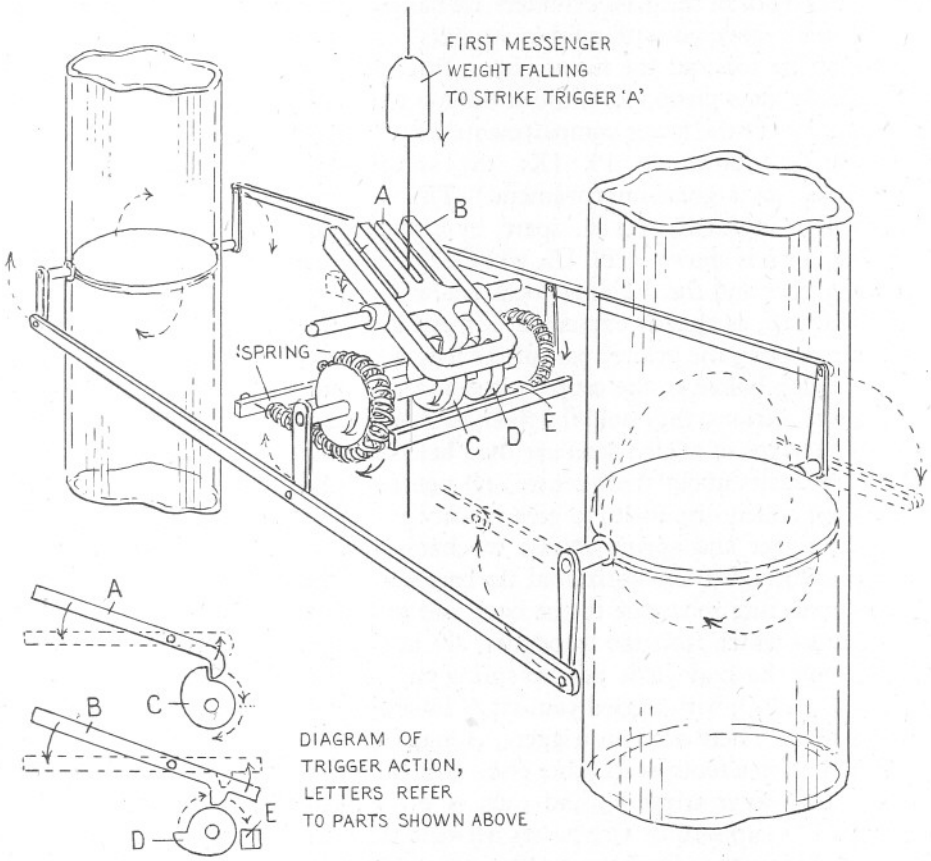


Fig. 3.

compartment of the other, so that the numbers moving up or down under similar conditions may be compared. The experiments described here are mainly of this nature. Again, and this is the ultimate object of the apparatus, we may use one side as a control, keeping the conditions as far as possible constant for a number of experiments, and alter one by one the conditions of the environment on the other side (e.g. *p*H, oxygen content, light and shade,



Text-fig. 2. Sketch of trigger and spring mechanism of Apparatus No. 1, with parts of the steel supporting frame omitted.

phytoplankton concentration, etc.) until the different factors which may affect the vertical migrations of the animals have been analysed. As yet only a small beginning has been made in this direction.

Detailed description

The cylinders have an internal diameter of 3 in. and are each made in three sections, two 18 in. long of glass $\frac{1}{4}$ in. thick and a short centre-piece which

holds the trapdoor and its spindle. This centre-piece was originally of glass, 4 in. long, as shown in Pl. X, fig. 3; but later it was made of metal (3 in. long) to ensure a better fit for the trapdoor, provide better bearings for the spindles and avoid the danger of cracking. Formerly the three sections were held together by metal clamping pieces lined with thick rubber, but latterly the two glass sections fitted into sockets at either end of the metal centre-piece. The distal ends of the glass cylinders are flanged to a thickness of $\frac{5}{8}$ in. to make broad seats (covered with rubber washers) against which are held the glass plates at the top and the metal plates, fitted with stopcocks, at the bottom. (Originally glass plates like those at the top were used also at the bottom, and the contents of the lower compartments were drained out through the corked bottle-necks shown in Pl. IX; the substitution of metal plates with stopcocks was a great improvement.) The two tripartite cylinders are held in position in parallel, 11 in. apart, by a metal frame. The apparatus in its original form is shown in Pl. IX, while Pl. VIII shows it fitted with the metal centre-pieces and the draining cocks below.

The frame, as already explained, is made as open as possible. Angled steel strips run along the greater part of the length of the cylinders at the back and front; being bolted to the centre-piece and to metal clamps round the upper and lower sections, they hold the three parts of each cylinder securely together. The two strips of angled steel are then held in parallel by horizontal steel tie bars, two pairs about their centre and one pair towards the bottom. Other strips are added diagonally to give rigidity as shown in Pl. IX.

The trigger and spring release mechanism, illustrated in Text-fig. 2, is mounted between the horizontal tie bars about the centre of the machine. The connecting rods, one to the back and one to the front, linking together the cranks which turn the trapdoors, are in addition each linked to a crank turned by the main axle of the spring mechanism. On this axle are two cams, *C* and *D*, with angled cam-stops into which fit the teeth of the trigger mechanism. There are two triggers, *A* and *B*, each with paired release arms and each with a tooth at its other end. One lies between the arms of the other (inner and outer triggers), and each is pivoted about two-thirds along its length. The supporting wire passes between their arms (to a clamping shackle below), and so they form the striking points for the messenger weights which slide down the wire. The main axle with its two cams is turned by two springs; these stretch over and are attached to drums on the axle, their other ends being fixed to a stationary bar a short distance away. When the trapdoors are set at 'position 1' for the beginning of an experiment the springs are at their maximum tension and held by the inner trigger tooth which is caught in its cam-stop *C*. When the first and smaller messenger strikes, the inner trigger *A* is depressed and its tooth raised; the axle immediately rotates through 90° and a second cam-stop *D* is caught by the tooth of the outer trigger. The trapdoors, being linked with the cam axle by connecting rods,

are also turned through 90° into 'position 2' giving free passage between the upper and lower parts of the cylinders. At the end of the experiment the second messenger is allowed to slide down the wire; being hollowed out to fit over the first messenger, and being so much larger, it strikes and depresses the arms of the outer trigger *B*. This raises the second tooth; the springs turn the axle through a further 90° bringing the trapdoor to 'position 3', and so close once more the passage between the two halves of the cylinders. Extra springs were added stretching between the connecting rods and the steel frame (see Pl. X, fig. 3). The two messengers are shown suspended on the wire in Pl. IX.

The trapdoors were originally made of two half circles of plate glass held on a metal spindle by circular metal rings (see Pl. X, fig. 3). The edges of the trapdoors were of rubber which bedded against the glass sides of the centre-piece. This proved to be an unsatisfactory arrangement, and in the winter of 1938–9 a modified centre-piece was introduced. The trapdoors and spindles are now all metal in one piece, with the edges of the doors bevelled to give a good fit against the inside of the centre-piece. This is also of metal, but where the trapdoor edges fit against it, there is a ring of rubber let into its walls. By the introduction of this modification each trapdoor is now watertight when closed, and there is no danger of the centre-piece becoming strained owing to the impact of the rotating trapdoors. The metal was brass, which was found to be highly toxic to Calanus. A good deal of time was spent in discovering why the Calanus died, but finally the trapdoors and centre-piece (as well as the metal bottom plates) were silver-plated, and the toxic effect was overcome.

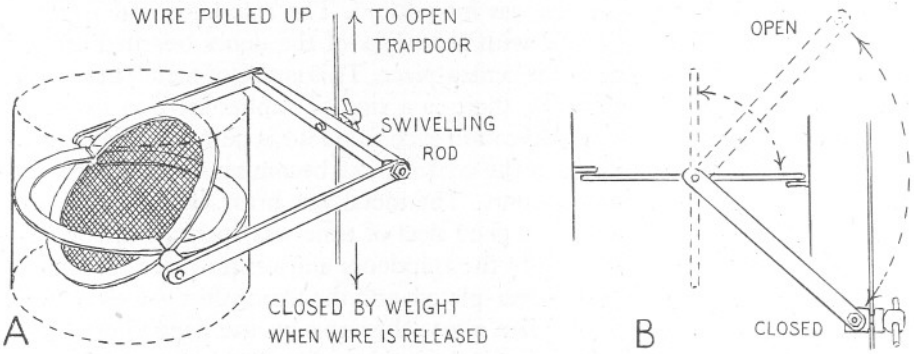
The top plates are of $\frac{1}{4}$ in. plate glass; they rest on the flanged lip of the cylinders with a flat rubber washer interposed, and are held in position by an open metal ring with two slotted wings opposite each other on the circumference, into which fit threaded arms with butterfly nuts. These arms are attached to the metal framework of the apparatus, and the nuts can be screwed down till the joint is watertight. There is essentially the same fitment at the lower end of each cylinder, but here the bottom plates are of silver-plated brass with centrally placed stopcocks. The inside of each of these is slightly concave so that the water and plankton may more easily be washed through the draining cock. The metal bottom plates and glass top plates with their metal rings are interchangeable end for end.

In the general set up the apparatus is suspended on a thin steel wire which is threaded between the trigger arms and attached by a shackle to a central bar at the base of the frame. Attached also to this bar is a heavy weight on a length of line, to keep the apparatus vertical and to prevent swinging due to water currents.

The whole apparatus is lowered over the side of the boat, and the wire let out over a recording sheave slung on a davit. A rope 'life line' is always attached to the frame in case the wire should break.

Apparatus No. 2

A modification of the original apparatus was made in the winter of 1938–9; it is shown in Pl. XI, figs. 1 and 2. A number of glass cylinders, in the present instance seven (but the number might be very much increased), each 18 in. long with an internal diameter of 3 in., is connected in series with intervening metal pieces (cylinders only 2 in. in length) which are not unsimilar to the centre-pieces of Apparatus No. 1. The ends of the glass cylinders butt up against the rims of these metal connecting pieces and a broad rubber band fits over the junction. This rubber band is in turn clasped above and below the joint by narrow bands of brass which may be tightened by thumbscrews. In each connecting piece is a circular trapdoor mounted on a spindle which passes through its walls to be attached to levers fixed at 45° to the plane of the trapdoor. Each trapdoor, which is of phosphor-bronze gauze set in a flat



Text-fig. 3. Trapdoor mechanism of Apparatus No. 2. A is a sketch showing the trapdoor in half open position; B is a diagrammatic side view.

metal ring, beds itself down against two semicircular flanges running round the inside of the connecting piece: one above the one-half of the trapdoor and to one side of its spindle, and the other below the other half and on the opposite side of its spindle (see Text-fig. 3). By lifting the levers through 90° the trapdoor is turned from its closed position, at right angles to the axis of the cylinder, to its open position in line with the axis. It can be turned no further. All the metal parts were silver plated to avoid the toxic effects which had been observed in Apparatus No. 1 before a similar remedy was applied (see above, p. 473).

The whole system of alternate glass and metal connecting pieces is suspended vertically in the water attached to a stout wire cable by means of thumbscrew clamps situated on the side of the connecting pieces (Pl. XI, fig. 2). A heavy weight on the end of the cable keeps the whole in alignment, while the rubber bands allow just sufficient flexibility to prevent any strain upon the glass pieces. The whole forms one cylinder nearly 12 ft. long containing six gauze

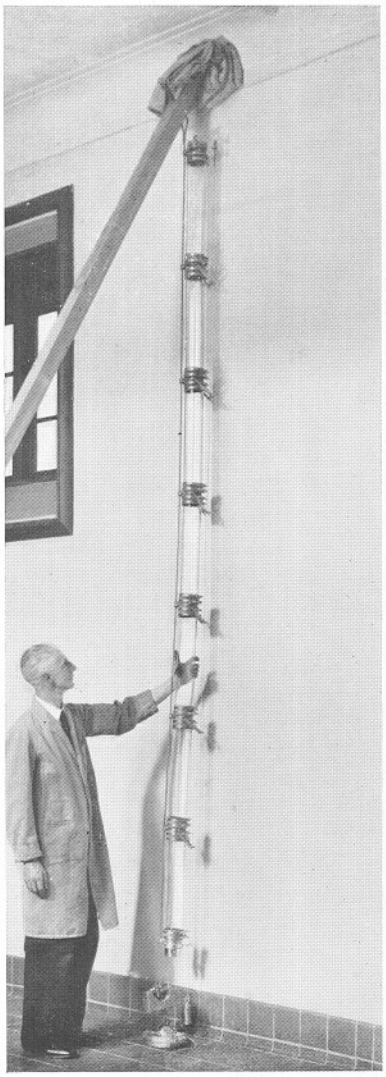


Fig. 1.

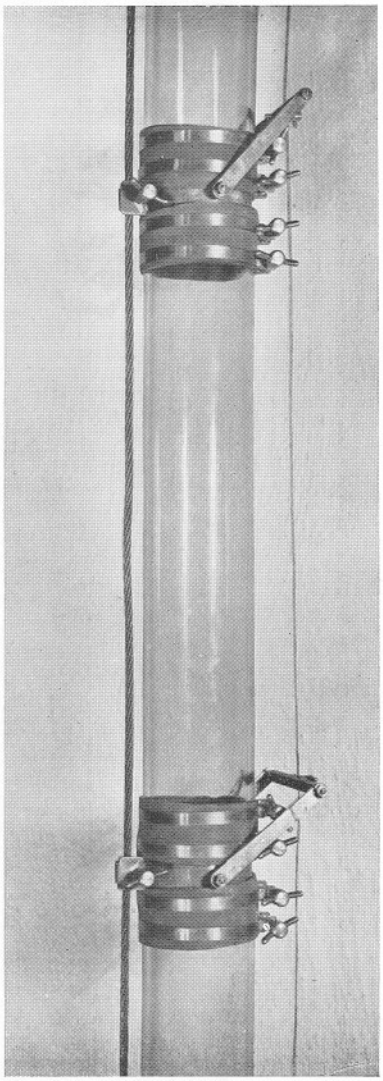


Fig. 2

trapdoors at intervals down its inside: its top and bottom are closed respectively by a glass plate and a metal gauze disk held in metal pieces. Into the sides of the top metal piece are let panels of phosphor-bronze gauze. Now if the whole apparatus (when it has been assembled as described below) is lowered slowly into the sea, the water will rise in it, passing up through the bottom gauze, through all the gauze trapdoors and out through the gauze side panels in the top piece. Thus by lowering it from a boat we enclose within it an actual column of the sea itself.

One other device must be described. All the levers which will turn the gauze trapdoors are secured by little swivelling screw clamps to a thin wire which has a small weight attached to its lower end and hangs down beside the apparatus (see Pl. XI, fig. 2). The upper end of this wire passes up to the boat above. As this wire is paid out the weight at its end holds all the levers hard down so that each gauze trapdoor is closed at the beginning of an experiment. Plankton (as will be explained below) may be introduced into any *one* of the compartments (top, bottom, or perhaps one of the intervening ones) cut off from the rest of the cylinder by the gauze trapdoors. When the apparatus has been lowered to the desired depth, the end of the thin wire is pulled up so that each of the levers rotates through 90° and all the trapdoors open in unison. The wire is secured in this position and the plankton animals are now free to travel vertically up or down the whole length of the cylinder. After a prearranged interval of time the wire is slackened so that the weight falls, and all the levers are pulled down; this closes all the trapdoors again and divides the cylinder as before into a series of separate compartments. The apparatus is now hauled up and as the water drains out through the gauzes so the plankton from each section is found on the gauze immediately below it, and is washed off and preserved separately as the cylinders are dismantled.

The whole device can readily be assembled or taken apart. In assembling, section after section is clamped to the supporting cable as it is lowered over the side of the boat; at the same time the trapdoor levers are secured one by one to the weighted operating wire which keeps them pressed down in the closed position. The plankton is introduced by a long rubber siphon when the appropriate section is partially submerged. When the plankton is placed in any but the top section care must be taken in lowering lest the surge of the water, as the apparatus fills, should cause the animals to be pressed against the gauzes and so damaged; the apparatus must be lowered very slowly.

Only five experiments with Calanus have so far been performed with this apparatus, and in each the top of the apparatus was sunk only about 6 in. below the surface;[1] the results are discussed on pp. 510–15.

[1] In experiments with fresh-water plankton animals made in Lake Windermere the apparatus was at times lowered to a depth of 10 m. and worked just as satisfactorily as near the surface. There is no reason why it should not be worked at much greater depths.

Methods

It will be most convenient to describe the procedure adopted in the preparation and carrying out of one typical experiment (with Apparatus No. 1) and later to give the modifications of this method in particular instances.

The plankton was usually caught between 8 and 9 o'clock in the morning by means of stramin ring nets (1 m. diameter) fished at a depth of between 60 and 90 m.;[1] it was known that the Calanus were generally most abundant at this range of depth at this time of the day. Usually two nets were attached to the towing warp about 10 ft. apart and towed horizontally for $\frac{1}{2}$ hr. The nets would fish very little on the way down because they were veered out at almost the same speed as the forward motion of the boat. They would, however, fish on the way up; but the time involved is small compared with that of the haul proper (7–10%). Occasionally more than one haul was necessary to secure sufficient animals, but generally the catches in the Clyde sea area are remarkable for the numbers of Calanus they contain.

It was desirable to interfere with the animals as little as possible, so that except in certain special experiments the Calanus were not individually picked out, but part of the plankton sample was used just as it was caught. This was possible because in most cases, being caught with a coarse-mesh net of stramin which let the smaller animals escape, the sample was composed almost entirely of this one species of copepod.

Since light was considered from the results of earlier workers to be the most important factor influencing the behaviour of the animals, precautions were taken to avoid exposing them at any moment to the above-surface daylight. The apparatus was always filled in the cabin of the boat with the skylights covered with cardboard screens. The cabin was so dark that it took the operator 2 or 3 min. to discern objects even dimly. It was found that no reading was given on a Cambridge Unipivot 'LX' galvanometer when coupled direct to a Weston photocell, even with appreciably brighter conditions in the cabin. When the nets were hauled to the surface, the cod-end, with its opaque (zinc) bucket attached, was lowered into this darkened cabin through the skylight which was then closed. The contents were then transferred to glass jars (breffits) from which they were later siphoned into the apparatus; care was always taken not to include the animals at the very bottom, since these might be in a moribund condition.

In a typical experiment the plankton (mainly Calanus) was introduced into the top compartment A of one side of the apparatus and the lower compartment β of the opposite side; the other two compartments B and α were filled with sea water filtered to exclude all plankton.

[1] Tests made with a depth recorder attached to the line just above the nets are described on p. 491. They show that the depth was usually between 60 and 70 m., but sometimes as deep as 90 m.

When loaded the apparatus was placed on a wooden frame with handles at either end just like a stretcher (Pl. X, fig. 2); it was necessary to have some such device to enable the machine to be handled easily without fear of breakage. As it was placed on the stretcher it was covered with a black cloak of calendered linen. The stretcher was then passed up through the skylight of the cabin, the apparatus taken off it and lowered to just below the surface of the sea (Pl. X, fig. 1). Only then was the black cover removed (by pulling a system of cords) and the machine lowered quickly to the required depth, say 5, 10 or perhaps 50 m. Though these precautions against abnormal illumination could not be continued to the depth of the experiment, it was felt that the protection afforded till the apparatus was below the surface would considerably reduce the stimulation from light to which the animals would otherwise be exposed. From the moment of capture to the time when they were lowered again below the surface of the sea the animals were never exposed to above-surface illumination.

The experiment was now begun by the first messenger weight being sent down the suspending wire to open the trapdoors. The animals were now free to move up and down the whole length of the cylinders. Usually at the end of an hour the second messenger was sent down to close the trapdoors again and prevent further migration between A and B and β and α. Very occasionally the experiment was of only half an hour's duration, and such exceptions will be specially noted.

The apparatus was then hauled up to the surface, taken below to the cabin, and the populations of Calanus in each compartment extracted, and preserved separately. Those from the top compartments were siphoned off; those in the lower compartments drained through the stopcocks. The samples were taken to the laboratory where they were counted, separated into sexes and developmental stages, and examined for food remains in the gut. The total of the animals found in A and B reveals the number introduced into A at the beginning of the experiment, and the number found only in B gives the number of those which have migrated *downwards* during the experiment. Similarly, the total found in α and β gives the number originally introduced into β, and the number in α alone shows those which have migrated *upwards* during the experiment. The numbers which have moved upward and downward can now each be expressed as a percentage of the total population in the appropriate side of the experiment. The results of all the experiments, together with particulars of date, time, position, weather, etc., are given in tables in the Appendix (pp. 524–6).

In all the experiments the general plan of procedure was as outlined above, but in some, as will be described later, certain modifications were introduced for special purposes.

All the experiments were made in the months August to November: Exps. 1–39 between 2 August and 11 November 1938, and 40–75 between

21 August and 22 November 1939. It had been hoped that the early summer months of 1939 could be used, but certain technical difficulties (see p. 473) as well as limitations of opportunity for sea work interfered.

Limitations of Method

The main purpose of these experiments was to examine the behaviour of Calanus under as natural conditions of illumination as possible. It is realized that the methods employed do hold considerable artificialities; yet it is felt that they are nearer to natural conditions than experiments in the laboratory. This contention is supported by the results of Exps. 68–75, in which individuals of the same original stock of Calanus showed a marked change of behaviour after being kept in the laboratory for 3 days. This does not seem to be due merely to a lowering of their vitality, since the whole of the remainder of the stock lived healthily for a fortnight, and many for 6 weeks, afterwards in the laboratory.

We have no means at present of telling how far the precautions taken, e.g. darkening of the cabin, cloaking of the apparatus, etc., are effective or necessary. The Calanus must have experienced some abnormal conditions during capture. The results of the experiments at any one depth, however, are with a few exceptions remarkably consistent.

The water used for the experiments was, nearly always, taken either from the surface or pumped from just below it. The fact that Calanus are thus introduced into water which may differ considerably (e.g. salinity, oxygen content, *p*H, etc.) from that from which they were caught may be a source of error. It would appear not to be great however, as on two occasions experiments were conducted using surface water in one side of the apparatus and water from 30 m. (drawn with a water bottle) in the other, and the difference in behaviour in the two sides was only slight (see p. 507).

Usually we attempted to use just over 100 Calanus in each side of the apparatus to allow the calculation of a true percentage. This was very difficult to judge in the dark, and the numbers used range between 20 and 1400. Each side of the apparatus holds about 2·8 litres of water which gives a range of population density from 7 to 500 Calanus per litre. The lowest figure probably fairly represents a density to be found in the sea (catches of Calanus in a water bottle have on occasions contained 6 per litre), but the higher value must represent abnormally crowded conditions. However, even at this high figure, such physical conditions as oxygen tension in the cylinder would probably not be significantly different at the end of 1 hr. Marshall, Nicholls & Orr (1935) show that the maximum respiration rate of female Calanus was 0·75 ml./l./hr. up to 3 hr. after capture. Using this figure the highest density in our experiments would produce a fall in oxygen tension of

0·39 ml./l./hr. Probably the actual value was below this, as a large proportion of our Calanus were Stage V, whose respiration rate is below that of adults, but in any case Marshall *et al.* found that Calanus were affected only after the tension had fallen by over 2 ml./l. Other chemical factors might be involved and, further, the population density in the tube might have a purely mechanical effect due to obstruction. However, when the results at any one depth are plotted against a scale of population density there is no correlation: a random distribution of the points is found.

There are various other ways in which these experimental conditions might affect the behaviour of the Calanus. In the first place they might be disturbed by bumping into the sides of the apparatus, or obstructed by the trapdoor in its vertical position. Again the surge produced by the rotation of the trapdoor might introduce a false distribution. Whether the first type of interference occurs to any extent can easily be ascertained. If the sides of the cylinder or the trapdoor do interfere with the movements of the animals, then, in standard-type experiments in which the plankton was introduced into A on one side and β on the other, one would expect at the end of an experiment to find a higher percentage in β than in B. Omitting experiments below 30 m. in which another factor (referred to later) may arise, there are eighteen such standard experiments performed between depths of 1 and 20 m.; in eight the percentage is higher in B and in ten it is higher in β: there is clearly no significant difference.

The 'surge' effect was examined in the laboratory. There is certainly some disturbance set up by the opening trapdoors, but it is felt that any result of this momentary effect would be counteracted by the stimulus of light or other factors operating for an hour. Also the effect would be the same on both sides of the apparatus.

The possible effects of shadow produced by the metal parts must be considered. The most important of these must be the shading from the trapdoors and centre-piece. If this was a considerable factor in the final distribution of Calanus in the cylinders, one would expect it again to show as a difference in the results of the two sides when the original place of introduction in each differed. We have just seen that in the upper 20 m. this is not so. The effects of shadow would seem to be too fine to be shown by these experiments. In 1938 the apparatus had a cylindrical glass centre-piece, while in 1939 this was replaced by a metal one. It was feared that this metal centre-piece would possibly create a shadow past which the Calanus might not move or in which they might collect. The results, however, from the two years are quite consistent; the illumination came of course vertically down the tube.

Such factors as are discussed above do not appear to have concealed the main outlines of behaviour.

Discussion of Results

In the following discussion only the results of the behaviour of the fifth copepodite stage are treated in detail. The other stages, including adults, occur in too small numbers to give comparable pictures, but in some cases there are sufficient males and females to give a rough comparison, and these are included in the discussion. A few results with the copepod *Euchaeta norvegica* Boeck are also given (p. 502). Unless otherwise stated the Calanus figures throughout will refer to Calanus Stage V.

The preliminary nature of the work so far accomplished is again emphasized; but for the outbreak of hostilities the experiments would have been carried much further before the publication of results. It is realized that there are too few experiments as a whole and that the special ones require further development. The main results, however, are felt to be of sufficient interest to record, and the more special side issues have been included as they indicate useful lines for future inquiry.

The results of sixty-five experiments with Apparatus No. 1 are here considered: Exps. 1–21, 23–39 and 49–75. Exp. 22 was made with *Thysanoessa* and, offering insufficient evidence, is excluded; Exps. 45–48 are also excluded because of the toxic effect of the new metal centre-pieces and bottom plates referred to on p. 473 and overcome in subsequent experiments by silver plating. Exps. 40–44 were made with Apparatus No. 2.

Standard experiments—statement of results

It will be convenient to deal first with the standard experiments which formed the main part of the work and were designed to study the behaviour of Calanus under the different light conditions met with at different depths in the sea. All those considered in this section were performed between 0800 and 1600 hr. (G.M.T.); other similar experiments made in the evening or hours of darkness will be described separately.

In these preliminary experiments it was felt that only relative light conditions need be considered; we had not the equipment to measure the exact intensity of light at each experimental depth. The relative light intensity at any given depth will not only vary from hour to hour, but also from day to day at the same hour according to various weather conditions. An indication of light penetration, however, was obtained by the use of the Secchi disk[1] with each experiment.

Under the heading 'Standard experiments' there are two kinds, which may be termed *double-* or *single*-standard experiments.

[1] The Secchi disk is a white disk used to measure the transparency of water. It is lowered below the surface on a line at the end of which it is suspended by three cords of equal length running to its circumference; below, supported by three similar cords, hangs a weight which keeps the disk horizontal and the line vertical. A measure of the transparency of the water, and so an indication of the relative light penetration, is obtained by lowering the disk and noting the depth at which it just disappears.

A *double* standard experiment is one in which both cylinders of the apparatus are subjected to the same conditions, but the Calanus are usually introduced into the upper compartment (A) of one side and into the lower compartment (β) of the other. The carrying out of such an experiment has already been described under the section on methods.

A number of other experiments have been performed in which the conditions in one cylinder are normal, as a control, but those of the other have been altered as part of the experiment. The results of the normal control cylinders will be considered along with those of their more special partners when these are dealt with later; but by themselves they may also be considered here as *single*-standard experiments.

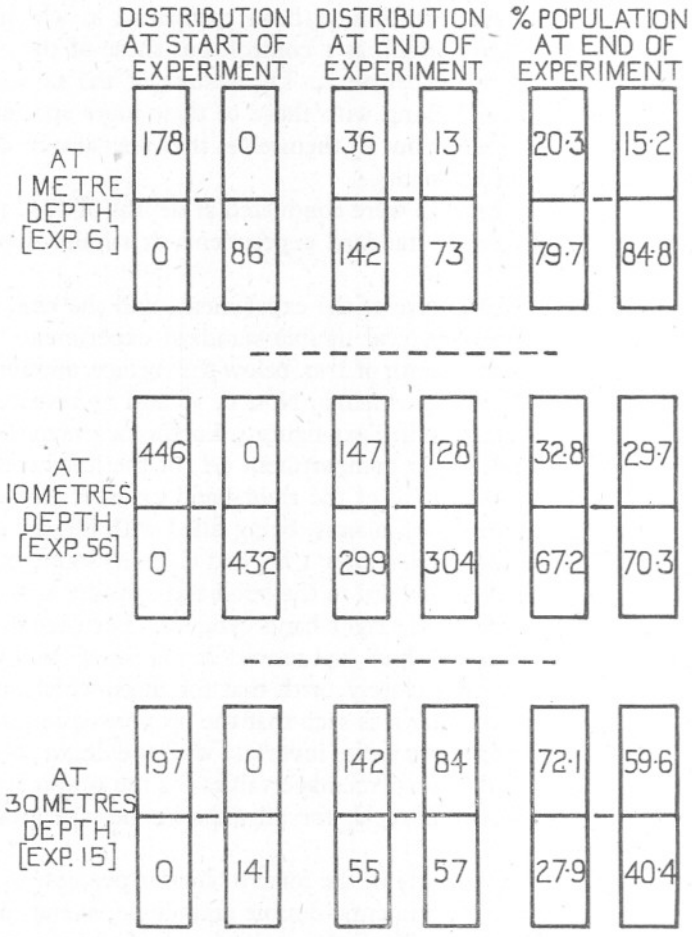
Double-standard experiments were conducted at depths of 1, 5, 10, 20, 30, 40, 50 and 100 m. and single-standard experiments at similar depths down to 30 m.

To make quite clear the nature of the experiments and the kind of results obtained, three examples of typical double-standard experiments may first be considered: one made at a depth of 1 m. below the surface, another at 10 m. and the third at 30 m. The experiments, Nos. 6, 56 and 15 respectively, are compared in diagrammatic form in Text-figure 4. Each experiment started with the Calanus placed in the upper compartment (A) of the left-hand cylinder and in the lower compartment (β) of the right-hand cylinder; the other two compartments (B and α) had no Calanus, being filled with filtered sea water. At the end of each experiment (i.e. after 1 hr. had elapsed) some, but not all, of the Calanus had moved downward in the left-hand cylinder and some, but not all, had moved upward in the right-hand cylinder. For each experiment the percentage value for those which had moved down on the one side corresponds, either closely or fairly closely, with that for those which had stayed down on the other side. Further it is seen that the proportion of those which had moved down or stayed down varies inversely with the depth at which the experiment was performed. The percentage values for the proportions found in the lower compartments, B or β, for all experiments are given in the Appendix, Table II.

Text-figure 5 shows graphically in the form of similar percentage diagrams the results of all standard experiments, double and single, averaged for each depth at which they were made. The left-hand column of each pair represents the cylinder of which the Calanus were introduced into the upper compartment, and the right-hand column that of which the Calanus were introduced into the lower compartment at the beginning of each experiment. The number of experiments of each kind averaged for each depth are shown by figures below each column. The use of average percentages gives a clear indication of the general change over in the proportions of the Calanus population which move up or down as the experiments are performed at different depths. The actual numbers for all experiments cannot be summed and averaged because

the totals used in different experiments vary widely and the experiments are performed over different dates under a range of different weather conditions.

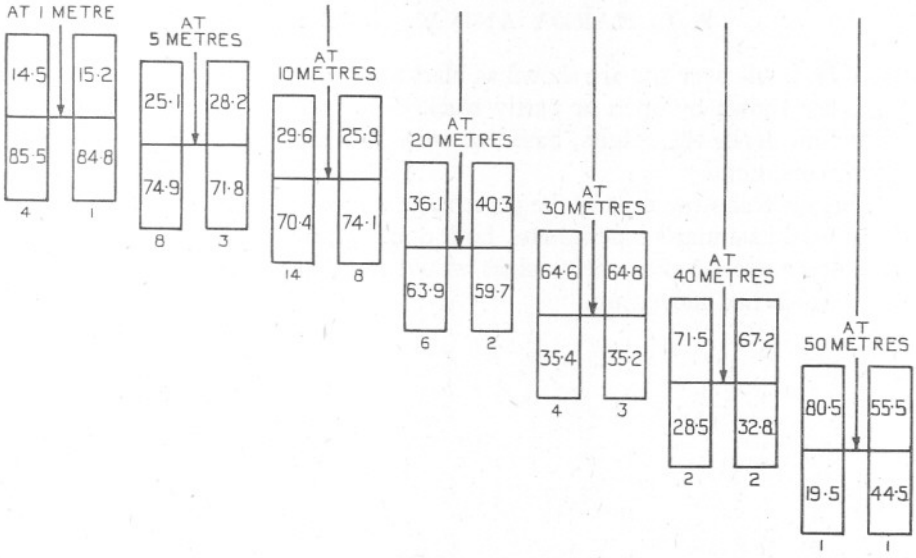
Text-figure 6 shows the individual results of all double-standard experiments. The positions of the blacked-in circles represent the percentage values



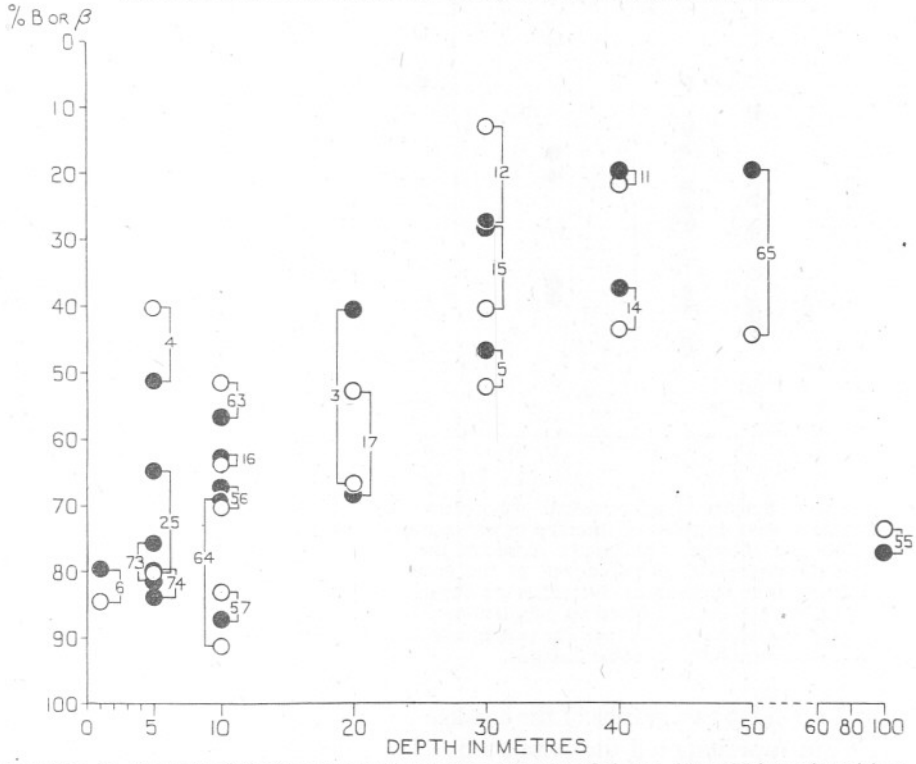
Text-fig. 4. Diagram of results of three standard experiments, Nos. 6, 56 and 15, performed respectively at depths of 1, 10 and 30 m.

for the Calanus which have moved down and the positions of the open circles the percentage values for those which have stayed down in the opposite cylinder of each experiment. The results from the two cylinders in any one experiment are linked together.

Text-figure 7 shows the percentage values of those which have moved down for all standard experiments, both double and single. The percentage values



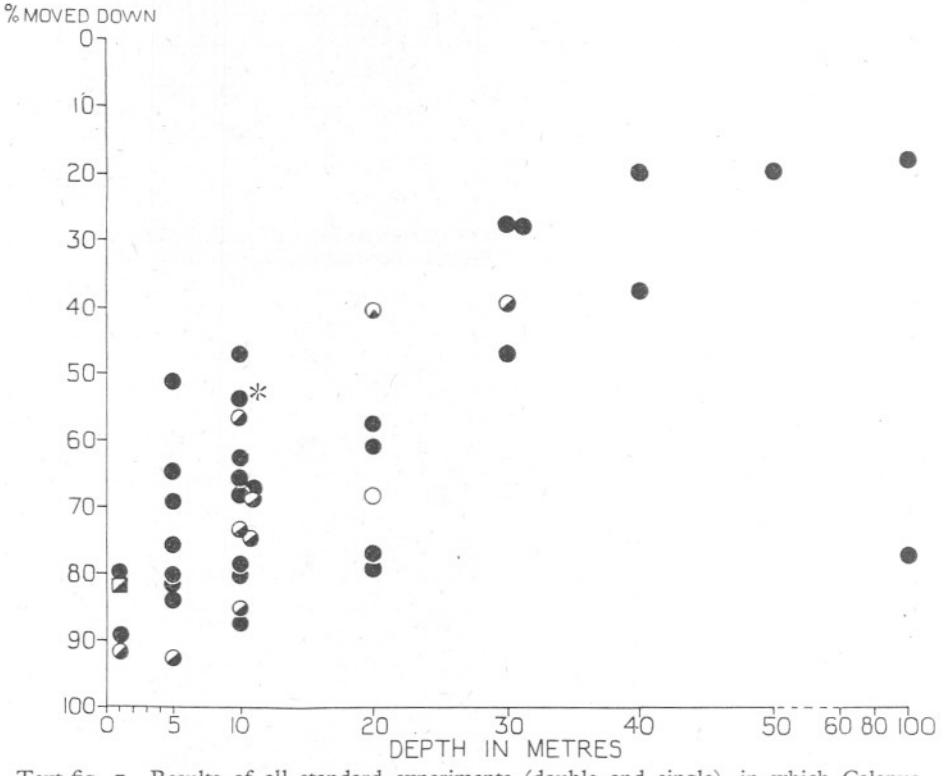
Text-fig 5. Diagram of the averaged results of all standard experiments performed between 0800 and 1600 hr. at depths of 1–50 m. For full explanation see text.



Text-fig. 6. Results of double-standard experiments with Calanus Stage V introduced into *A* on one side and *β* on the other (except in Exps. 73 and 74, in which they were introduced into *A* and *α*) carried out in daylight between 0800 and 1600 hr. The blacked-in circles represent the percentage Calanus which have moved down (into *B*) and the open circles the percentage Calanus which have stayed down (in *β*). The two results for each experiment are linked together with its reference number.

based on totals over 100 are shown as blacked-in circles, those based on lesser totals are shown by open or partly blacked-in circles (see legend to figure). At 100 m. depth the results, based on only two experiments, are seen to be very inconsistent.

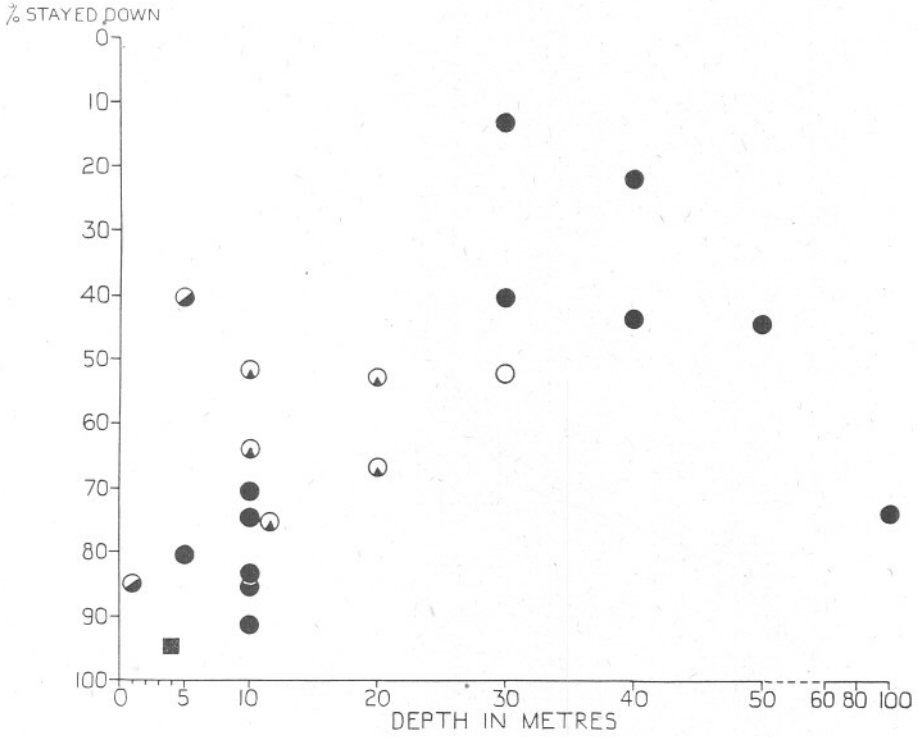
Text-fig. 8 shows similarly the percentage values of those which have stayed down for all standard experiments, both double and single. If the percentage scale was reversed then their values would naturally give the percentage of those which had moved up.



Text-fig. 7. Results of all standard experiments (double and single), in which Calanus Stage V were introduced into the upper compartment, carried out in daylight between 0800 and 1600 hr. The circles represent the percentage Calanus found in the lower compartment (i.e. moved down) at the end of each experiment. The single square represents an experiment (No. 40) with Apparatus No. 2 (see p. 513). Blacked-in circles represent percentages based on populations > 100, half-blacked 51–100, quarter-blacked 26–50 and open circle 21–25. The percentage result with an asterisk is a little too low due to an accidental loss of some Calanus.

In Text-fig. 9 two graphs of the average percentage values from Text-figs. 7 and 8 are superimposed for comparison. The numbers against the points on the graphs show the number of experiments averaged. The percentage values are also shown in Table I. At 50 m. there is only one experiment of each kind

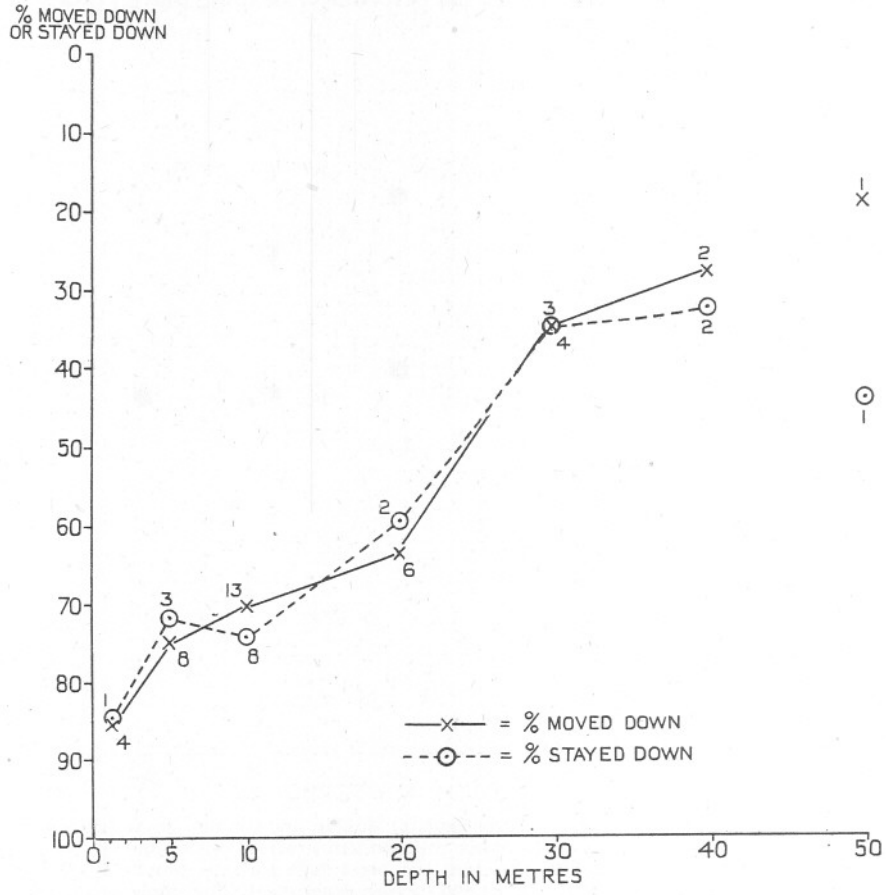
(one double experiment); while it is unwise to draw conclusions from just one experiment there is a suggestion, for future investigation, that at this depth more Calanus tend to remain in the compartment into which they were introduced. Against this latter suggestion is the result of the double experiment at 100 m. (Text-fig. 6), where the percentages of those moved down and stayed down are closely similar.



Text-fig. 8. Results of all standard experiments (double and single), in which Calanus Stage V were introduced into the lower compartment, carried out in daylight between 0800 and 1600 hr. The circles represent the percentage Calanus found in the lower compartment (i.e. stayed down) at the end of each experiment. The single square represents an experiment (No. 41) with Apparatus No. 2 (see p. 513). Blacked-in circles represent percentages based on populations > 100, half-blacked 51–100, quarter-blacked 26–50 and open circle 21–25.

Text-fig. 10 shows together the percentage values of male and female Calanus which have moved down or stayed down for the limited number of experiments in which there were numbers worth considering (over twenty, see reference in figure legend). The percentage values of those moved down are shown as circles and of those stayed down as squares. Clearly the number of experiments and the number of adult Calanus available are too small to point to any definite conclusion, but there is a suggestion that the trend of

their behaviour is in the same direction as that for Stage V but in a much less marked degree. Where there are sufficient males to be included their percentages are usually very similar to those of the females in the same experiments.



Text-fig. 9. The crosses, connected by a continuous line, represent the average percentage values of Calanus Stage V moved down in all standard experiments (i.e. the average of the values shown in Text-fig. 7), and the points within circles, connected by a broken line, represent the average percentage which have stayed down (i.e. the average of the values shown in Text-fig. 8). The number of results averaged is shown in each case. The diverse results at 50 m. depth are based on only one experiment of each kind.

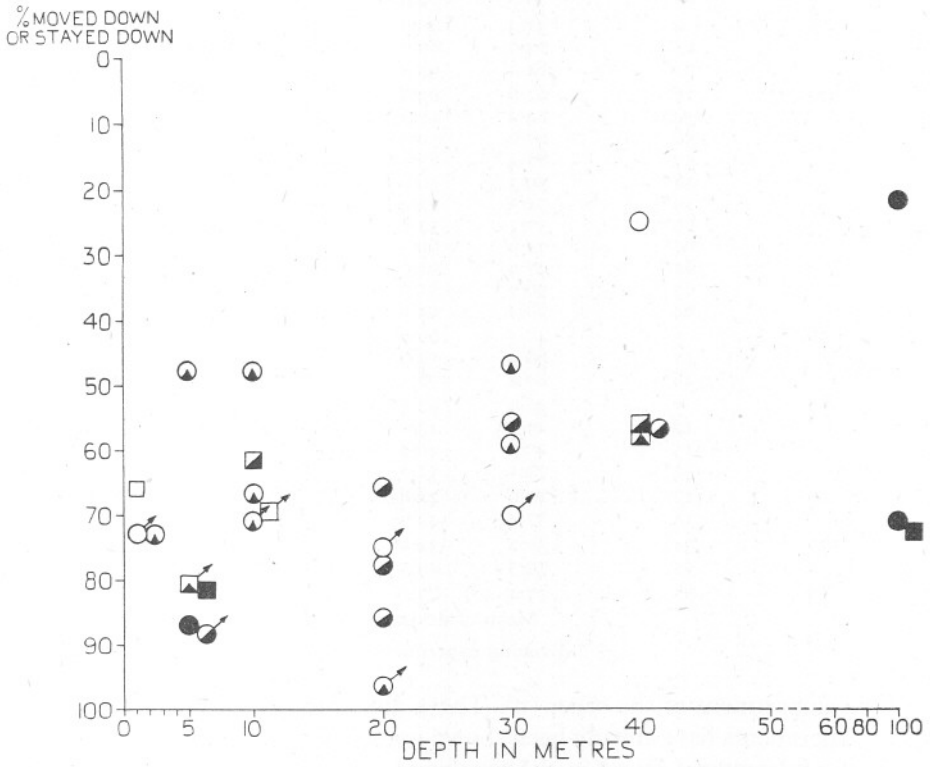
Significance of standard-experiment results

After this brief digression to look at experiments with male and female Calanus we may return to consider further the results obtained with Calanus Stage V, and now, as before, unless otherwise stated the term Calanus will always refer to Stage V only.

TABLE I. THE AVERAGE PERCENTAGES OF CALANUS STAGE V WHICH HAVE MOVED DOWN OR STAYED DOWN IN STANDARD EXPERIMENTS AT DIFFERENT DEPTHS IN THE DAYTIME (BETWEEN 0800 AND 1600 HR.)

Depth of exps. in m.	Average % moved down	Average % stayed down	Average % both moved and stayed down
0·5–1	$85·5^{4}$	$84·8^{1}$	$85·4^{5}$
3·5–5	$74·9^{8}$	$71·8^{3}$	$74·0^{11}$
10	$70·4^{13}$	$74·1^{8}$	$71·8^{21}$
20	$63·9^{6}$	$59·7^{2}$	$62·9^{8}$
30	$35·4^{4}$	$35·2^{3}$	$35·3^{7}$
40	$28·5^{2}$	$32·8^{2}$	$30·6^{4}$
50	$19·5^{1}$	$44·5^{1}$	$32·0^{2}$
100	$47·4^{2}$	$73·7^{1}$	$56·1^{3}$

Note. The index numbers refer to the number of experiments averaged.



Text-fig. 10. Results of standard experiments in which male and female adult Calanus were introduced into the upper compartments (shown as circles) or into lower compartments (shown as squares) carried out in daylight between 0800 and 1600 hr. The circles and squares represent the percentage Calanus found in the lower compartment (i.e. moved down or stayed down respectively) at the end of an experiment. The arrows attached to the symbols distinguish the male results from the female results. Blacked-in circles or squares represent percentages based on populations > 100, half-blacked 51–100, quarter-blacked 26–50 and open circles or squares 21–25.

Here will be a convenient place at which to discuss the nature of the difference that is found between the results of the two sides of the apparatus, in such double-standard experiments as we have been discussing, where the conditions on the two sides have been the same except that the Calanus have been introduced into the upper compartment of one side (A) and into the

TABLE II. SHOWING THE DIFFERENCE BETWEEN THE RESULTS OF THE TWO SIDES (AB AND $\alpha\beta$) OF ALL DOUBLE-STANDARD EXPERIMENTS IN WHICH CALANUS WERE INTRODUCED INTO THE UPPER COMPARTMENT (A) OF ONE SIDE AND INTO THE LOWER COMPARTMENT (β) OF THE OTHER

Depth in m.	Reference no. of exp.	% Calanus at end of exp. B	% Calanus at end of exp. β	Deviation of B and β from their mean	Mean of deviations at each depth
1	6	79·7	**84·8**	2·5	
5	4	**51·4**	40·3	5·6	
	25	64·9	**80·3**	7·7	
	32*	81·1	**93·1**	6·0	6·4
10	16	62·6	**63·8**	0·6	
	54*	84·3	**97·3**	6·5	
	56	67·2	**70·3**	1·6	
	57	**87·4**	83·1	2·2	
	58*	**59·3**	50·0	4·7	
	59*	72·3	**73·4**	0·6	
	60*	37·1	**57·8**	10·4	
	61*	**71·6**	69·5	1·1	
	62*	**97·4**	93·6	1·9	
	63	**56·7**	51·6	2·6	
	64	68·4	**91·2**	11·4	4·0
20	3	40·5	**66·6**	13·1	
	17	**68·4**	52·9	7·8	
	28*	**80·2**	76·1	2·1	7·7
30	5	46·9	**52·1**	2·6	
	12	**27·5**	13·0	7·3	
	15	27·9	**40·4**	6·3	
	30*	71·1	71·1	0·0	4·1
40	11	19·6	**21·8**	1·1	
	14	37·4	**43·7**	3·2	2·2
50	31*	30·2	**32·5**	1·2	
	65	19·5	**44·5**	12·5	6·9
100	55	**77·1**	73·7	1·7	—
			Mean of deviations at all depths		4·6

* Evening experiments.

lower compartment of the other (β). These differences for the standard daylight experiments have already been shown graphically in Text-fig. 6. Table II gives the percentages found in the two lower compartments (B and β) at the end of all these experiments together with those of other similar ones (marked with an asterisk) taken in the evening. The latter, which will be discussed in a later section (pp. 500–4), are here included because, although taken in dusk or darkness, the conditions of the two sides of the apparatus are the same in any one experiment. The table also gives the deviations of the percentages

on the two sides of each experiment from their mean; these range from 0 to 13·1, and the mean of the deviations for all the experiments is 4·6. The higher of the two percentages (in B and β) in each experiment is shown in heavy type; we see that down to and including 20 m. there are eighteen experiments of which eight have the higher percentage in B and ten have it in β. For 30 m. and below there are nine experiments, and out of these six have the higher percentage in β. It may be that at the greater depths there is a slight tendency for more Calanus to remain in the compartment in which they were placed at the beginning of the experiment, but there are too few results to warrant any conclusion on this and the one result at 100 m., the deepest of all, is against it.

At the end of the season in 1939 a series of experiments (68–75), in which the Calanus were introduced into the top compartment of both sides of the apparatus, were made for the special purpose of (*a*) comparing the differences in the results found on the two sides of these experiments with those of the standard experiments just discussed, and (*b*) providing a comparison for later experiments in which the conditions on one side of the apparatus would be modified. Unfortunately, these experiments were left until very late in the programme, 18–22 November 1939; then it was difficult to collect Calanus in sufficient numbers off Millport, so that all but two were performed with stocks of Calanus which had been collected in Loch Striven, brought to the laboratory and kept in large containers for 1, 2 or 3 days. The effects of being so kept are discussed in a later section (p. 508);[1] here we are simply considering the differences in the percentages of Calanus, with exactly the same history, introduced into the top compartments of the two sides of the apparatus and subjected to exactly the same conditions. The Calanus used were always selected from the same level in the containers to eliminate individual differences as far as possible. The results are shown in Table III. The deviations of the two percentages from their mean in each experiment range from 0·9 to 12·8, and the mean of these deviations is 4·8; these figures compare very closely with those just given above for the standard experiments. It is seen that the position of introduction at the beginning of the experiment on either side makes little difference to the result.

We are working with a population in which a certain proportion of the individuals shows a tendency to move upward and a certain proportion to move downward at a particular depth and time. Taking two random samples from such a population for purpose of experiment it is not surprising that we do not get exactly similar results on the two sides; rather is it remarkable that they differ so little from one another. The difference seen between the results of the two sides of any experiment is clearly of the nature of an experimental error due to sampling. Out of the total of thirty-five experiments given in

[1] The results of these experiments, because of the effects described later, have not been included with the standard experiments just described.

Tables II and III, twenty-one show deviations between 0 and 4·9, nine between 5 and 9·9, and only five between 10 and 13·1 (the highest).

Having obtained some measure of this experimental error we can now look more closely at the standard experiments performed in daylight, i.e. between 0800 and 1600 hr.

Neglecting the experiments at 50 and 100 m. which are too few to offer conclusive results, it is seen from Table I and Text-fig. 9 that the deeper the experiments are made, from 1 to 40 m., then the smaller is the average proportion of the population which has moved down or stayed down at the end of each experiment; and the larger is the average proportion which has moved up or stayed up in the apparatus.

TABLE III. SHOWING THE DIFFERENCE BETWEEN THE RESULTS OF THE TWO SIDES (AB AND $\alpha\beta$) OF DOUBLE EXPERIMENTS IN WHICH CALANUS WERE INTRODUCED INTO THE UPPER COMPARTMENTS (A AND α) OF EACH SIDE

Depth in m.	Reference no. of exp.	% Calanus at end of exp. B	% Calanus at end of exp. β	Deviation of B and β from their mean	Mean of deviations at each depth
5	73	**81·5**	75·6	3·0	
	74	80·0	**84·0**	2·0	2·5
10	68*	63·2	**75·7**	6·3	
	69*	69·8	**86·8**	8·5	
	70*	74·1	**81·1**	3·5	
	71†	**18·4**	15·0	1·7	
	72†	3·5	**29·0**	12·8	
	75*	**35·6**	33·8	0·9	5·6
			Mean of all deviations		4·8

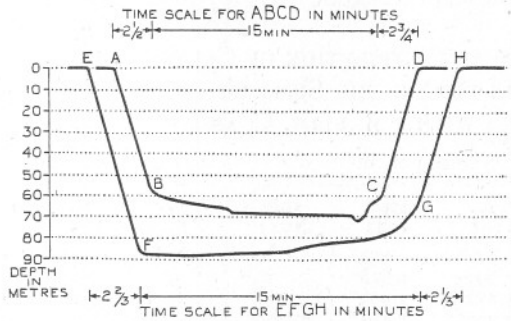
* Calanus experimented with from 21 to 26 hr. after capture.
† Calanus experimented with from 72 to 74 hr. after capture.

(See discussion of these experiments on p. 508.)

If nothing definite had been known about the actual depth from which the Calanus were originally collected, a very simple explanation of these results could be suggested. At 1 m. depth it was found that on an average 14·6% of the population in the apparatus moved upward or stayed up; it might be suggested that this 14·6% of the population had in fact been collected from just below the surface as the nets came up. At 5 m. depth experiments showed 26% of the population up in the apparatus, so it might be suggested that there would on an average be 11·4 (i.e. 26 − 14·6%) of the population caught between depths of 5 and 1 m. So on as we pass to lower depths; at 30 m. an average of 64% moved up or stayed up in the experiments, suggesting that this proportion of the population was actually caught above 30 m. Such a simple explanation, however, is not possible; we know from what follows that the majority of the Calanus were collected at a much greater depth.

It became a matter of the utmost importance to have an exact record of the depth at which the nets fished when the Calanus were collected for the

experiments. A depth recorder, similar to that used by Russell (1925) for determining the depths of his nets when studying vertical migration at Plymouth, was kindly lent by the Admiralty. A graph of the depth at which the recorder is towed is traced on a paper mounted on a clockwork drum in a watertight chamber within its streamline body. The tests were made at the same place, in the Cumbrae Deep (the deep water between Garroch Head and Kilchattan Bay) from which the Calanus were usually collected for the experiments. The two 1 m. diameter tow-nets were used just as they had always been used: placed on the towing rope 10 ft. apart with a weight just below the lower net and 60 fathoms of rope let out. The only addition was the depth recorder placed between the weight and the lower net; being small and streamlined, and having neutral buoyancy, it would make little difference to the normal path of the nets when towing. The boat and windlass were handled



Text-fig. 11. Two tracings from an Admiralty Depth Recorder showing the path of the collecting tow-nets below the surface on two occasions: curve *ABCD* is a tow against the tide (as was the custom whenever possible) and curve *EFGH* is a tow at slack water. *AB* and *EF* represent the path of the nets while the towing rope is being veered out, *BC* and *FG* their path during the actual tow, and *CD* and *GH* while being hauled in. The duration of the collecting period (i.e. between the time when the rope was fully out and the time when hauling in began) was exactly 15 min. in each case; a separate time scale is given for *ABCD* above the figure and for *EFGH* below, a difference in scales due to the varying rate of turning of the recorder clockwork.

by the same two boatmen who always worked them so that the nets were towed and hauled up at the same speed as usual. A first tow was made against the tide as had been the practice whenever possible in the past; a second test was then made in the opposite direction, but by that time it was almost slack water and the nets fished deeper. The two curves traced by the recorder are shown superimposed in Text-fig. 11 with the depth scale alongside. Curve *ABCD* is the first tow: that against the tide. *AB* represents the descent of the net while the rope is being veered out; *BC* is the path of the net during the tow and is seen to lie (except for a very small fraction) between depths of 60 and 70 m.; *CD* is the net being hauled to the surface. In the same way the curve *EFGH* represents the path of the net during the second test, that at slack water; the depth during tow was now deeper, starting at about 87 m.

and rising to about 62 m. at *G*, where the transition to the regular steep climb during hauling can be seen. The haul *FG* appears to be of longer duration than *BC*, but actually this is due to an acceleration in the clockwork mechanism[1]—the two were timed to be 15 min. each. The tests show conclusively that the nets were fished during towing at a depth of between 60 and 90 m. and more usually between 60 and 70 m., because they were towed against the tide whenever possible.

The nets, being veered out at almost the same speed as the forward motion of the boat, would hardly fish on the way down; they would, however, fish well while being hauled up, but the time taken in hauling is less than 3 min. In the tests the duration of the tow was 15 min., but in actual collecting it was always half an hour; thus the time taken in hauling was just under 10% of the fishing time. It is almost inconceivable that nets fishing for 90% of the time below 60 m. should capture some 70% of their Calanus above 40 m. in the

TABLE IV. VERTICAL DISTRIBUTION OF CALANUS IN THE CUMBRAE DEEPS IN THE DAYTIME DURING THE SUMMERS OF 1942 AND 1943 AS SHOWN BY 15 MIN. HAULS WITH 1 M. DIAM. COARSE MESH NETS AT VARIOUS DEPTHS

	Average nos. in				Same results as percentages				Average % at
Depth in m.	July 1942	Aug. 1942	Sept. 1942	July 1943	July 1942	Aug. 1942	Sept. 1942	July 1943	each depth
1	400[1]	672[4]	112[2]	0[1]	2·8	1·2	0·7	0	**1·2**[8]
30	470[4]	697[12]	1,618[5]	72[1]	3·2	1·2	10·7	0·4	**3·9**[22]
55	5,010[4]	15,882[12]	1,967[8]	2,253[3]	34·5	27·2	13·0	9·9	**21·1**[27]
90	8,603[3]	41,202[8]	11,425[6]	20,600[3]	59·5	70·4	75·6	89·7	**73·8**[20]

The index figures indicate the number of samples averaged.

short interval of time during which they are hauled up. They are hauled at a speed of just over 1 m. in 3 sec. The Calanus would have to be exceedingly rich near the surface to yield 14·6% of the catch in the top metre (in 3 sec. tow). In fact we know that this is not so except on very rare occasions. Repeatedly it has been found impossible to collect heavy samples of Calanus in the daytime except by fishing below 50 m.

During the summers of 1942–3 the senior author carried out a study of the yield of Calanus in the Clyde Sea area;[2] a number of horizontal tow-net hauls were made with 1 m. diameter nets at depths from 1 to 90 m. in the area of the Cumbrae Deeps, just where the Calanus were collected for the present experiments. Table IV shows the results of these hauls for the months of July, August and September. From 60 to 90% of the Calanus were below 55 m. depth in the daytime with less than 10% in the upper 30 m.

[1] Similar variations in the recorder clockwork are also shown by Russell (1925).

[2] This was part of an investigation into the possibility of harvesting the plankton as a means of increasing the country's protein supply for livestock food in wartime; it was not found to be a practical proposition (as will be recorded in a later paper).

These two lines of evidence make it clear that the bulk of the Calanus used in the standard experiments had in fact come from depths of some 60 m. or more. One is presented with an unexpected result; when samples of this deep population are taken for purposes of experiment nearer the surface, between 1 and 40 m., there is a regular change in the proportions of the population which move upwards and of those which move downwards. We will return to this problem in the general discussion at the end.

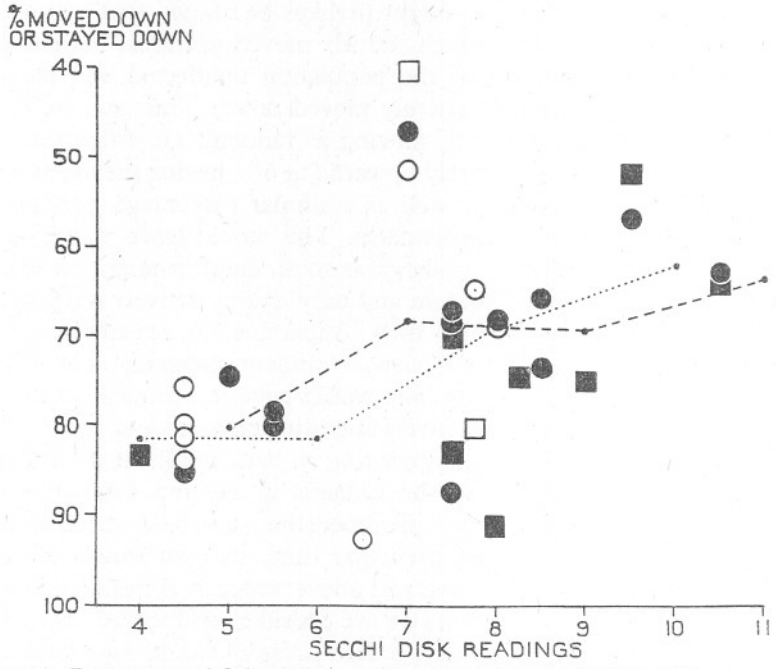
Regarding the upper levels it might perhaps be argued that one need not assume that there were some which actively moved upwards, but rather that there might be a proportion of the population unaffected and moving at random and only some which actively moved down. Thus at 1 m. depth it might be said there were 29·2% moving at random, i.e. twice the 14·6% appearing to have migrated actively upward (14·6% having moved at random into the upper compartment as well as a similar percentage having moved at random into the lower compartment). This would leave 70·8% actively moving down at 1 m. depth. Similarly, at 10 m. depth it might be suggested that 56·4% were moving at random and only 43·6% actively moving down. However the evidence of the long tube (Apparatus No. 2) experiments to be described on p. 510 is against this view of random movement and when one comes to consider events at 30 m. one would have to assume that there had been a change over with 29·4% actively migrating upwards and 70·6% moving at random (i.e. twice the 35·3% appearing to have migrated downwards).

If it should be assumed that the Calanus in the top compartment are photopositive and the remainder photonegative, it would mean that each individual would have, for that particular time, its own threshold of light intensity below which it is positive and above which it is negative in action. If this was so then the populations we are considering must be characterized by nicely graded threshold values: a few Calanus would be photopositive under all experimental conditions, and more and more would reach their positive threshold at each successive reduction in light intensity with increasing depth. So far no direct evidence has been presented to show that these changes in behaviour in relation to different depths are due to differences in the light intensity at all. All that has been demonstrated so far is that there is a change of behaviour in the population varying with depth.

In the next section under the heading of 'Mirror experiments' evidence will be given to show that light is truly a factor of importance; but before passing to these there is other evidence from those experiments already described which must be considered and which, together with the mirror experiments, suggest that differences in light intensity have but little to do with the changes in behaviour observed at different depths. Two lines of evidence from the present experiments are available.

In Text-figs. 7 and 8 it is seen that the results of different experiments at any given depth spread over a considerable range of values. If the differences

in the intensity of the light were an important factor in determining the animals' behaviour at different depths, then it might be expected that differences in behaviour at the same depth, but on different days, might in part be due to differences in the light conditions on these different occasions. At the one depth it would be expected that the brighter the intensity of light then the smaller the proportion of the population moving upward in the apparatus. With each experiment readings were taken with the Secchi disk (see p. 480)



Text-fig. 12. Percentages of Calanus Stage V in the lower compartments of the apparatus at the end of standard experiments at 5 and 10 m. between 0800 and 1600 hr. plotted against Secchi disk readings. Percentages of Calanus which have moved down are shown as circles and those which have stayed down as squares; the observations at 5 and 10 m. depth are distinguished by open and blacked-in symbols respectively. The broken line connects points which are the averages of the percentage values falling between Secchi disk readings of 4–5·9, 6–7·9, 8–9·9 and 10–11·9; similarly, the dotted line shows the averages when the Secchi disk readings are grouped as 3–4·9, 5–6·9, 7–8·9 and 9–10·9.

to give some measure of the transparency of the water and hence the relative penetration of light. The full set of readings will be found in the Appendix, Table I. A greater number of standard experiments were made at 5 and 10 m. than at any other depths. In Text-fig. 12 the percentage values of Calanus which were in the lower compartments at the end of these experiments (i.e. either moved down or stayed down) are plotted against their Secchi disk readings. The Secchi disk method is undoubtedly a crude one; but, while not a measure of light intensity, in general a shallower disk reading indicates a poorer penetration of light due to increased opacity on that particular day.

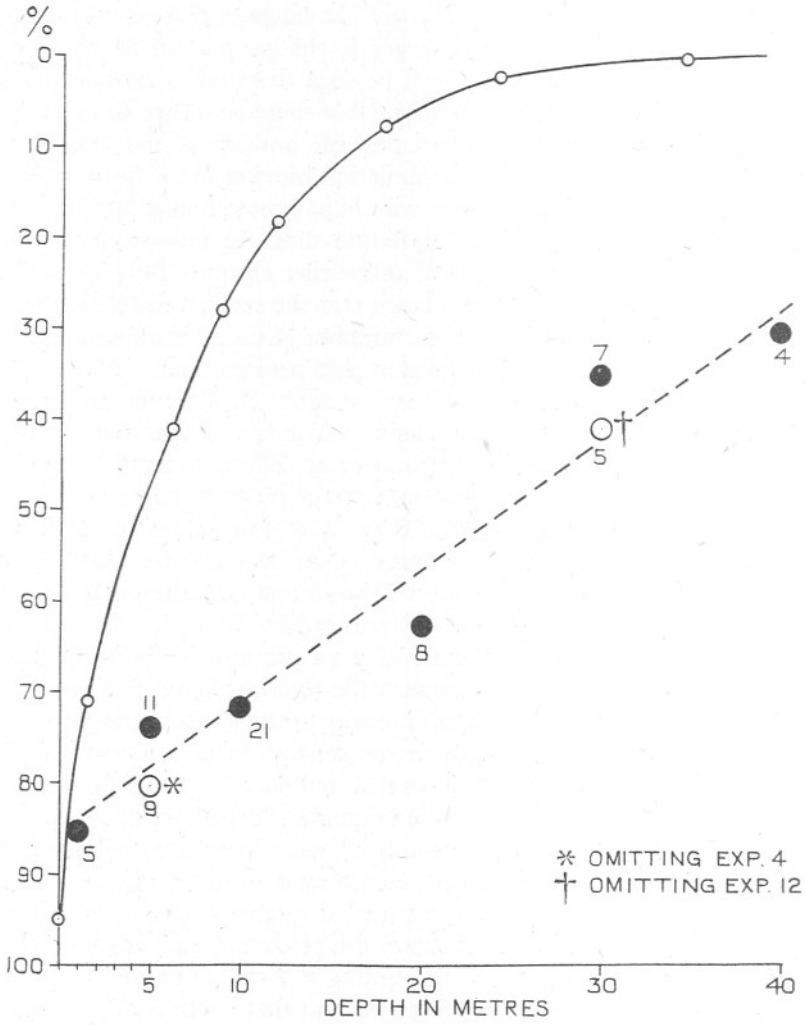
If there is any correlation shown here between the behaviour of the Calanus and the differences in the penetration of light it is only a slight one—and if so, then it is a correlation in the unexpected direction. The broken line and dotted line graphs in the figure connect the points which represent the average percentage values for each two degrees of the Secchi disk readings grouped either as 4–5·9, 6–7·9, etc., or 3–4·9, 5–6·9, etc. It suggests that on an average the greater the light penetration the larger is the proportion of photopositive individuals in the population. It will be seen from other experiments to be described later that there are indications that there are other factors (possibly physiological conditions dependent upon the amount of food taken) which may affect the proportions of the population moving up or down at any one depth so that any marked correlation with light penetration at one depth would not be expected. This possible correlation must be investigated by future experiments with an exact means of measuring absolute light intensity; for the moment it is sufficient to have shown that the reverse correlation does not hold here: there is no sign of a larger number of Calanus moving downward when the Secchi disk indicates a greater light penetration.

The second line of evidence has more weight. In Text-fig. 13 are plotted the average percentage values of Calanus which have either moved down or stayed down in the standard experiments at different depths. As already pointed out it is virtually a straight line correlation with depth; it becomes so if we omit two double experiments (Exp. 4 at 5 m. and Exp. 12 at 30 m.) which gave exceptionally low percentages. Now in the same figure, using the same percentage scale, there is plotted for comparison the curve of relative light intensity below the surface as determined by Poole & Atkins (1926) off Plymouth expressed for each depth as a percentage of the light intensity immediately below the surface (see also the figure in Russell, 1927, p. 248). Although the actual subsurface light intensity in the Clyde sea area may differ somewhat from that off Plymouth, its percentage reduction with depth will be of the same general order as that shown by Poole & Atkins. It seems quite clear from this that the progressive alteration in the behaviour of the population of Calanus as one goes deeper is in direct linear correlation with depth and not in such direct correlation with diminution of light intensity. This is further emphasized in Text-fig. 14 where the same average percentages of Calanus, moved down and stayed down, are plotted directly against the scale of percentage light intensity, e.g. the results at 1 m. are plotted opposite the value of the percentage light intensity found at that depth by Poole & Atkins (82·5%), those at 5 m. opposite the percentage light intensity at that depth (46%) and so on.

Mirror experiments

In these experiments the sides of one whole cylinder of the apparatus were tightly covered with black opaque paper and its metal bottom plate

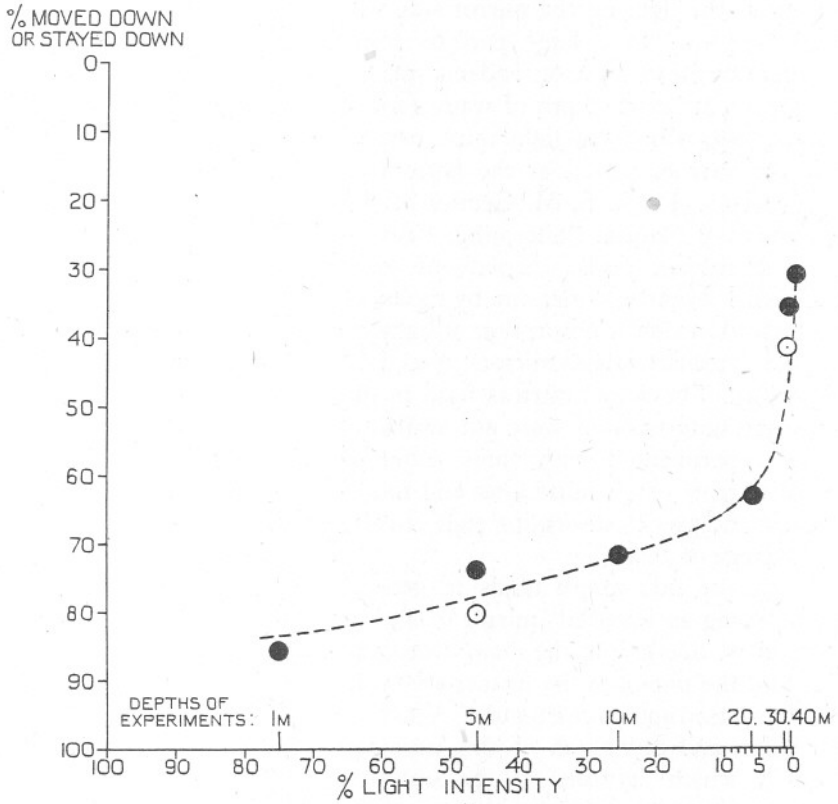
interchanged with its top glass plate. Thus in one cylinder all light was excluded *except from below*, and here mirrors at right angles to one another were arranged to reflect the daylight from above vertically *up the cylinder* from below as shown in the diagram in Text-fig. 15. In this way light was played



Text-fig. 13. The blacked-in circles show the average percentage values of Calanus which have either moved down or stayed down in standard experiments at depths of 1–40 m. (i.e. the two graphs in Text-fig. 9 combined). The figures against them indicate the number of experiments averaged at each depth. Their distribution suggests a straight-line correlation with depth. The continuous line curve indicates the relative light intensity below the surface as determined off Plymouth by Poole & Atkins (1926) expressed for each depth as a percentage of the light intensity immediately below the surface. See discussion in text.

upwards against gravity on one side of the apparatus while the cylinder on the other side was normal and acted as a control.

In Text-fig. 16 the right-hand graph shows the percentage of Calanus which moved down (circles) or stayed down (squares) in the normal side of the apparatus according to whether they were placed in the upper or the lower half of the cylinder at the start. This graph is therefore that of a selected

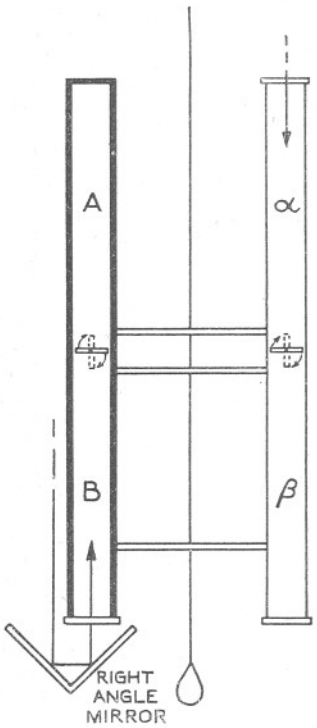


Text-fig. 14. The same percentage values of Calanus moved down or stayed down as shown in Text-fig. 13 but plotted against a scale of percentage light intensity. They are plotted against points on the scale corresponding to the light intensities found by Poole & Atkins (1926) at the same depths at which the experiments were performed. See discussion in text.

number of single-standard experiments, and their results conform closely with the general trend of those shown by the total of such standard experiments (compare with Text-figs. 7–9). In the left-hand graph are shown the percentages of Calanus that have moved down or stayed down in the mirror side of the apparatus in the same number of experiments. The reference number of each experiment is given so that the members of each pair of experimental results may be compared. In both sides of the apparatus the majority of the

Calanus in the experiments at the lesser depths of 1 and 5 m. have been found at the end of the experiment in the compartment away from the direction of the light, but to do this in the mirror side they have had to go up (or stay up) against gravity. This clearly shows that light is playing an important part.

The only difference in the conditions of the two sides of each experiment relate to light: first, the direction of the light is reversed, and secondly, the intensity of the light on the mirror side will be the less, due in a large part to some absorption by the two mirrors and in a smaller part due to the extra depth of water (about 1 m.) through which the light must pass to reach the mirrors placed at the bottom of the apparatus. Dr A. E. M. Geddes of the Department of Natural Philosophy, University of Aberdeen, kindly carried out some experiments recently to measure by means of a photoelectric cell the absorption of light by two such ordinary glass mirrors placed at right angles. The actual mirrors used in the experiment unfortunately were not available, but he experimented with three different pairs of mirrors of a similar kind and found 28·8, 30·0 and 30·5 % absorption respectively, or an average of 29·8 %.

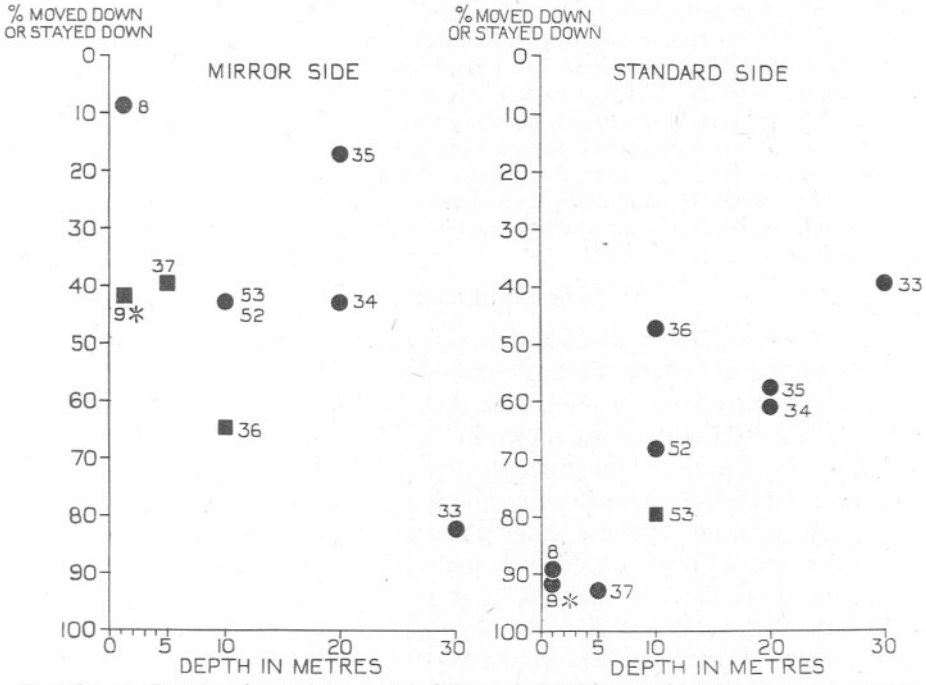


Text-fig. 15. Apparatus No. 1 adapted for the 'mirror experiments'. For explanation see text.

The mirror side graph tends in general towards being an inverted 'mirror image' of the standard side graph, the main difference being that the points in the former are more widely dispersed and more irregular. A further explanation and discussion of this irregular dispersal, which appears to be only of secondary importance, is given in a note in smaller type which follows. While many more such mirror experiments should be made to test these results, those here described, together with the former standard experiments, appear to indicate: (*a*) that light more than gravity is the influence towards which or away from which the animals move at different depths, and (*b*) that it is not the intensity of the light which determines the proportion moving towards or away from it. Such differences as there are between the two graphs, regarding them as inverted 'mirror images' of one another, can hardly be explained by the 30 % reduction in the light intensity (due to the mirrors) in the one as compared with the other. In Exps. 8 and 34 the results are almost perfect inversions of one another.[1]

[1] See however Addendum, p. 521.

Some special though minor features concerning the dispersal of the points in the mirror side graph may now be noted. In Exps. 8 and 9 the same Calanus were used twice. In Exp. 8, 92 Calanus were put into the top compartment of the mirror side at the beginning (i.e. away from the light) and 84 (91·3%) remained there; 111 Calanus were put into the top compartment of the normal side (i.e. towards the light) and 98 (89·2%) went down into the lower compartment (away from the light). In Exp. 9 the 84 Calanus which had stayed up (away from the light) in the mirror side of Exp. 8 were now put into the top compartment of the normal side and 77 (91·6%) went down; in the mirror side the 98 Calanus which had gone down in the normal side in Exp. 8 were put into the lower compartment (i.e. towards the light), and at the end of the experi-



Text-fig. 16. Results of experiments with Calanus Stage V in one side of the apparatus which was blacked-out except for light reflected from a mirror below and in the other side under standard conditions. The circles represent the percentage Calanus which have moved down and the squares the percentage which have stayed down in different experiments. The figures against each indicate the reference numbers of experiments. The Calanus in Exp. 9 (marked with asterisk) were used on opposite sides of the apparatus in Exp. 8.

ment only 57 (58·2%) had moved up into the compartment away from the light. It is possible that either the Calanus were suffering from fatigue or that the light intensity on the mirror side was not sufficiently high to stimulate them fully when they had previously been exposed for an hour to the greater light intensity of the open side in the former experiment. This latter suggestion implies that a good part of them had become adapted to a higher value. Johnson (1938), working on *Acartia clausi*, found that in the laboratory this copepod reacted rather to rate of change of light intensity than to absolute intensity, and further that a return to a random distribution occurred between changes of stimulation except when the period between them was less than half an

hour. In other words the copepods became adapted to the presented light condition in about half an hour, but if the next alteration of stimulus occurred within 15 min. adaptation was not complete and a certain summation of reaction was noticeable. It should, however, be remembered that the present experiments must not be compared closely with laboratory experiments which do not take into account the factor of depth which would seem here to be so important. Actually in the present instance the time interval between the end of Exp. 8 and the beginning of Exp. 9 was 1 hr. 57 min.

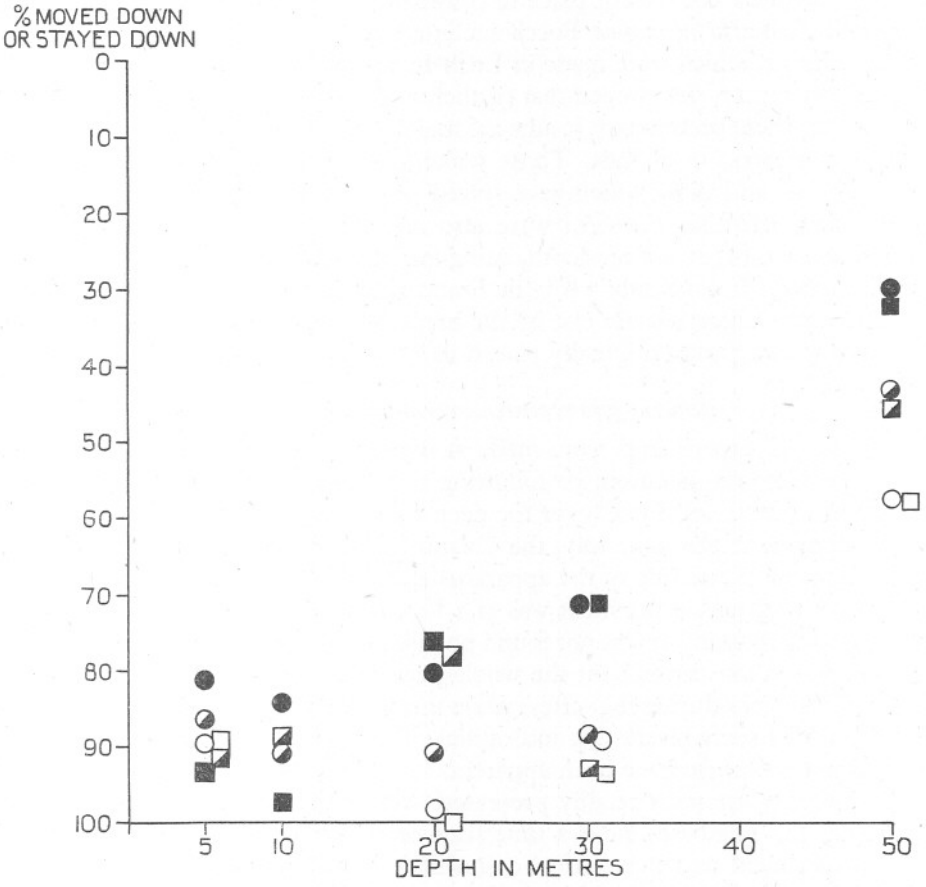
In the other experiments of the series the Calanus were used only once. The percentage down on the mirror side in Exp. 35 at 20 m. is exceptionally low; there is an experimental defect which might have given rise to this. The following is a quotation from the log-book of the experiments: 'The first messenger failed to work the trapdoor to begin with; the apparatus was hauled up and released at the surface and sent down again.'[1] For a very short period the experiment began like one just below the surface and this brief exposure may have had a lasting effect through the experiment. Any such abnormalities in other experiments are few and are recorded in the Appendix. No obvious explanation appears for the abnormality of Exp. 36 at 10 m. depth; on the mirror side the percentage down is exceptionally high, whereas on the other side it is correspondingly low. The reversal of values on the two sides would be expected, but not that they should be abnormally high and low; the Calanus used in this experiment were caught at the same time as those used in Exp. 35 which was performed only an hour earlier.

Experiments at night and dusk

Apart from experiments which were repeated at the same depth throughout a 24 hr. period and which will be described in the next section, a few standard experiments were made at dusk or in darkness at different depths from 5 to 50 m. The results of these are shown in Text-fig. 17. In each experiment the Calanus were introduced into the upper compartment of one cylinder and into the lower one on the other side. The graph shows the percentages found in the lower compartments at the ends of the experiments: circles represent those which had moved down on one side and squares those which had remained down on the other. In addition to results for Stage V, those for female Calanus and the copepod Euchaeta (see p. 502) are also shown. Only one experiment was performed at each depth. The data regarding times and dates of experiments and times of sunset are shown in Table V.

There are too few experiments to discuss in detail; they are merely recorded for future reference when it is hoped many more may be made at night. They do, however, again suggest a relation with depth rather than light intensity. On the whole the percentages down are greater than those of daylight experiments when the light intensity was so much higher, but this may be due to the fact that for all experiments, except Exp. 30, the Calanus were collected between 1830 and 2015 hr. from deep water when the majority of the population may have already migrated leaving below a stock 'less inclined' to move upwards (see similar suggestion in next section).

[1] One could always tell whether the trapdoors had been opened by feeling on the wire for the vibration caused by the working of the springs and cranks following the striking of the messenger.



Text-fig. 17. Results of experiments made at dusk and at night with Calanus Stage V (blacked-in circles or squares), female Calanus (half-blacked circles or squares) and *Euchaeta norvegica* (open circles or squares). The percentage moved down shown as circles, those stayed down as squares. The experiments at 5, 20 and 50 m. were made at night and experiments at 10 and 30 m. at dusk (1910 and 1700 hr. respectively). See Table V below.

TABLE V. DATA FOR EXPERIMENTS MADE AT NIGHT AND DUSK

Depth in m.	Date	Reference no. of exp.	Time of exp. (hr.)	Time of collection of Calanus (hr.)	Time of sunset (hr.)
5	15. ix. 38	32	2210	1900	1838
10	23. viii. 39	54	1910	1830	1937
20	14. ix. 38	28	2108	2015	1840
30	15. ix. 38	30	1700	1100	1838
50	15. ix. 38	31	2039	1900	1838

Here will be a convenient place to consider a few results obtained with the copepod *Euchaeta norvegica* Boeck included in these same experiments, 28, 30, 31 and 32, which were made in Loch Fyne. The results are shown in the same Text-fig. 17. It is hoped that further work will be done with *Euchaeta* in the future; these preliminary results are merely indications, but are thought of sufficient interest to include. Those which have moved down are shown as open circles, and those which have stayed down as open squares. It may be mentioned here that *Euchaeta* were also recorded in Exp. 29 made in the daytime (1300 hr) at 100 m. depth, being introduced into A on one side and β on the other. It gave only 7·6% in B and none in β (93 were used in AB; sample α was unfortunately lost by the breakage of the cylinder so we do not know how many were originally placed in β).

Experiments repeated over a 24-hour period

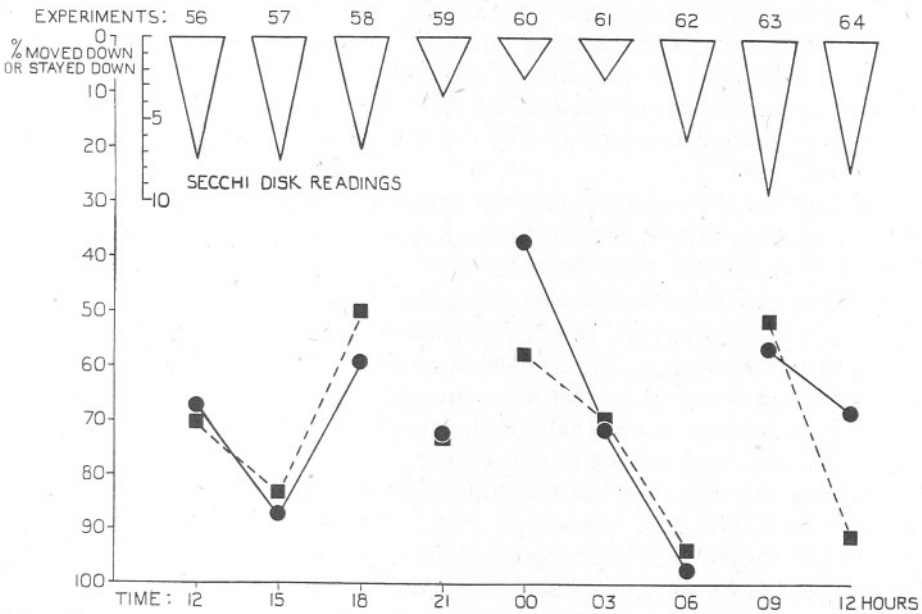
A series of experiments were made at intervals of 3 hours from noon on 24 August 1939 to noon on the following day. These were all made at 10 m. depth in upper Loch Fyne (over the deep water opposite Strachur pier), and were all made in the same way, the Calanus being introduced into the upper compartment of one side of the apparatus and into the lower compartment of the other, and each experiment was of 1 hr. duration. A Secchi disk reading was taken with each. It was not found possible to keep a sufficient single stock of Calanus to last throughout the whole period so that fresh hauls had to be taken three times during the series; while this was an unfortunate complication it has yielded some interesting indications of the behaviour of Calanus which would not otherwise have been apparent.

The results are most readily presented in graphic form and are shown in Text-fig. 18. The base-line is a time scale on which are marked the times of each experiment and the vertical co-ordinate is an inverted scale indicating the percentage Calanus found in the lower compartments in each experiment. The percentage values for the Calanus that have moved downwards in each experiment are shown as usual as blacked-in circles and those which, in the opposite cylinders of the apparatus, have stayed down are shown as blacked-in squares. The percentage values of those moved down (circles) in experiments made with Calanus collected at the same time are linked by a continuous line; the results of the opposite sides of the same experiments are linked by a broken line. At the top of the figure an indication of the variation in light penetration is given by a series of triangles the varying depths of which correspond to the depths (in metres) at which the Secchi disk disappeared from view.

The Calanus for the first three experiments were collected at 0830 hr. from a depth of 60–70 m. and kept in the dark until required. The first experiment at noon yielded similar results in each side of the apparatus, 67·2% moving down and 70·3% remaining down. At 1500 hr. the results of the two sides were again closely similar to each other, but the values down were considerably

higher, 87·4% moving down and 83·1% remaining down. In the third experiment at 1800 hr. there was a marked change, only 59·3% moved down and only 50% remained down on the other side. This clearly shows a change in behaviour with the passage of time as evening approaches: from noon to 1500 hr. an increasing proportion of the population were moving downward—at 1800 hr. the proportion moving up had greatly increased.

After the experiment at 1800 hr. it was found that the remaining stock of Calanus was insufficient for another experiment, and a fresh supply was collected at 1900 hr. again from 60–70 m. depth. The catch was now a very much smaller one, only sufficient for one experiment, that made at 2100 hr.



Text-fig. 18. Results of Exps. 56–64 made at 10 m. depth throughout a 24 hr. period; for explanation see text.

Here the results with this new stock of Calanus gave 72·3% moved down and 73·4% remained down; almost identical results but markedly different from those obtained with the former stock at 1800 hr. An explanation of this is suggested: at 1900 hr. the number of Calanus was very much less than was caught before, they would be those left below when the majority had begun their upward evening migration and so might be expected to yield a large proportion moving down or staying down when experimented with at 10 m. Sunset was at 1935 hr.

It was now necessary to obtain yet a further stock of Calanus and, since the majority had apparently left the lower layers, a fresh haul was made at 2200 hr. from 20 m. depth; now sufficient were again obtained to last for the next three

experiments, those at midnight, 0300 and 0600 hr. At midnight only 37·1% moved down, whereas 57·8% stayed down; this suggests that at midnight there may be little tendency to go up or down, perhaps a general scattering effect (cf. Russell, 1925), with a slight majority on each side tending to remain in the compartments into which they were introduced at the beginning of the experiment. At 0300 hr. there was once more a striking similarity in the results of the two sides of the apparatus, 71·6% moving down and 69·5% remaining down. This tendency for the majority to move down had set in well before sunrise (which was at 0505 hr.), and when there was no increase in light penetration indicated by the Secchi disk reading. This agrees with the findings of several workers (cf. Esterly, 1912; Clarke, 1936, p. 10) that Calanus tend to leave the surface layers around midnight, although the light has not yet started to increase. At 0600 hr. the results in the two sides of the apparatus were again remarkably similar but this time showing nearly the whole population either moving down (97·4%) on one side or remaining down (93·6%) on the other.

To continue the experiments it was again necessary to collect a fresh stock of Calanus and, since the vast majority had been moving downward, the haul was made at 0800 hr. from 60–70 m. The results of the 0900 hr. experiment were again consistent for the two sides, but the percentages down were very much less than at 0600 hr., 56·7% moved down and 51·6% stayed down. This suggests that at 0900 hr. the downward migratory impulse of those collected at 60–70 m. had ceased, so that when brought up to 10 m. there was almost a random movement in each side of the apparatus. However, using Calanus from the same stock for the last experiment at noon a greater percentage was found down in each side, but the values differed markedly from one another, 68·4% had moved down whereas 91·2% had remained down. The percentage which had moved down corresponded very closely with the percentage that had moved down in the experiment at noon the previous day (67·2%), but the percentage which had remained down was very different.

Clearly more experiments on these lines must be performed before one can draw many conclusions; they do, however, give definite evidence of a change in the behaviour of Calanus throughout the 24 hr., changes in the proportions of the population moving upward or downward at different times, not the whole population rising and falling together. They also show that the downward migration begins before there can be any marked increase in the light intensity.

Experiments with 'fed' and 'starved' Calanus

In the hypothesis of 'animal exclusion' already referred to on p. 468, it was suggested that the vertical migration of plankton animals might be modified by varying concentrations of phytoplankton in the upper layers. Apart from effects on the environment brought about by the plants such as the known

changes in *p*H and oxygen content of the water, or possibly by their excreting some at present unrecognized substance, it was thought that perhaps the behaviour of the animals might be modified according to whether they were well or poorly fed. If the phytoplankton was abundant so that they obtained sufficient food in a short time they might remain for a shorter period in the phytoplankton zone than when it was scarce; or if they had recently been well fed they might not show the same tendency to migrate upwards as those that were 'hungry'. A few experiments were made to compare the vertical migrational behaviour of Calanus which were well fed and those which had been starved. They were preliminary experiments, exploring for the most suitable method, intended to prepare for more systematic ones, and are only included to give a complete record of the work. The results are quite inconclusive and indeed impossible to interpret, both because of the number of variables in so few experiments and because it has later been shown, on p. 508, that keeping Calanus in the laboratory may have a most disturbing effect upon their behaviour. They do, however, give some indications suggesting future lines of work.

The following was the general procedure in preparing the cultures of 'fed' and 'starved' Calanus, the details of variations being given in Table VI. For a stock of 'fed' Calanus about 200 were picked out and placed in about 10 l. of outside sea water to which was added, for different experiments, varying quantities from 50 to 1000 c.c. of a medium strength culture of the diatom *Nitzschia*. The container was darkened and cooled by standing in running water. They were kept for varying periods from 35 to 90 hr. For the 'starved' stocks the Calanus were washed in several changes of sea water which had been filtered through a Berkefeld filter and were then placed in a container in about 10 l. of the filtered sea water darkened and kept cool as for the 'fed' stock. In Exps. 10, 23 and 24 both sets were kept in plunger jars instead of ordinary containers.

In Exps. 19 and 24 the behaviour of the 'fed' Calanus was compared with that of outside Calanus collected just before the experiment.

The results are shown in Table VI. With so many variables and in view of the already referred to effect of keeping Calanus in the laboratory, it is not surprising that they are somewhat inconsistent. Three features may be pointed out. The deviations in the results of members of a pair from their mean are more often than not considerably larger (average 11·8) than the deviations due to the random sampling, the experimental error, found in standard experiments (averaging 4·6); their treatment, whether due to feeding and starving or not, *has* influenced their vertical migrational behaviour. Secondly, it will be seen that four out of five stocks of starved Calanus give very similar results (61·0, 61·6, 61·8 and 67·4%) in spite of being experimented with at different depths of 5, 10 and 30 m. Does starving tend to produce an 'apathy' towards different conditions? Lastly, at 10 m. depth there is seen what might appear to be a

TABLE VI. DATA REGARDING EXPERIMENTS WITH 'FED' AND 'STARVED' CALANUS

Reference no. of exp.	Time and date of capture of Calanus	Strength of culture for 'fed' Calanus: c.c. of *Nitzschia* added to 10 l. of water	Length of time in culture in hr.	Time and date of exp.	Depth of exp. in m.	Percentage found in lower compartments. (The letters U or L indicate that the Calanus were introduced into upper or lower compartments)			Deviation of the two percentages from their mean
						'Fed' Calanus	'Starved' Calanus	Outside Calanus	
7	1030, 9 Aug.	50	45½	1036, 11 Aug.	10	51·7 (L)	81·2 (L)	—	14·8
10	0830, 23 Aug.	100	72*	1055, 26 Aug.	10	59·8 (U)	— †	—	—
18	1330, 29 Aug.	200	66	1032, 1 Sept.	10	85·1 (L)	61·6 (L)	—	11·8
19	1330, 29 Aug.	200	68	1221, 1 Sept.	10	87·2 (U)	—	65·6 (U)‡	10·8
23	1600, 8 Sept.	200	89*	1139, 12 Sept.	30	31·0 (U)	61·8 (U)	—	15·4
24	1600, 8 Sept.	200	91*	1326, 12 Sept.§	5	77·9 (U)	—	69·1 (U)‡	4·4
26	0930, 12 Sept.	1000	35‖	1325, 14 Sept.	30	35·0 (U)	67·4 (U)	—	16·2
27	0930, 12 Sept.	1000	40‖	1720, 14 Sept.§	5	50·7 (U)	61·0 (U)	—	5·2
								Mean of deviations	11·8

* Cultures kept in 'plunger jars'.
† Sample lost through accident to container.
‡ Outside Calanus collected on same morning as experiment.
§ Duration of experiment only ½ hr., remainder 1 hr.
‖ Stocks of Calanus kept for 12 hr. in laboratory before being put into culture.

correlation between the behaviour of the 'fed' Calanus and the strength of the *Nitzschia* culture in which they were kept: the stronger the culture added (50, 100 or 200 c.c.), the larger is the percentage that have moved down or stayed down; this, however, is not supported by the results at 5 and 30 m.

Experiments with waters of different alkalinity

Loeb (1906) showed that Copepoda became positively phototropic with a reduction in the alkalinity of the water. Rose (1925), however, found that the natural range of *p*H had little effect on their reactions to light, though artificial ranges did. He says that the maximum sensitivity to light appears very clearly in the neighbourhood of neutrality. Marshall *et al.* (1935) found that Calanus can withstand ranges of *p*H from 6·7 to 8·5 and that changes in *p*H did not affect their respiration rate.

Two experiments were made with artificially produced *p*H: Exps. 38 and 39, both at 10 m. depth. In the former Calanus were introduced on one side into more alkaline sea water (*p*H 8·75) produced by adding drops of *N*/10 solution of NaOH and their behaviour compared with that of Calanus in outside sea water (*p*H 7·90) in the other side of the apparatus. In the second experiment they were put into less alkaline water (*p*H 7·57) and compared with those in outside sea water; the former condition was produced by bubbling CO_2 into the sea water and shaking till the required *p*H was obtained. In each experiment the Calanus were introduced into the top compartments of the apparatus. The percentages of the populations found down in the lower compartments of each experiment were as follows:

Exp. 38:	In alkaline water	*p*H 8·75,	84·0%
	In outside water	*p*H 7·90,	80·1%
Exp. 39:	In less alkaline water	*p*H 7·57,	86·1%
	In outside water	*p*H 7·92,	78·5%

The deviations are well within the experimental error; it is clear that, in spite of the small number of experiments, such differences in *p*H do not markedly affect their behaviour.

Experiments with surface and deeper water

In all the experiments hitherto described the sea water used was obtained from the surface, or as in a few cases, when heavy rain in Loch Fyne or Loch Striven had produced a layer of less saline water at the surface, it was obtained with closing water bottles from 10 m. below the surface. Unless otherwise stated all the Calanus for the experiments have been collected from a depth of 60 m. or more. Two experiments, Nos. 66 and 67, at 10 m. depth, were made to compare the behaviour of Calanus in water from the surface with the behaviour of those in water taken by a water bottle from 30 m. In one

experiment (No. 66) the Calanus were introduced into the upper compartments of both sides of the apparatus and in the other into the lower compartments. The two experiments were made on the same day at 1112 and 1310 hr. The percentages in the lower compartments at the ends of the experiments were as follows:

Exp. 66: in surface water, 85·1%; in 30 metre water, 72·3%
Exp. 67: in surface water, 83·4%; in 30 metre water, 74·2%

The difference in the results of the two sides is not large, well within the range of experimental error; the fact, however, that the two sides in the two experiments should give such closely similar results suggests that the difference in the nature of the water may have some slight effect: another matter to be investigated further.

TABLE VII. RESULTS OF EXPERIMENTS WITH CALANUS WHICH HAD BEEN KEPT IN THE LABORATORY FOR VARYING PERIODS

Reference no. of exp.	Length of time kept hr. min.	Percentages of Calanus found in lower compartments at the end of experiments	
68	21 49	63·2	75·7
69	23 54	69·8	86·8
70	26 04	74·1	81·1
71	72 15	18·4	15·0
72	74 06	3·5	29·0
75	21 22*	35·6	33·8

* These Calanus had a different history from the rest (see text).

Experiments with Calanus kept for a day or more in the laboratory

In November 1939, when it was difficult to collect sufficient in the Cumbrae Deep, a quantity of Calanus was caught in Loch Striven, brought to the Millport Station laboratory and kept in large containers until required for experiments. They were kept under similar conditions as those used in the 'fed' and 'starved' experiments except that they were given two changes of outside water each day, the bulk of the old water being siphoned off through a gauze, concentrating the Calanus for a very short time before the fresh sea water was added.

The experiments made with them are those referred to on p. 489; all were made at 10 m. depth, and in each the Calanus were introduced into the upper compartments of the two sides of the apparatus. The results are shown in Table VII together with those of Exp. 75, the Calanus of which had a somewhat different history. Exps. 68–72 were made with Calanus caught on 17 November, brought to the laboratory and kept as described; those used in Exp. 75 were also caught in Loch Striven but on 21 November and kept till the next day in a darkened accumulator jar, with two changes of water, in the cabin laboratory of the station's research boat *Nautilus*.

In the series 68–72 we see a marked change in the behaviour of those Calanus kept in the laboratory for more than 70 hr. when compared with those kept in a similar manner but for only 21–26 hr. In Exp. 75 the Calanus, which were kept under rather different conditions on the boat, but again for only 21 hr. 22 min., gave results more approaching those of the Calanus kept for 70 hr. in the main laboratory. This change of behaviour does not appear to be due merely to a lowering of their vitality since the whole of the remainder of the stock, from which the Calanus for Exps. 68–72 were taken, lived healthily in the laboratory for a fortnight and many of them lived for as long as 6 weeks.

Experiments with Calanus in complete darkness

In these experiments (Nos. 49–51), which were performed in the daytime in August 1939, the top, bottom and sides of one cylinder were completely covered with black paper so that all light was excluded from it, while the other was left open and normal as a control. It is most unfortunate that only three such experiments were made, and all at 10 m. depth. It was our intention to

TABLE VIII. RESULTS OF BLACKED-OUT CYLINDER EXPERIMENTS

(Data for blacked-out cylinder in heavy type, for control cylinder in normal type)

Reference no. of exp.	Total Calanus in control cylinder	Total Calanus in blacked-out cylinder	Percentages of Calanus found in lower compartments at the end of exps.	
49	68	**74**	72·1	**59·7**
50	68	**157**	73·5	**81·5**
51	36	**200**	75·0	**81·0**
		Average	73·5	**74·1**

carry out many more at different depths, but the war intervened. In Exps. 49 and 50 the Calanus were put into the top compartment of each cylinder, and in Exp. 51 into the bottom compartments. The results are given in Table VIII, where the data relating to the blacked-out cylinder are shown in heavy type. Each experiment was of 1 hr. duration.

Exp. 49 was made at 1041 hr. off Millport with Calanus caught at 0830 hr. from 60–70 m. in the Cumbrae Deep; Exps. 50 and 51 were made at 1139 hr. in Upper Loch Fyne with Calanus caught also at 0830 hr. from 60–70 m. In spite of the difference in the origin of the stocks used the percentage down in the open control cylinder in all three experiments is remarkably similar; the behaviour of the two stocks in complete darkness is markedly different: 59·7% down for the Cumbrae stock as compared with 81·5 and 81·0% down for the Loch Fyne stock.

With either stock, however, there is really no very marked difference between the results of the control and darkened sides: with the Cumbrae stock the percentage down on the darkened side is 12·4 less than that of the control, in Loch Fyne those of the darkened side are 8·0 and 6·0 more than those of the

control side. The average deviations of the pairs from their mean is only 4·4, no more than the average experimental error of standard experiments. Further, the averages of the percentages of Calanus moved down or stayed down in the darkened side of the apparatus is 74·1%; this compares very closely with the average of the percentages of Calanus moved down or stayed down in the control sides of these experiments, 73·5%, and with a similar average for all standard experiments at 10 m., 71·8%.

In spite of this the results of Exps. 50 and 51 appear to show quite clearly that the distribution of the Calanus in the dark is not just a chance one due to movement at random. In Exp. 50, being introduced into the lower compartment, 81·5% of the Calanus stayed down and 18·5% actively moved up; in Exp. 51, being introduced into the upper compartment, 19·0% stayed up and 81·0% moved down. The same stock gave just as close results in the open side but showed slightly higher values for those having moved up or stayed up. The difference between the presence of light and its complete absence has made a real difference, but not a very marked one. It is surely very significant that in complete absence of light a population of Calanus will still segregate into two groups of individuals: one moving up and the other moving down—and that in two experiments with the same stock at the same depth the proportions up and down vary only by 0·5%.

These results, which are very puzzling in view of the mirror experiments, if confirmed by others, would seem to show that light has only a little to do with the proportions found up or down at the end of an experiment. It will be important to find out what happens when such black-out experiments are repeated at depths of 1, 5, 20 and 30 m. as we had originally intended. Actually there are two experiments which were made with the long-tube Apparatus No. 2, when the whole tube was blacked-out, and may in fact be taken to correspond to experiments made with the blacked-out cylinder of Apparatus No. 1; these were performed just below the surface. Further discussion of the dark-cylinder results just given will therefore be reserved until those with the long tube have been examined in the next section.

Experiments with the long-tube Apparatus No. 2

Only five experiments, Nos. 40–44, were made with Calanus in the long-tube Apparatus No. 2, the construction of which has been described on pp. 474–5, and illustrated in Pl. XI, figs. 1, 2. They were made off Millport on 20, 21 and 22 July, 1939 with Calanus collected from 60–70 m. in the Cumbrae Deep on the morning of each day at 0830 hr.; in each experiment the top of the apparatus was sunk just below the surface. Many more such experiments must be made at different depths and would have been but for the war; few as they are these five experiments are included here because it is considered that their results must be taken into account in any attempt to interpret the results with Apparatus No. 1.

Apparatus No. 2, it will be remembered, consists essentially of a long vertical tube made up of seven sections, each being a glass cylinder corresponding in diameter and length to one of the upper or lower compartments of Apparatus No. 1. We will denote these seven consecutive compartments by the letters *A*, *B*, *C*, *D*, *E*, *F* and *G*; they are linked to one another by a series of short connecting pieces fitted with gauze trapdoors which can all be opened or closed together by a control wire. The Calanus may be introduced into any one compartment, and then by opening the trapdoors at the beginning of an experiment they are free to migrate up and down the whole length of the tube; by closing the trapdoors at the end of the experiment we can separate any migration column into seven parts for subsequent analysis. The method of extracting the Calanus at the end of an experiment has already been described (p. 475).

The results of the five experiments are shown in Table IX and Text-fig. 19; each was of 1 hr. duration. Throughout the figures refer only to Calanus Stage V; the numbers of adults and other stages were too small to be considered.

At the start of Exp. 40 the Calanus, 98 of them, were placed in the top compartment *A* and none in the lower ones; at the end of the hour only eighteen remained in *A*, smaller numbers in *B* to *F* and thirty-nine in the bottom compartment *G*. The numbers in each compartment, together with the percentage proportion of the whole column that they represent, are given for each experiment in the table.

In the next experiment 340 Calanus were put into the bottom compartment *G*. After an hour it was found that 322 had remained there and small numbers had moved up into all the others, four reaching the top compartment *A*; the total length of the tube is just 12 ft.

In Exp. 42 the whole tube was blacked out so that the column of water was in complete darkness, and 137 Calanus were put at the start into the bottom compartment *G*. At the end 133 (97·0%) remained in *G* and only one went up as far as *D*, none was found in *E* but three in *F*.

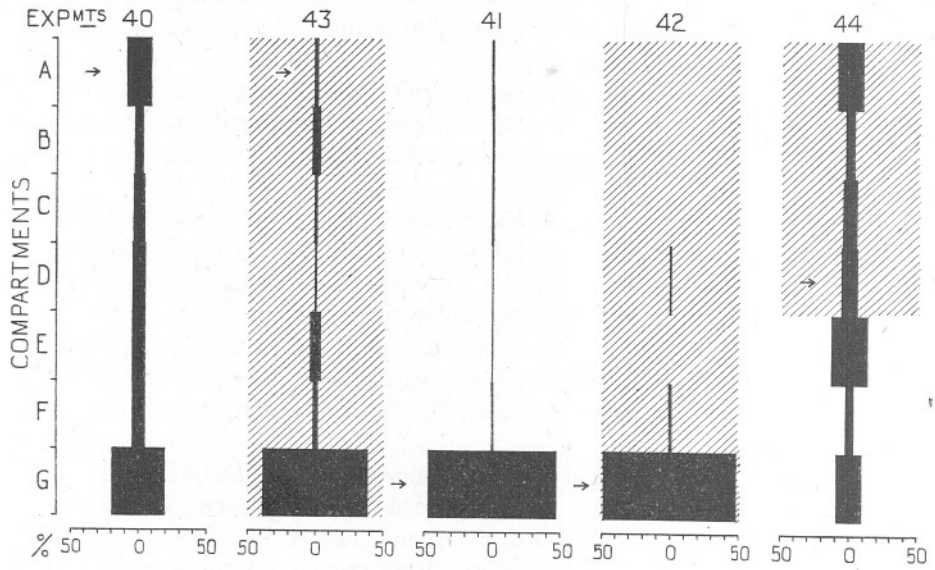
Exp. 43 was blacked out just as in Exp. 42, but the Calanus, 125, were introduced at the start into the top compartment *A*; at the end only four remained in *A*, small numbers in *B*, *C*, *D*, *E* and *F*, and ninety-six had gone down to *G*.

Exps. 40 and 41 were carried out on the same day with Calanus from the same sample; Exps. 42 and 43 were made the next day with Calanus from another sample but caught at the same place, depth and time of day. It was impossible to do all four experiments with Calanus from the same sample on the same day because of the time necessary to prepare the completely blacked-out tube. The object of Exps. 40 and 41, as planned, was to compare the vertical movement of Calanus upward and downward, as had been done in the two sides of Apparatus No. 1, but through a greater range of depth; to do this it was

TABLE IX. SHOWING THE DISTRIBUTION OF CALANUS STAGE V IN THE DIFFERENT COMPARTMENTS *A–G* IN THE LONG-TUBE APPARATUS NO. 2 AT THE BEGINNING (*a*) AND END (*b*) OF EXPS. 40–44.

The whole tube in Exps. 42 and 43, and compartments *A*, *B*, *C* and *D* in Exp. 44, were covered with black paper to exclude all light.

Exps....	40		41		42		43		44	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Time (hr.)...	1111	1211	1443	1543	1133	1233	1354	1454	1015	1115
Compartments										
A	98 100 %	18 18·4 %	—	4 1·15 %	—	—	125 100 %	4 3·2 %	—	25 18·8 %
B	—	6 6·1 %	—	3 0·9 %	—	—	—	7 5·6 %	—	10 7·5 %
C	—	8 8·1 %	—	3 0·9 %	—	—	—	2 1·6 %	—	14 10·5 %
D	—	9 9·2 %	—	2 0·6 %	—	1 0·75 %	—	1 0·8 %	133 100 %	16 12·0 %
E	—	9 9·2 %	—	2 0·6 %	—	—	—	10 8·0 %	—	35 26·4 %
F	—	9 9·2 %	—	4 1·15 %	—	3 2·25 %	—	5 4·0 %	—	8 6·0 %
G	—	39 39·8 %	340 100 %	322 94·7 %	137 100 %	133 97·0 %	—	96 76·8 %	—	25 18·8 %



Text-fig. 19. Results of Exps. 40–44 made with Apparatus No. 2. The arrows point to the compartment into which the Calanus were introduced at the beginning of each experiment. The width of each blacked-in histogram represents the percentage of the population found in each compartment at the end of an experiment. The shaded areas indicate that the whole apparatus or part of it was blacked out for purposes of the experiment. Exp. 43 is placed next Exp. 40 to make comparison easier. For further explanation see text.

necessary to use the same stock of Calanus for such a pair of experiments. Since Exps. 40 and 41 were taken with Calanus from one stock, and Exps. 42 and 43 with those from another, the differences between their behaviour in Exps. 40 and 43 or again between 41 and 42 may be due either to the effect of light and darkness or to the Calanus being of different origin. In future such experiments must be made with Calanus from the same stock, but to do this satisfactorily two separate long tubes would be necessary, one uncovered as a control, the other already blacked out. The blacking out of the tube sections and the precautions taken to cut out light with baffle plates and screens, as it was assembled and the Calanus introduced without being exposed to light, need not be described in detail; the difficulties, however, were considerable and the process took time.

Exp. 44 was of a special kind and will be more conveniently dealt with after we have considered the relation of the results of the four experiments just described to those obtained with Apparatus No. 1.

If we compare Exp. 40 with a standard one using Apparatus No. 1 which has only the two compartments, upper *A* and lower *B* (or α and β), then the top compartments *A* of each, into which the Calanus have been introduced, will correspond; further, all the Calanus found in the sections *B*, *C*, *D*, *E*, *F* and *G* in Apparatus No. 2 will correspond to those which would be found at the end of an experiment in the lower compartment (*B*) of Apparatus No. 1. This would correspond to an Apparatus No. 1 result of 81·6% moved down. Had the tube of Apparatus No. 2 been still longer it seems likely that many of the thirty-nine found in *G* would have descended deeper. The long tube amplifies the information provided by Apparatus No. 1: the population is not simply analysed into those which stay up and those which go down—but the latter are seen to be made up of individuals graded in their reactions during a 1 hr. period.

Similarly, if we compare Exp. 41 to a standard experiment with Apparatus No. 1, then the compartment *G*, into which the Calanus were introduced, will correspond to the compartment β of No. 1 and the Calanus found in the compartments *F*, *E*, *D*, *C*, *B* and *A* of No. 2 will correspond to those that would be found in compartment α at the end of an experiment. We would have a result in Apparatus No. 1 of 94·7% having stayed down and 5·3% having moved up. Since the results of these two experiments (Nos. 40 and 41) can be considered to provide data strictly comparable with those from standard experiments, these percentages have been inserted into the graphs in Text-figs. 7 and 8, shown as squares instead of circles to distinguish them from the rest, Exp. 40 being entered as at $\frac{1}{2}$ m. depth and Exp. 41 as at $3\frac{1}{2}$ m. depth.[1]

[1] In these experiments the top of the apparatus was just below the surface so that the bottom of compartment *A* and the top of compartment *G* will respectively be $\frac{1}{2}$ and $3\frac{1}{2}$ m. below the surface; it is these points which correspond to the middle of Apparatus No. 1 when the experiments are compared.

If we treat the darkened Exps. 42 and 43 in the same way we have results for comparison with those of Apparatus No. 1 as follows: Exp. 42 gives 97·0% stayed down (=β) and 3% moved up (=α); Exp. 43 gives 96·8% moved down (=B) and 3·2% stayed up (=A). The two populations were from the same stock, but selected at random; it is remarkable that the percentages should be so closely similar. Exp. 42 corresponds to an experiment with Apparatus No. 1 at $3\frac{1}{2}$ m. and Exp. 43 with one at $\frac{1}{2}$ m., as just explained. The three experiments with blacked-out cylinders performed with Apparatus No. 1 (described in the preceding section) were all at 10 m. depth and gave percentage values for Calanus, moved down or stayed down, having an average of 74·1%; this we have seen corresponded closely with the average for their control sides which was 73·5%. The results of the two blacked-out experiments (Nos. 42 and 43) just described, regarded as results with Apparatus No. 1, at $3\frac{1}{2}$ and $\frac{1}{2}$ m., give percentages down of 97·0 and 96·8 respectively compared with those of the uncovered cylinders at the same depths of 94·7 and 81·6%. These results, so expressed, again show no significant difference. Although one can see some difference between the behaviour of the Calanus over the *whole length* of the long tube when it is uncovered and when it is blacked out, one is led once more to doubt if light is in fact a predominating influence; yet how can such a view be reconciled with the results of the mirror experiments? The results of the fifth long-tube experiment (No. 44) may now be considered.

In Exp. 44 the four compartments *A*, *B*, *C* and *D* were blacked out, but the lower three, *E*, *F* and *G*, were uncovered. The Calanus, 133 of them, were introduced into compartment *D*. At the end of the hour's experiment they were distributed as shown in the last column of Table IX; 12·0% remained in *D*, 36·8% had moved upwards (10·5% into *C*, 7·5% into *B* and 18·8% reached the top compartment *A*) and 51·2% moved downwards (26·4% into *E*, 6·0% into *F* and 18·8% into the bottom compartment *G*). Certainly this peculiar distribution must be due to the distribution of light and shade which is peculiar to the experiment. Light could only enter the darkened part of the tube from below; here conditions were similar to those in the mirror experiments except that the light was scattered light and not the direct overhead illumination reflected upwards. Some of the Calanus apparently responded to this and moved upwards away from the light, for far more moved up than did so in a completely blacked-out tube; others, the largest number in any compartment (26·4%), were found in *E* in the shade just below the darkened part; the rest went further down into compartments *F* and *G* (6·0 and 18·8% respectively).

Exp. 44, adding support to the evidence from the mirror experiments with Apparatus No. 1, certainly shows that light is a factor influencing the vertical migrational behaviour of Calanus. Schallek (1943), as the result of his laboratory experiments with the copepod *Acartia tonsa*, has put forward the view that such animals only react to direct light and in diffuse light sink passively under

the influence of gravity. Our Exp. 44 does not support this in regard to Calanus. In any further consideration of the problem, we must bring together in review the results of all the experiments with both types of apparatus; the place for this is in the general discussion which follows.

General Discussion and Conclusions

The standard experiments in the daytime, between 0800 and 1600 hr., with Apparatus No. 1 (pp. 480–95), showed that populations of Calanus, caught at depths of 60 or more metres and experimented with at depths of 1, 5, 10, 20, 30 and 40 m., behaved in the following manner: at each successive depth the members of the population segregated into those which moved upwards and those which moved downwards. The proportions of those moving upwards or downwards, while showing considerable variation between results on different days, on an average increased or decreased respectively in direct relation to depth and not in relation to diminished light intensity.[1]

This would appear to indicate that Calanus, and possibly other animals which show a similar vertical migration, have a sense of depth. Whether they have some as yet undiscovered pressure organ for this purpose or whether there is some metabolic chemical reaction the rate of which varies with pressure remains to be investigated. The possibility that they react to chemical differences in the water which vary with depth seems unlikely from experiments made with waters either of different alkalinity or taken from different depths (pp. 507–8). It is likely that chemical differences in the water may modify their behaviour—but hardly that such differences will form a regular gradient sufficiently often to produce an average behaviour reaction directly correlated with depth.

The mirror experiments (pp. 495–500), in which the natural overhead illumination was reflected vertically upwards into an otherwise darkened cylinder, showed that light *is* an important factor: that it is towards or away from the light that Calanus moves at the different depths rather than in response to gravity. But again these experiments do not support the view that the response varies in relation to differences in the intensity of the light.

Experiments performed at night or dusk (pp. 500–2) showed results very similar to those of daylight experiments, again suggesting that the difference in the intensity of the light is of little significance.

Experiments repeated at 3-hourly intervals at 10 m. depth (pp. 502–4) showed that there is a change in the behaviour of Calanus with the passage of time through a 24 hr. period. They showed a marked increase in the proportion of Calanus moving up with the approach of night, and an equally marked downward movement after midnight but before any apparent increase in light intensity. At 0600 hr. some 95% were moving downward.

[1] See however, Addendum, p. 521.

Experiments with 'fed' and 'starved' Calanus (pp. 504–7) were too few and too varied; they gave inconclusive results, but suggested that physiological changes may alter the animal's more normal behaviour to some extent. Experiments with Calanus kept for periods of 1–3 days in the laboratory showed marked changes in the behaviour of those kept longest (pp. 508–9).

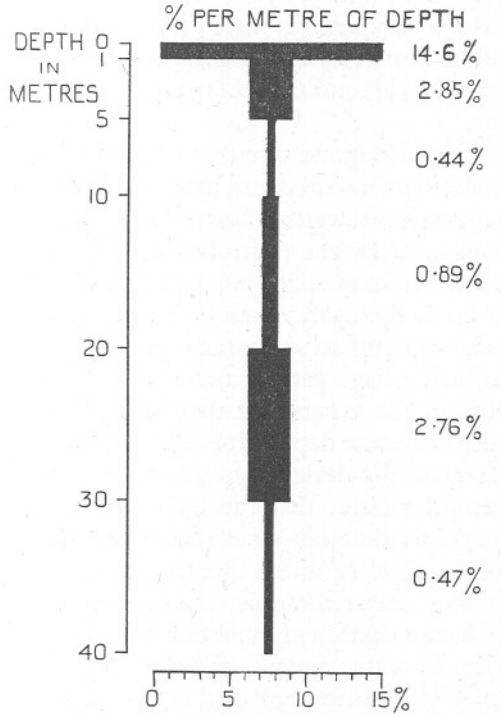
Two outstanding puzzles are presented. First, how is it that a population of Calanus, which was known to have been caught at a depth of some 60 m. or more at 0800 or 0900 hr., should segregate out into proportions apparently positively and negatively phototactic when experimented with at varying depths much nearer the surface, i.e. from 1 to 40 m. deep, and further that the positive and negative proportions should vary directly with depth? How is it that in nature they did not take up a depth distribution in accordance with these phototactic tendencies, being invariably found by us at these times in deep water?

The second outstanding puzzle is that in experiments, made with both Apparatus No. 1 and No. 2, in which the Calanus were in complete darkness, there was no fundamental difference between their behaviour in darkness and their behaviour in the control uncovered cylinders at the two ranges of depth at which the experiments were made: 0·5–3·5 and 10 m. (pp. 509–14). How can these results be reconciled with those of the mirror experiments and of Exp. 44 with the long tube (p. 514) which clearly show the importance of light?

As already stated in the introduction, the experiments would have been carried very much further before the publication of results if the war had not intervened. It is not our intention at present to elaborate a theory to cover all the results; this must wait until a number of hypotheses suggested by the work have been tested by further experiment. It may be of interest, however, to outline one such tentative hypothesis, and valuable if it provokes discussion and criticism.

May it not be possible that the Calanus have a diurnal rhythmic habit of vertical migration: that as evening approaches, whether or not started off by a *change* of light intensity which is most rapid at sunset (cf. Clarke's experiments with *Daphnia*, 1930), they move upwards, and after a certain time spent nearer the surface make their descent to deeper water again where they remain until the upward urge sets in once more? Now if this is so, and if artificially they are removed from their normal depth in the daytime and carried upwards, is it not possible that they may react as if they had themselves made the migration, endeavouring to distribute themselves in relation to depth as they would have done if they had made the journey upwards in the evening? May it not be that in nature, having started this migration, they move upwards towards the light, irrespective of its intensity, until certain lesser depths are reached which satisfy the migrational urge of different particular individuals on that particular day?

If this hypothesis is correct then we could reconstruct from our results a general picture of their more normal distribution at night. From Table I we see the average percentage proportions moving or staying up at each successive depth; thus between 1 m. and the surface would be 14·6% of the population, between 5 and 1 m. 11·4% or 2·85% per m. of depth, between 10 m. and 5 m. 2·2% or 0·44% per m. of depth, and so on. These percentage values per metre depth are shown graphically in Text-fig. 20 down to a depth of 40 m. Nicholls (1933), using vertical closing nets in the Clyde sea area (Loch Fyne) in July,



Text-fig. 20. Hypothetical distribution at night. For explanation see text.

found the distribution of Calanus Stage V at 2200 hr. as follows: 17·1% between 0 and 30 m., 0·6% between 30 and 60 m., 0·9% between 60 and 80 m., 6·4% between 80 and 100 m., 45·2% between 100 and 120 m. and 29·5% below 120 m. At 0100 hr. for similar ranges of depth he found percentages as follows: 16·7, 7·3, 0·9, 4·7, 54·5 and 15·9. The bulk of his Calanus Stage V remained below 100 m. throughout his 24 hr.; but the distribution he found in his population above 80 m., the region from which our samples were taken, on the whole was not unsimilar to our hypothetical reconstruction suggested above.

Physiological changes may govern the variation in depth to which individuals may go on different days; the 'fed' and 'starved' experiments have given a

hint of such a modification of behaviour. It may be that if light plays the part of attracting them upwards when once the evening migrational urge has set in, they may be inclined, if anything, to go slightly farther up in a higher light intensity than they would in a lower. Such a view might be supported by (1) the slight but positive correlation found between the percentages in the lower compartments of the apparatus at 5 or 10 m. depth and the Secchi disk readings (p. 494), and (2) the fact that the percentages in the lower compartments at night were on the whole higher than those in the daytime at corresponding depths (cf. Text-figs. 9, 17).

The depth to which they sink on their downward morning migration may indeed be determined in part by the intensity of the light as suggested by the work of Russell (1926, 1934) and Clarke (1933); we have no evidence from our work regarding this.

If when they begin to migrate upward it is movement towards the light which guides them until a sense of depth determines how far they go, how is it that they go still higher up towards a lesser depth in the mirror experiments when normally, as shown by the control side of the apparatus, they would move downwards away from the light into a greater depth? It is possible that, with the reversed light, the cylinder was not long enough to allow them to appreciate the change of depth in so short a range. Their movement *away from the light* would *normally* have carried them to a greater depth—under the abnormal conditions of the experiment their movement away from the light actually carried them to a lesser depth. It is idle to speculate; more experiments must be made systematically designed to test the various points suggested.

What of the second puzzle: that the behaviour of Calanus in complete darkness is not markedly different from their behaviour in light? Again we can suggest an hypothesis to be tested by experiment. In the absence of light it is possible that they may still adjust themselves to depth by reaction to gravity. They may have a rhythm of migration which will assert itself for some time in the absence of light; indeed, Esterly (1917) demonstrated such a rhythm in the copepod *Acartia* kept in a tall jar in darkness all day in the laboratory. We may recall other similar rhythms recorded for marine animals, e.g. the tidal rhythm in *Convoluta roscoffensis* observed by Gamble & Keeble (1903) for several days after specimens had been removed to the laboratory or the diurnal rhythm of luminescence observed by Moore (1909) in plankton animals kept in the dark. There is perhaps some evidence in support of this hypothesis from the results of the long-tube experiments shown in Table IX (p. 512). Comparing Exps. 41 and 42, in which the Calanus were introduced into the bottom compartment of each, we see that practically the same proportion has moved up from this compartment in each, 5·3 and 3%; but that in the uncovered tube some have travelled to the very top towards the light, whereas in the complete darkness of Exp. 42 none has travelled more than half-way. Similarly in Exps. 40 and 43, in which the Calanus were introduced

into the top compartment of each, 81·6% moved down from that compartment in the uncovered tube and 96·8% in the completely blacked-out tube, but in the former only 39·8% reached the bottom compartment, whereas in the latter, in the dark, 76·8% went to the bottom. In Text-fig. 19 (p. 512) the percentage proportions in the different compartments at the end of Exps. 40–44 are shown graphically, the arrows indicating the compartments into which they were originally introduced; Exp. 43 is placed next to Exp. 40 with which it compares, Exp. 42 comparing with Exp. 41. It is seen that in general their behaviour in the darkened tubes (Exps. 43 and 42) is similar to that in the uncovered tubes, but that they tend to go somewhat deeper in the absence of light. Again this seems to fit in with the suggestion that, while it is the depth itself which is the major factor in determining their upward distribution, they may tend to be a little higher up in a greater light intensity than in a lesser. The distribution in Exp. 43 is more like that in Exp. 40; they have not all sunk from compartment *A* in spite of the complete absence of light. The distribution in Exp. 42 is most like that in Exp. 41; in spite of the darkness some have migrated upwards.

The problem is a complex one, but that it can in time be solved by experimental analysis cannot be doubted. It would seem that the experiments must be made in the sea itself since depth appears to be such an important factor and since other conditions in the laboratory present so many artificialities. The experiments here described are to be regarded as but the beginning of such an approach.

Summary

Experiments were made with apparatus, largely of glass, specially designed to study the vertical movements of plankton animals under as natural conditions as possible at various depths in the sea. The animals were introduced in darkness into the apparatus which was kept covered with a black cloth until it was lowered below the surface so that from the time they were caught, in the opaque tow-net bucket, to the time they were returned to the sea in the apparatus, they were never subjected to above-surface illumination. The experiments were begun and ended at the required depth by the dispatch of messenger weights down the suspending wire from above. The copepod *Calanus finmarchicus* (Gunn.) was used, but a few experiments were also made with another copepod, *Euchaeta norvegica* Boeck.

The apparatus is described in detail; it takes two forms. No. 1 consists of two vertical parallel glass cylinders *AB* and $\alpha\beta$ closed at the top by a glass plate and at the bottom by a metal one, and having trapdoors at the middle of each which divide them into upper and lower compartments, *A* and *B* in one, and α and β in the other. They were filled with sea water and the copepods were introduced into only one compartment of each cylinder, in standard

experiments into *A* on one side and *β* on the other. The apparatus was now lowered to the required depth and the trapdoors opened so that the copepods were free to move up or down the whole length of the cylinders. At the end of an experiment the trapdoors were closed again so that the percentage proportions that have moved up or down under different conditions could be estimated. In experiments other than standard, one side was left normal as a control and in the other the conditions were altered for the purpose of the experiment, e.g. darkened or the *p*H of the water increased or decreased. Apparatus No. 2 is a modification, a long tube of seven compartments each separated by a controlled trapdoor.

Standard experiments in the daytime (between 0800 and 1600 hr.) made at depths of 1, 5, 10, 20, 30 and 40 m. showed that populations of Calanus, caught at a depth of 60 m. or more, segregated into those moving upwards and those moving downwards, and that their proportions on an average increased and decreased respectively in direct relation to depth and not to light intensity. Calanus would appear to have a sense of depth.[1] Experiments at 50 and 100 m. were too few to give conclusive results.

Mirror experiments, in which the natural overhead illumination was reflected vertically upwards from below (against gravity) into an otherwise darkened cylinder, showed that light is an important factor. It is towards or away from light that Calanus moves rather than in response to gravity.

Experiments at night showed results on the whole similar to those in the daytime.

Experiments repeated at 3-hourly intervals at 10 m. depth showed that there is a marked change in the behaviour of Calanus with the passage of time through a 24 hr. period: an upward movement with the approach of night and a downward movement with the approach of day.

In other experiments those made with 'fed' and 'starved' Calanus were too few and varied to give conclusive results. Those made with waters of different *p*H and waters from different depths revealed no significant difference in the behaviour of Calanus.

A few experiments made in complete darkness are puzzling in that the behaviour of Calanus is not markedly different in the dark from that in the light: a tentative explanation is suggested in the general conclusions.

The few experiments made with the long-tube Apparatus No. 2 enable the vertical migrational behaviour of Calanus to be analysed in greater detail.

The experiments must be continued further before a theory can be elaborated to cover all the observations; some tentative hypotheses are, however, suggested in the general conclusions. This account, to record the results so far obtained, was thought desirable since the work was interrupted by the war, and it is uncertain when it may be continued (see the preface).

[1] See however Addendum on next page.

ADDENDUM

The late Lieut. Neil Paton made some experiments on freshwater plankton animals with both Apparatus No. 1 and No. 2 in Lake Windermere in the summer of 1939, but was not able to analyse the results before taking his commission in the R.N.V.R. Since going to press Mr D. H. Cushing in my Laboratory (at Oxford) has completed their analysis. He finds that *Cyclops strenuus* (but not *Diaptomus gracilis*) has a very similar behaviour to that of Calanus in that the proportions moving up or down in different experiments (in Apparatus No. 1) *appear* directly correlated with the depths at which the experiments are made. Some results with *Cyclops* in Apparatus No. 2 however seem to tell against the 'sense of depth' hypothesis. He suggests however that instead of behaving in direct relation to depth, the animals are reacting in relation to the *logarithm* of the light intensity at the different depths and so giving the appearance of a straight line correlation with depth. While at present it does not seem possible to reconcile such a view with some of the Calanus experiments described in the foregoing paper, this note is added to emphasize that the 'sense of depth' hypothesis must be regarded as entirely tentative until both it and that suggested by Mr Cushing have been tested by further experiments specially designed for the purpose. It is hoped that these will be made in the coming year.

REFERENCES

CLARKE, G. L., 1930. Change in phototropic and geotropic signs in *Daphnia* induced by changes in light intensity. *Journ. Exper. Biol.*, Vol. 7, pp. 109–31.

—— 1933. Diurnal migration of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. *Biol. Bull.*, Vol. 65, pp. 402–36.

—— 1934*a*. Further observations on the diurnal migration of copepods in the Gulf of Maine. *Biol. Bull.*, Vol. 67, pp. 432–55.

—— 1934*b*. The diurnal migration of copepods in St George's Harbour, Bermuda. *Biol. Bull.*, Vol. 67, pp. 456–60.

—— 1936. Light penetration in the western North Atlantic and its application to biological problems. *Cons. Perm. Internat. Explor. Mer, Rapp. et Proc. Verb.*, Vol. 101, 2ne partie, No. 5.

ESTERLY, C. O., 1911. Diurnal migrations of *Calanus finmarchicus* in the San Diego region during 1909. *Intern. Rev. Hydrobiol. Hydrogr.*, Vol. 4, pp. 140–51.

—— 1912. The occurrence and vertical distribution of the Copepoda of the San Diego region. *Univ. Calif. Public. Zool.*, Berkeley, Vol. 9, pp. 253–340.

—— 1917. Specificity in behaviour and relation between habits in nature and reactions in the laboratory. *Univ. Calif. Public. Zool.*, Berkeley, Vol. 16, pp. 381–92.

—— 1919. Reactions of various plankton animals with reference to their diurnal migrations. *Univ. Calif. Public. Zool.*, Berkeley, Vol. 19, pp. 1–83.

GAMBLE, F. W. & KEEBLE, F., 1903. The bionomics of *Convoluta roscoffensis*. *Quart. Journ. Micro. Sci.*, Vol. 47, pp. 363–431.

GARDINER, A. C., 1933. Vertical distribution in *Calanus finmarchicus*. *Journ. Mar. Biol. Assoc.*, Vol. 18, pp. 576–610.

HARDY, A. C., 1936. Plankton ecology and the hypothesis of animal exclusion. *Proc. Linn. Soc.*, Session 1935–6, Pt. 2, pp. 64–70.

—— 1938. Change and choice: a study in pelagic ecology. In *Evolution: Essays on Aspects of Evolutionary Biology*. Oxford: Clarendon Press.

HARDY, A. C. & GUNTHER, E. R., 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–7. *Discovery Reports*, Vol. XI, pp. 1–456.

JOHNSON, W. H., 1938. The effect of light on the vertical movements of *Acartia clausi* (Giesbrecht). *Biol. Bull.*, Vol. 75, pp. 106–18.

LOEB, J., 1906. Ueber die Erregung von positivem Heliotropismus durch Saure, insbesondere Kohlensaure und von negativem Heliotropismus durch ultraviolette Strahlen. *Arch. ges. Physiol.*, Vol. 115, pp. 564–81.

MARSHALL, S. M., NICHOLLS, A. G. & ORR, A. P., 1935. On the biology of *Calanus finmarchicus*. Part IV. Oxygen consumption in relation to environmental conditions. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 20, pp. 1–27.

MICHAEL, E. L., 1911. Classification and vertical distribution of the Chaetognatha of the San Diego region. *Univ. Calif. Public. Zool.*, Berkeley, Vol. 8, pp. 21–186.

—— 1913. Vertical distribution of the Chaetognatha of the San Diego region in relation to the question of isolation versus coincident distribution. *American Naturalist*, Vol. 47, pp. 17–49.

MOORE, B., 1909. Observations on certain marine organisms of (*a*) variations in relation to light and (*b*) a diurnal periodicity of phosphorescence. *Biochemical Journal*, Vol. 4, pp. 1–29.

MURRAY, J. & HJORT, J., 1912. *The Depths of the Ocean*. London: Macmillan and Co.

NICHOLLS, A. G., 1933. On the biology of *Calanus finmarchicus*. III. Vertical distribution and diurnal migration in the Clyde Sea-area. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 19, pp. 139–64.

POOLE, H. H. & ATKINS, W. R. G., 1926. On the penetration of light into sea water. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 14, pp. 177–98.

ROSE, M., 1925. Contribution à l'étude de la biologie du plankton, le problème des migrations verticales journalières. *Archiv. Zool. Expér. Génér.*, Vol. 64, Fasc. S, pp. 387–542.

RUSSELL, F. S., 1925. The vertical distribution of marine macroplankton. An observation on diurnal changes. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 13, pp. 769–809.

—— 1926. The vertical distribution of marine macroplankton IV. The apparent importance of light intensity as a controlling factor in the behaviour of certain species in the Plymouth area. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 14, pp. 415–40.

—— 1927. The vertical distribution of plankton in the sea. *Biological Reviews*, Vol. 2, pp. 213–62.

—— 1928*a*. The vertical distribution of marine macroplankton VI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 15, pp. 81–103.

—— 1928*b*. The vertical distribution of marine macroplankton. VII. Observations on the behaviour of *Calanus finmarchicus*. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 15, pp. 429–54.

—— 1931*a*. The vertical distribution of marine macroplankton. X. Notes on the behaviour of *Sagitta* in the Plymouth area. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 17, pp. 391–414.

RUSSELL, F. S., 1931*b*. The vertical distribution of marine macroplankton. XI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 17, pp. 767–84.

—— 1934. The vertical distribution of marine macroplankton. XII. Some observations on the vertical distribution of *Calanus finmarchicus* in relation to light intensity. *Journ. Mar. Biol. Assoc.*, N.S., Vol. 19, pp. 569–84.

SOUTHERN, R. & GARDINER, A. C., 1932. The diurnal migrations of the Crustacea of the plankton in Lough Derg. *Proc. Roy. Irish Acad.*, Vol. 40, B, pp. 121–59.

SCHALLEK, W., 1943. The reaction of certain crustacea to direct and diffuse light. *Biol. Bull.*, Vol. 84, pp. 98–105.

WORTHINGTON, E. B., 1931. Vertical movements of freshwater macroplankton. *Int. Rev. Hydrobiol. Hydrogr.*, Vol. 25, pp. 394–436.

EXPLANATION OF PLATES

PLATE X

Fig. 1. Apparatus No. 1 covered with a black cloth about to be sent down for an experiment; the cloth is removed when the apparatus is below the surface.

Fig. 2. The apparatus on the 'stretcher' being lowered into the cabin at the end of an experiment.

Fig. 3. Details of trigger mechanism of Apparatus No. 1, the trapdoors (in their original form) are in the open position.

PLATE XI

Fig. 1. Apparatus No. 2 suspended attached to cable as in an experiment below the surface.

Fig. 2. Details of the levers and wire operating two of the trapdoors of Apparatus No. 2; the trapdoors are in the open position.

APPENDIX

TABLE I. SHOWING THE CONDITIONS AND TYPE OF EACH EXPERIMENT

Unless otherwise stated in a footnote all experiments were of 1 hr. duration, and the Calanus used were caught from a depth of 60–90 m. The compartments into which the Calanus were introduced (*A* or *B* and α or β) are shown with the results of each experiment in Table II

No. of exp.	Date 1938	Depth in m.	Time of beginning of exp. G.M.T.	State of weather: Beaufort symbols	State of sea	Transparency of sea: Secchi disk reading in m.	Temperature of sea at surface °C.	Time at which Calanus were caught	Date on which Calanus were caught	Type of exp.	Origin of the water used in the two cylinders *AB*	Origin of the water used in the two cylinders $\alpha\beta$
1	2. viii.	20	1100[c]	b.z.	0	—	—	0830	2. viii.	Standard	Surface water	Surface water
2	2. viii.	20	1236[c]	o.	0	8·5	—	0830	2. viii.	Standard	Surface water	Surface water
3	8. viii.	20	1029	o.p.	1–2	7·75	—	0800	8. viii.	Standard	Surface water	Surface water
4	8. viii.	5	1306	o.	2	7·0	—	0800	8. viii.	Standard	Surface water	Surface water
5	10. viii.	30	1032	b.z.	0	8·25	15·3	0800	10. viii.	Standard	Surface water	Surface water
6	10. viii.	1[b]	1256	b.z.	0	—	15·6	0800	10. viii.	Standard	Surface water	Surface water
7	11. viii.	10	1006	b.	0	8·4	14·6	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
8	12. viii.	1[b]	1054	c.	1	6·25	13·9	0800	12. viii.	Mirror	Surface water	Surface water
9	12. viii.	1[b]	1351	b.c.	1–2	7·5	13·5	0800	12. viii.	Mirror	Surface water	Surface water
10	26. viii.	10	1025	b.c.z.	0	11·0	14·6	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
11	26. viii.	40	1225[c]	b.c.z.	0	9·5	14·6	0800	26. viii.	Standard	Surface water	Surface water
12	26. viii.	30	1353[c]	b.c.z.	0	11·5	14·6	0800	26. viii.	Standard	Surface water	Surface water
14[a]	30. viii.	40	1140	b.	0	10·5	—	0730	30. viii.	Standard	Surface water	Surface water
15	30. viii.	30	1349	b.c.	1–2	8·5	—	0730	30. viii.	Standard	Surface water	Surface water
16	31. viii.	10	1020	b.	0–1	10·5	13·6	0730	31. viii.	Standard	Surface water	Surface water
17	31. viii.	20	1200	b.	1	11·0	—	0730	31. viii.	Standard	Surface water	Surface water
18	1. ix.	10	1002	b.c.	0	8·0	13·8	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
19	1. ix.	10	1151	b.c.	0–1	8·5	14·0	—[f]	—[f]	'Fed' and outside Calanus	Culture water[f]	Surface water
20	1. ix.	10	1330[c]	c.p.	1	8·25	14·0	0730	1. ix.	Standard	Surface water	Surface water
21	7. ix.	20	1030	c.z.	1	7·25	13·8	0800	7. ix.	Standard	Surface water	Surface water
23[a]	12. ix.	30	1109	o.	1–2	6·5	13·8	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
24	12. ix.	5	1311[c]	c.z.	2–3	8·0	13·8	—[f]	—[f]	'Fed' and outside Calanus	Culture water[f]	Surface water
25	12. ix.	5	1433[c]	c.z.	2–3	7·75	13·8	0830	12. ix.	Standard	Surface water	Surface water
26	14. ix.	30	1255	b.c.	1	—	13·8	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
27	14. ix.	5	1705	b.	0	7·5[d]	12·6	—[f]	—[f]	'Fed' and 'starved' Calanus	Culture water[f]	Filtered water[f]
28	14. ix.	20	2108	b.	0	—	—	2015	14. ix.	Standard	Surface water	Surface water
29	15. ix.	100	1245[c]	c.p.	0–1	—	—	1100[g]	15. ix.	Standard	From 10 m.	From 10 m.
30	15. ix.	30	1700	b.c.	1	6·0	—	1100[g]	15. ix.	Standard	From 10 m.	From 10 m.
31	15. ix.	50	2039	b.c.	0	—	—	1900	15. ix.	Standard	From 10 m.	From 10 m.
32	15. ix.	5	2210	b.c.	0	—	—	1900	15. ix.	Standard	From 10 m.	From 10 m.
33	19. x.	30	1158	b.c.z.	1	8·0	11·6	1025	19. x.	Mirror	Surface water	Surface water
34	19. x.	20	1358	c.	1	8·0	11·6	1025	19. x.	Mirror	Surface water	Surface water
35	25. x.	20	1202	b.z.	1	7·25	11·9	1030	25. x.	Mirror	Surface water	Surface water
36	25. x.	10	1355	b.z.	1	7·0	11·9	1030	25. x.	Mirror	Surface water	Surface water
37	27. x.	5	1153	b.c.	1	6·5	11·6	1030[b]	25. x.[b]	Mirror	Surface water	Surface water

38	9. xi.	10	1145	o.	1–2	5·5	—	0930	9. xi.	Alkaline	See p. 507	Surface water
39	11. xi. 1939	10	1215	b.z.	1	5·5	—	—[i]	—[i]	Acid	See p. 507	Surface water
40	20. vii.	0·5	1111	b.z.	0	5·5	—	0830	20. vii.	Long-tube experiment	Surface water	—
41	20. vii.	0·5	1443	o.	0	5·0	13·9	0830	20. vii.	Long-tube experiment	Surface water	—
42	21. vii.	0·5	1133	o.	0	—	—	0830	21. vii.	Long-tube experiment	Surface water	—
43	21. vii.	0·5	1354	o.	0	—	—	0830	21. vii.	Long-tube experiment	Surface water	—
44	22. vii.	0·5	1015	o.p.	1–2	5·5	12·5	0830	22. vii.	Long-tube experiment	Surface water	—
49[e]	21. viii.	10	1041	b.c.	0	5·0	13·8	0800	21. viii.	$\alpha\beta$ completely darkened	Surface water	Surface water
50	23. viii.	10	0944	b.	0	8·5	15·0	0900	23. viii.	$\alpha\beta$ completely darkened	From 10 m.	From 10 m.
51	23. viii.	10	1139	b.	0	9·0	15·6	0900	23. viii.	$\alpha\beta$ completely darkened	From 10 m.	From 10 m.
52	23. viii.	10	1356	b.	0	7·5	*c.* 15	0900	23. viii.	Mirror	From 10 m.	From 10 m.
53	23. viii.	10	1556	b.	0	—	*c.* 15	0900	23. viii.	Mirror	Surface water	Surface water
54	23. viii.	10	1910	b.	0	6·5	*c.* 15	1830	23. viii.	Standard	Surface water	Surface water
55	24. viii.	100	0939	o.	1	7·5	15·6	0730	24. viii.	Standard	Surface water	Surface water
56	24. viii.	10	1139	o.	1	7·5	14·8	0730	24. viii.	Standard	Surface water	Surface water
57	24. viii.	10	1439	b.	1	7·5	*c.* 15	0730	24. viii.	Standard	Surface water	Surface water
58	24. viii.	10	1732	b.	1	7·0	*c.* 15	0730	24. viii.	Standard	Surface water	Surface water
59	24. viii.	10	2035	b.c.	0	3·5	15·4	1900	24. viii.	Standard	Surface water	Surface water
60	24. viii.	10	2333	b.c.	0	2·5	16·0	2230[j]	24. viii.	Standard	Surface water	Surface water
61	25. viii.	10	0230	b.c.	0	2·5	15·6	2230[j]	24. viii.	Standard	Surface water	Surface water
62	25. viii.	10	0537	b.c.	0	6·25	15·7	2230[j]	24. viii.	Standard	Surface water	Surface water
63	25. viii.	10	0834	b.z.	0	9·5	16·4	0730	25. viii.	Standard	Surface water	Surface water
64	25. viii.	10	1133	c.	0	8·0	14·8	0730	25. viii.	Standard	Surface water	Surface water
65	25. viii.	50	1332	o.	0	6·5	15·8	0730	25. viii.	Standard	Surface water	Surface water
66	30. viii.	10	1042	b.c.	0	4·5	—	0830	30. viii.	Deep *v.* surface water	From 30 m.	Surface water
67	30. viii.	10	1240	o.	0	4·0	—	0830	30. viii.	Deep *v.* surface water	From 30 m.	Surface water
68	18. xi.	10	0949	c.	0	5·25	—	1200	17. xi.	Standard (control)	Surface water	Surface water
69	18. xi.	10	1154	c.	0	6·0	—	1200	17. xi.	Standard (control)	Surface water	Surface water
70	18. xi.	10	1404	c.	0	5·5	—	1200	17. xi.	Standard (control)	Surface water	Surface water
71	20. xi.	10	1215	c.	0	5·25	—	1200	17. xi.	Standard (control)	From 10 m.	From 10 m.
72	20. xi.	10	1406	c.	0	5·0	—	1200	17. xi.	Standard (control)	From 10 m.	From 10 m.
73	21. xi.	5	1154	o.r.	1	4·5	—	1030	21. xi.	Standard (control)	From 10 m.	From 10 m.
74	21. xi.	5	1356	o.r.	1	4·5	—	1030	21. xi.	Standard (control)	From 10 m.	From 10 m.
75	22. xi.	10	1042	o.r.	2	5·5	—	1300[k]	21. xi.[k]	Standard (control)	Surface water	Surface water

(Exps. 68–75: Standard (control) — see p. 506)

[a] Exps. 13 and 22 were done with *Thysanoessa* and are not included in this paper.
[b] Middle of apparatus 1 m. (top ½ m.) below surface.
[c] Experiment of 30 min. duration instead of usual 60 min.
[d] Experiment in shallow water, Secchi disk seen resting on bottom at 7·5 m.
[e] Exps. 45–48 were invalidated by toxic effects (see p. 473).
[f] For details of origin and treatment of Calanus in these experiments see Table VI in the text.
[g] Calanus caught at 100–120 m.
[h] Calanus had been kept in jar standing in running water and fed on *Nitzschia*.
[i] Calanus in *AB* were from same stock as those used in Exp. 38 and had been kept 2 days in the laboratory; those used in $\alpha\beta$ were caught on the morning of the experiment.
[j] Calanus caught at 20 m. (see p. 503).
[k] Calanus kept in darkened jar on boat with two changes of water.

TABLE II. SHOWING THE NUMBERS OF CALANUS (TOTAL, STAGE V AND FEMALE) USED IN CYLINDERS *AB* AND $\alpha\beta$ IN EACH EXPERIMENT TOGETHER WITH THE PERCENTAGE OF THOSE FOUND IN THE LOWER COMPARTMENTS *B* AND β AT THE END OF THE EXPERIMENTS.

The experiments are grouped according to depth; particulars of date, time, weather conditions, origin of Calanus, etc., for each experiment will be found in Table I. The Calanus were introduced into compartments *A or B* and α *or* β in each experiment as shown in columns 3 and 10.

Depth in m.	No. of exp.	No. of Calanus introduced into compartments *A or B* at beginning of exp. Comp.	Total	V	♀	% Calanus in *B* at end of exp. Total	V	♀	No. of Calanus introduced into compartments α *or* β at beginning of exp. Comp.	Total	V	♀	% Calanus in β at end of exp. Total	V	♀
1	6	*A*	241	178	30	75·3	79·7	72·8	β	123	86	24	80·5	84·8	66·6
	8	A^m	118^m	92^m	13^m	$11·8^m$	$8·7^m$	$30·7^m$	α	132	111	6	87·1	89·2	66·6
	9	B^m	115^m	98^m	4^m	$46·0^m$	$41·8^m$	100^m	α	104	84	9	93·3	91·6	100
5	4	*A*	200	136	43	50·0	51·4	47·7	β	80	57	16	45·0	40·3	56·2
	24	*A*	548	372	166	83·0	77·9	96·9	α	292	280	8	69·1	69·1	75·0
	25	*A*	1120	834	230	70·7	64·9	86·9	β	1243	1057	152	80·5	80·3	81·5
	27	*A*	227	219	6	48·9	50·7	33·3	α	265	259	6	61·1	61·0	66·6
	32	*A*	417	297	110	82·2	81·1	86·3	β	450	351	91	92·6	93·1	91·2
	37	B^m	75^m	71^m	3^m	$38·6^m$	$39·4^m$	0^m	α	84	83	1	92·8	92·7	100
	73	*A*	412	411	1	81·5	81·5	—	α	276	275	0	75·6	75·6	—
	74	*A*	106	105	1	80·0	80·0	—	α	134	134	0	84·0	84·0	—
10	7	*B*	77	56	13	50·6	51·7	38·4	β	73	64	3	83·5	81·2	100
	10	*A*	152	107	31	67·7	59·8	90·3	α	—[a]	—	—	—[a]	—	—
	16	*A*	150	107	40	58·0	62·6	47·5	β	41	36	4	63·4	63·8	50·0
	18	*B*	560	540	7	85·3	85·1	100	β	506	481	14	64·0	61·6	78·0
	19	*A*	282	275	1	87·6	87·2	100	α	367	355	6	65·9	65·6	50·0
	20	*A*	291[b]	262[b]	17[b]	52·9[b]	53·8[b]	41·2[b]	β	397	370	16	73·8	74·5	68·7
	36	B^m	71^m	65^m	3^m	$66·2^m$	$64·6^m$	$66·6^m$	α	149	144	5	47·6	47·2	60·0
	38	*A*	85	75	9	84·7	84·0	100	α	130	111	15	80·8	80·1	86·6
	39	*A*	89	67	19	92·1	86·1	100	α	185	168	16	80·0	78·5	93·7
	49	*A*	67	59	8	76·1	74·6	83·3	α	84	74	10	61·9	59·7	80·0
	50	*A*	89	68	8	74·1	73·5	87·5	α	202	157	33	79·4	81·5	75·7
	51	*B*	60	36	17	61·7	75·0	58·8	β	252	200	28	84·2	81·0	92·8
	52	*A*	434	313	12	67·5	68·1	58·3	β^m	236^m	201^m	4^m	$41·9^m$	$43·8^m$	$50·0^m$
	53	*B*	288	254	2	79·5	79·5	50·0	α^m	872^m	712^m	16^m	$42·3^m$	$42·6^m$	100^m
	54	*A*	141	128	11	85·1	84·3	90·9	β	173	152	18	96·5	97·3	88·8
	56	*A*	524	446	48	67·9	67·2	66·6	β	514	432	52	69·8	70·3	61·5
	57	*A*	240	207	19	87·0	87·4	73·7	β	228	201	8	83·3	83·1	100
	58	*A*	229	214	4	57·2	59·3	25·0	β	420	397	9	49·7	50·0	11·2
	59	*A*	640	528	77	73·7	72·3	76·6	β	545	422	84	78·3	73·4	70·2
	60	*A*	275	254	19	37·4	37·1	42·1	β	209	185	18	55·5	57·8	33·3
	61	*A*	105	88	14	68·5	71·6	64·3	β	222	197	25	69·3	69·5	68·0
	62	*A*	83	79	4	97·5	97·4	100	β	191	174	17	92·6	93·6	82·3
	63	*A*	98	67	4	68·3	56·7	100	β	43	31	2	55·8	51·6	0
	64	*A*	213	76	2	82·6	68·4	50·0	β	274	149	3	89·7	91·2	33·3
	66	*A*	293	246	15	73·0	72·3	86·6	α	81	54	4	81·4	85·2	100
	67	*B*	429	396	15	74·1	74·2	73·3	β	347	333	8	83·5	83·4	100
	68	*A*	275	275	0	63·2	63·2	—	α	681	681	0	75·7	75·7	—
	69	*A*	608	606	1	69·8	69·8	—	α	450	450	0	86·8	86·8	—
	70	*A*	368	368	0	74·1	74·1	—	α	302	302	0	81·1	81·1	—
	71	*A*	93	93	0	18·4	18·4	—	α	108	107	1	15·0	15·0	—
	72	*A*	58	58	0	3·5	3·5	—	α	100	100	0	29·0	29·0	—
	75	*A*	137	135	2	35·6	35·6	—	α	80	80	0	33·8	33·8	—
20	1	*B*	—[a]	—	—	—[a]	—	—	α	28	22	5	64·3	68·1	40·0
	2	—[c]	—	—	—	—	—	—	α	589	470	78	80·3	79·3	85·9
	3	*A*	62	37	17	48·4	40·5	64·7	β	53	36	12	56·6	66·6	25·0
	17	*A*	29	19	7	62·0	68·4	28·5	β	44	34	6	52·3	52·9	33·3
	21	*B*	—[a]	—	—	—[a]	—	—	α	194	109	67	72·6	77·0	65·6
	28	*A*	101	76	22	82·1	80·2	90·9	β	124	88	32	76·8	76·1	78·1
	34	A^m	219^m	198^m	19^m	$43·8^m$	$42·9^m$	$57·8^m$	α	206	123	59	67·4	60·9	77·9
	35	A^m	159^m	153^m	4^m	$17·1^m$	$17·0^m$	25^m	α	212	193	15	56·8	57·5	69·2
30	5	*A*	236	179	27	50·4	46·9	59·1	β	34	23	7	44·1	52·1	28·5
	12	*A*	661	559	88	31·6	27·5	55·6	β	350	323	16	14·3	13·0	18·7
	15	*A*	254	197	47	34·0	27·9	46·7	β	161	141	14	44·1	40·4	71·4
	23	*A*	368	338	17	33·6	31·0	47·0	α	142	118	23	61·9	61·8	60·8
	26	*A*	231	220	8	34·6	35·0	25·0	α	259	252	5	67·5	67·4	80·0
	30	*A*	418	322	86	74·4	71·1	88·3	β	523	399	118	74·3	71·1	92·6
	33	A^m	189^m	171^m	17^m	$81·4^m$	$82·3^m$	$76·3^m$	α	83	66	17	42·1	39·3	52·9
40	11	*A*	411	382	24	19·9	19·6	25·0	β	361	316	28	25·2	21·8	57·1
	14	*A*	161	112	37	43·5	37·4	56·7	β	305	249	50	45·9	43·7	56·0
50	31	*A*	564	436	115	34·0	30·2	43·4	β	947	755	184	35·3	32·5	45·6
	65	*A*	371	262	4	17·5	19·5	75·0	β	337	216	1	41·5	44·5	0
100	29	*A*	1873	1238	619	19·2	17·6	21·9	β	—[a]	—	—	—[a]	—	—
	55	*A*	1205[d]	959[d]	225[d]	75·6[d]	77·1[d]	71·1[d]	β	1147	972	159	72·1	73·7	72·9

[a] Sample discarded (or lost) due to faulty working of apparatus.
[b] Some of the Calanus from compartment *B* were lost making the percentage in *B*, also estimate of numbers introduced into *A*, too low.
[c] Cylinder *AB* out of action.
[d] Cork came out of cylinder *A* on the way up (at end of experiment) so that a few Calanus may have escaped.
[m] Mirror experiments: the cylinder indicated (*AB* or $\alpha\beta$) was blacked out at top and sides and provided with a mirror system below reflecting light *upwards* (see p. 495).

NOTES ON THE INSHORE PLANKTON OF PLYMOUTH

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From the Plymouth Laboratory

(Text-fig. 1)

CONTENTS

Introduction

During the years 1940–5 plankton samples were examined regularly from inside the Plymouth Breakwater, with the exception of a few months. Although it was not possible to do any quantitative work, special attention was given to larval forms, especially of the decapods, molluscs and annelids. The presence of these larvae gave a good idea of the breeding seasons of the various species. As it is only recently that many of these larvae have been identified, this is the first time that detailed specific notes have been made of their presence; and it is thought to be worth while to publish these results. To help those who wish to identify the larvae, a reference to a description of each species is given whenever possible, in square brackets after its name. It should be clearly understood that the absence of any species from these notes does not necessarily imply that it might not have been there, although all the samples were carefully examined. Most of the Coelenterates, the Cirripedia, Copepoda, and young fishes, are omitted here. Of the remaining ingredients of the plankton, various records were kept; and the occurrence of the more noteworthy of these forms, according to months, is shown in Table I.

Very rarely there was an indication of an inflow of Atlantic water, or of windborne Atlantic organisms, for instance, *Doliolum* in August and September 1942, and a very young *Velella* float in February 1943, on which separate comment is made (Lebour, 1947). *Sagitta setosa* was, as is to be expected, the

prevailing species of this genus, but *S. elegans* occurred in 1941 on 1 January and 3 February; in 1943 on 13, 17 and 18 May; in 1945 on 21 February, 13 (in numbers) and 17 April. On 21 August 1940, Mr O. D. Hunt reported that *Salpa fusiformis* Cuv. was abundant in tow-nettings from the mouth of the River Yealm. At this time *Muggiaea atlantica* Cunningham was specially abundant in the Plymouth inshore waters and a few specimens of *Stephanomia bijuga* (Della Chiaje) were also seen.

Muggiaea atlantica Cunningham [Cunningham, 1892], regarded by Russell as an inhabitant of south-western waters, occurred in any month except February and March in the present samples: in 1940 from August to October (the plankton was not examined earlier in the year); in 1941 from June to December; in 1942 in January and from July to December; in 1943 from April to October; in 1944 in May and June only; in 1945 from June to November.

TABLE I. OCCURRENCES OF CERTAIN PLANKTONIC ORGANISMS

Month ...	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Noctiluca	×	×	×	×	×	×	×	×	×	×	×	×
Muggiaea atlantica	×	.	.	×	×	×	×	×	×	×	×	×
Stephanomia bijuga	.	×	.	.	.	.	.	.	.	.	.	.
Oikopleura dioica	×	×	×	×	×	×	×	×	×	×	×	×
Fritillaria sp.	.	×	×	×	×	.	×	×	×	×	×	×
Doliolum	.	.	.	.	.	.	.	×	×	.	.	.
Sagitta setosa	×	×	×	×	×	×	×	×	×	×	×	×
S. elegans	×	×	.	×	×	.	.	.	.	.	.	.

It is usually abundant in summer and autumn, rare or absent in winter and spring. Its occurrence in January in 1942 probably indicated the remnant of the autumn growth. In April and May 1943, and in May 1944, when it only began to be abundant at the end of that period, it may have been unusually early, or possibly very late. Russell (1934) states that this species and also *M. kochi* (Will) occurring in our waters generally first appear towards the end of the summer and often continue on through the autumn to the January or February in the following year. Russell (1934) has shown that *M. atlantica* and *M. kochi* occur in alternating periods, and one species does not overlap the other. *M. atlantica* occurred in an unbroken series from 1913 to 1924 (excepting 1915 when none was seen); in 1925 *M. kochi* appeared and *M. atlantica* was no longer there. *M. kochi* stayed until 1936 (excluding 1932), and during the whole of that period no *M. atlantica* were seen. After January 1936 *M. atlantica* was again abundant (Russell, 1938) and *M. kochi* absent. Probably *M. atlantica* has occurred from 1936 onwards to the present time—a period of ten years.

DECAPOD LARVAE

Table II marks the larvae present throughout the year in months. The only species present in every month are *Carcinus maenas*, *Portunus depurator*, *Macropodia* sp. and *Hippolyte varians*. *Crangon vulgaris*, *Porcellana longicornis*, *Galathea strigosa*, *Portunus puber*, Pagurid larvae *indet.*, and *Spirontocaris* sp.

are present in every month except December. The other larvae appear in various months, some of them very definite in their seasons. The majority abound in

TABLE II

Larvae present

Month ...	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Carcinus maenas	×	×	×	×	×	×	×	×	×	×	×	×
Portunus depurator	×	×	×	×	×	×	×	×	×	×	×	×
P. puber	×	×	×	×	×	×	×	×	×	×	×	.
P. pusillus	×	×	×	×	×	×	.	.	.	.	.	.
P. holsatus	.	.	.	.	×	×	.	.	.	.	.	.
P. marmoreus	.	.	×	.	×	×	.	.	.	×	.	.
Cancer pagurus	.	.	.	×	×	×	×	×	×	.	×	.
Atelecyclus septemdentatus	.	×	×	×	×	×	×	×	×	×	×	.
Pilumnus hirtellus	.	.	.	.	×	×	×	×	×	×	×	.
Portumnus latipes	.	.	.	.	.	×	×	×	×	.	.	.
Xantho spp.	.	.	.	.	.	×	×	×	.	.	.	.
Thia polita	.	.	.	.	.	.	.	×	×	.	.	.
Corystes cassivelaunus	×	×	×	×	×	.	.	.	.	.	.	.
Gonoplax rhomboides	.	.	.	.	.	×	×	×	×	.	.	.
Pinnotheres veterum	.	.	.	.	.	×	×	×	×	.	.	.
Ebalia spp.	.	×	×	.	×	×	×	×	×	×	×	.
Eurynome aspera	.	.	.	.	.	.	×	×	.	×	.	.
Maia squinado	.	.	.	×	.	×	×	×	×	×	.	.
Inachus spp.	.	.	.	.	×	×	×	×	×	×	.	.
Macropodia spp.	×	×	×	×	×	×	×	×	×	×	×	×
Hyas coarctatus	.	.	×	.	.	.	.	.	.	.	.	.
Porcellana longicornis	×	×	×	×	×	×	×	×	×	×	×	.
P. platycheles	.	.	.	×	×	×	×	×	×	.	.	.
Pagurid larva *indet.*	×	×	×	×	×	×	×	×	×	×	×	.
Galathea strigosa	×	×	×	×	×	×	×	×	×	×	×	.
G. squamifera	×	×	×	×	×	×	×	×	×	×	.	.
Munida banffica	.	.	×	.	×	.	.	.	×	.	.	.
Homarus vulgaris	.	.	.	.	.	×	×	×	.	.	.	.
Palinurus vulgaris	.	.	.	.	.	×	×	×	.	.	.	.
Jaxea nocturna	.	.	.	.	.	.	×	.	.	.	.	.
Callianassa subterranea	.	.	.	.	.	×	×	×	×	×	.	.
Upogebia spp.	.	.	.	×	×	×	×	×	×	×	×	.
Alpheus ruber	.	.	.	.	.	×	×	×	×	×	.	.
Axius stirhynchus	.	.	.	.	×	×	×	×	×	×	.	.
Athanas nitescens	.	.	.	.	.	×	×	×	×	×	.	.
Crangon vulgaris	×	×	×	×	×	×	×	×	×	×	×	.
C. allmanni	.	×	.	×	.	.	.	.	.	.	.	.
Philocheras fasciatus	.	.	.	.	×	×	×	×	×	.	.	.
P. trispinosus	.	.	.	.	.	.	×	.	.	.	.	.
P. bispinosus	.	.	×	.	×	×	×	×	×	×	.	.
Leander serratus	×	×	×	×	×	×	×	×	×	×	.	.
L. squilla	.	.	.	.	×	×	×	×	×	.	.	.
Hippolyte varians	×	×	×	×	×	×	×	×	×	×	×	×
Spirontocaris sp.	×	×	×	×	×	×	×	×	×	×	×	.
Caridion steveni	.	.	.	×	×	×	.	.	.	×	.	.
Pandalus montagui	.	×	×	.	×	×	×	×	×	×	.	.
Pandalina brevirostris	×	×	×	×	×	×	×	×	×	×	.	.
Processa edulis	.	.	.	.	×	×	×	×	×	×	.	.
P. canaliculata	.	.	.	×	×	×	×	×	×	.	.	.
Nyctiphanes couchii nauplius	.	.	.	.	×	×	.	.	.	.	.	.
Do. calyptopis and furcilia larvae	×	.	×	×	×	×	.	.	×	×	×	.

the spring and summer, but nearly all the Thalassinids and the Alpheids are present from June to October only, *Corystes* from January to May, *Portumnus latipes*, *Pinnotheres veterum* and *Gonoplax* from June to September, and *Thia* in

August and September. These are much the same in all years, showing definite breeding seasons. *Portunus depurator* zoea is much the commonest of the portunids inshore, *P. puber* coming next, but the others were not so easily recognizable and many may have been missed. The same applies to *Xantho*. The species of *Ebalia* were not differentiated, but are probably all *E. tuberosa*. *Inachus* and *Macropodia* were also recorded as *sp.indet.*, *Inachus* is probably *dorsettensis* and *Macropodia* probably *M. rostratus*. The larva of the common lobster, *Homarus vulgaris*, is seldom seen, and then usually singly. The Phyllosoma of *Palinurus*, being a more outside form, occurs only occasionally, and several other outside species recorded here are not usual inhabitants of the inshore waters. Such species are *Thia polita*, *Jaxea nocturna*, *Crangon allmanni*, *Philocheras trispinosus*. *Nyctiphanes couchii*, placed here with the decapods, must occasionally breed not far from shore for nauplii were found once, and calyptopis and early furcilia stages several times.

The number of species recorded below which may be present in each month is: January 16, February 19, March 23, April 24, May 34, June 42, July 40, August 39, September 37, October 30, November 16, December 4. Thus December has the fewest, January and November coming next, and June has the largest number. First larvae are much more numerous than late stages.

Carcinus maenas (Pennant) [Lebour, 1928] is already known to breed throughout the year. The present records show larvae in the plankton in every month, with large numbers in June 1941, May, July 1942, May, July, Sept. 1943, Jan., Feb., Mar., May 1944, Jan., Feb., Mar., June 1945. Fewest numbers occur in October, November and the beginning of December, when the numbers begin to rise.

Portunus depurator (L.) [Lebour, 1928] is already known to breed in any month. The present records show larvae in every month, but they are much more numerous outside the Sound. There are few in January and February in the inshore waters, but they may be numerous from March to September, dwindling markedly in October to December. Large numbers occurred in July 1941, May 1942, March to August 1943, May and July 1944. They are never so abundant inshore as the zoeae of *Carcinus*.

Portunus pusillus Leach [Lebour, 1928]. The records of this species are probably not at all complete for the small Portunid zoeae are so much alike that it is difficult to be sure of their identity, and unidentified small Portunids have not been recorded. It is one of the earliest crabs in berry and continues at least to August. Zoeae were noted in the inshore plankton in January and February 1942, March to May 1943, February to July 1944, with large numbers in April, and only once in July 1945.

Portunus puber (L.) [Lebour, 1928] is already known to breed chiefly in spring and summer. The present records show larvae in the plankton from January to November, but those in autumn and winter are very rare. The

largest numbers of zoeae occur in March to July, specially plentiful in July 1941 and 1942, March and May 1943, and May 1944.

Portunus holsatus Fab. [Williamson, 1911; Lebour, 1928]. Larvae have already been recorded in spring and summer. The present records are few and the zoeae were only seen in May and June, and then only in very small numbers.

Portunus marmoreus Leach [Lebour, 1928]. The larvae have already been recorded in spring and summer. The present records are few and the zoeae were only seen in March to June, and in October, and usually in very small numbers.

Portumnus latipes (Pennant) [Lebour, 1944*a*]. The larvae are found occasionally in the plankton from inshore from June to September.

Cancer pagurus L. [Lebour, 1928] breeds in spring and summer. The present records show the larvae in the inshore plankton from April to November, the largest numbers in May and July. None was seen in October, but they occur rarely as late as November.

Atelecyclus septemdentatus Leach [Lebour, 1928] is usually in the plankton from April to August. The present records show that it may be present as early as February and as late as November, but it usually occurs from March to September, the largest numbers in May to July.

Corystes cassivelaunus (Pennant) [Gurney, 1903; Lebour, 1928] is one of the earliest zoeae in the plankton, previous records showing it occurs from March to June, rarely later. The present records are from January to May. The largest number seen were in March 1941, but they are never very numerous so close inshore. Very large numbers sometimes occur in the outside waters.

Xantho spp. [Lebour, 1928]. The species of *Xantho* were not distinguished from one another. They are rarely seen in the plankton, occurring in summer only.

Pilumnus hirtellus (L.) [Lebour, 1928]. Zoeae in the inshore plankton were seen from May to November, never very abundant. Largest numbers occurred in July.

Thia polita Leach [Lebour, 1928] is rare and only the adult is found in outside waters. Zoeae were seen in the inshore plankton only in August and September 1941.

Gonoplax rhomboides (L.) [Lebour, 1928]. Zoeae were seen in the inshore plankton from June to September, never very numerous. The largest numbers occurred in July.

Pinnotheres veterum Bosc [Lebour, 1928]. Zoeae were seen in the inshore plankton from June to September, but always singly.

Ebalia spp. [Lebour, 1928]. The species of *Ebalia* zoeae were not distinguished, but most of them are almost certainly *Ebalia tuberosa* (Pennant) [Lebour, 1928]. Zoeae occurred in the inshore plankton from February to November, but never in large numbers, and chiefly from July to September.

Maia squinado Herbst [Lebour, 1927; 1928]. Zoeae were rarely seen in the inshore plankton, occurring in the present records from April to October.

Eurynome aspera Leach [Lebour, 1928]. Zoeae were rarely seen in the inshore plankton from July to October. They are much more frequent outside the Sound.

Hyas coarctatus (Leach) [Lebour, 1928]. Zoeae are usually seen in early spring. In the present records they were only noted once, in March.

Inachus spp., probably *dorsettensis* (Pennant) [Lebour, 1927; 1928]. The species of *Inachus* zoeae were not specially identified. They occur in the present records from May to October, but never in large numbers. Outside they are far more numerous.

Macropodia spp., probably chiefly *rostratus* (L.) [Lebour, 1928]. *Macropodia* zoeae, the species not identified, were found in the inshore waters in every month of the year, but never in numbers.

Porcellana longicornis (L.) [Lebour, 1943]. Larvae occur in the inshore plankton in every month except December. They are commonest in the summer months, with a fair number in spring and very few in autumn and winter.

Porcellana platycheles (Pennant) [Lebour, 1943]. The larvae have a more restricted season than those of *P. longicornis*, occurring from April to September, and are most numerous in June.

Galathea squamifera Leach [Lebour, 1931*a*]. These are some of the earliest larvae and occur in the inshore plankton from January to October. They are most numerous in April and May, but may be fairly plentiful up to July. Very few are recorded for August, rather more in September, and they were only seen once in January and October. May is usually the maximum month for breeding.

Galathea strigosa (L.) [Lebour, 1930*a*]. The larvae, like those of *G. squamifera*, may be in the inshore plankton from January to October; also, very rarely, in November. Again they are most numerous in April and May, but they are not so common as *G. squamifera*, and probably occur much more often in the outside waters.

Munida banffica (Pennant) [Lebour, 1930*a*]. This is an outside species, the adult not recorded from the Sound. Larvae were seen in the inshore plankton once in March, May and September.

Pagurid larvae. These were not identified, but probably were *Eupagurus bernhardus* (L.) [Sars, 1889], *E. prideauxi* (Leach), and, possibly, *Anapagurus laevis* (Thompson). They occur, but not in large numbers, in the inshore plankton from January to November.

Homarus vulgaris Milne-Edwards [Sars, 1875; Lebour, 1944*a*]. Larvae usually occur singly and not frequently. The present records show them in the inshore plankton from June to September.

Palinurus vulgaris Latreille [Bouvier, 1914*a*; Lebour, 1945]. The *Phyllosoma* larvae occur commonly in the outside plankton from February to September. The present records show them rarely in the inshore plankton from June to August.

Axius stirhynchus Leach [Webb, 1921]. Larvae occur in the inshore plankton from May to October, the largest numbers in July.

Jaxea nocturna (Chiereghin) [Bouvier, 1914*b*]. The larvae are rarely found in the inshore plankton, usually outside the Sound, in summer. They only occurred once in the present records, in July.

Callianassa subterranea (Montagu) [Webb, 1921]. Previous records show larvae in the plankton to be very common in summer and early autumn. The present records show them in the inshore waters from June to October, chiefly in July.

Upogebia spp., including *U.* (*Gebiopsis*) *deltaura* Leach and *U. stellata* (Montagu) [Webb, 1919]. The two species have not been separated. Previous records show larvae in the plankton to be very common in spring and summer. Webb (1919) found that *U. stellata* breeds rather earlier than *U. deltaura*. The present records show the larvae in the inshore plankton from April to November, commonest in July to September.

Athanas nitescens (Montagu) [Sars, 1906; Webb, 1921; Lebour, 1932]. Previous records show the larvae to be common in the plankton in summer and autumn, especially summer. The present records show them occurring from June to October, commonest in July, August and September.

Alpheus ruber Milne-Edwards [Lebour, 1932]. Previous records, which are for summer and early autumn, probably include the larvae of *A. macrocheles* (Hailstone). The present records of *A. ruber* in the inshore plankton are from June to October, fairly frequently, but never in large numbers.

Crangon vulgaris L. [Sars, 1890; Lebour, 1931*b*]. Larvae were previously known to occur practically throughout the year. The present records show that they are present from January to November, especially spring and summer. They may be numerous in any month from April to August, dwindling towards the autumn.

Crangon allmanni (Kinahan) [Sars, 1890; Lebour, 1931*b*]. This is an outside species. Its larva is always early, and was found in the inshore plankton on only two occasions, in February and April.

Philocheras fasciatus (Risso) [Gurney, 1903; Lebour, 1931*b*]. Previous records show larvae in the plankton from March to August. The present records show them in the inshore plankton from May to September, but never in numbers.

Philocheras trispinosus (Risso) [Gurney, 1903; Lebour, 1931*b*]. This is an outside species, the larvae occurring in spring and summer. There is only one record from the inshore plankton, in July.

Philocheras bispinosus (Hailstone & Westwood) [Sars, 1890, as *P. nanus*; Lebour, 1931*b*]. Previous records show larvae from June to September. The

present records show them in the inshore plankton from March to October, but never in numbers.

Hippolyte varians Leach [Sars, 1912; Lebour, 1931*b*]. Larvae were present in the inshore plankton throughout the year, the largest numbers in September and October.

Spirontocaris spp., including *S. cranchii* (Leach) and *S. occulta* Lebour [Lebour, 1936*a*]. The two species have not been distinguished. They occur in the inshore plankton from January to November, chiefly in spring, summer and early autumn, most common in August to October.

Caridion steveni Lebour [Lebour, 1930*b*]. Previous records show larvae in the plankton from early spring to the middle of August. The present records from inshore plankton show they occur from April to June and in October, but never in numbers.

Pandalus montagui Leach [Webb, 1921; Sars, 1900; Lebour, 1940]. The larvae occur commonly in the outside waters, in spring and summer, and a few in autumn. The present records show them in the inshore plankton from February to October, usually singly.

Pandalina brevirostris (Rathke) [Webb, 1921; Sars, 1900; Lebour, 1940]. Previous records show the larvae to be very common in the plankton in spring and summer. The present records from inshore plankton show that they occur from January to October, the largest numbers in July.

Processa edulis (Risso) and *P. canaliculata* Leach [Lebour, 1936*b*]. Larvae of *P. canaliculata*, almost certainly mixed with *P. edulis*, were formerly recorded in large numbers from the outside plankton from April to September. The present records from inshore waters agree in the seasonal distribution as formerly known, extending for *P. edulis* to October. Apparently *P. edulis* is more numerous in the inshore plankton than *P. canaliculata*.

Leander serratus (Pennant) [Lebour, 1944*b*]. Gurney (1923) states that all the *Leander* larvae in the plankton from December to nearly the end of June may confidently be assigned to this species. The present records from inshore waters show that the larvae occur from January to October, with the largest numbers in June, July and August.

Leander squilla (L.) [Gurney, 1924]. There are no certain previous records for early larvae of this species from Plymouth. The present records, however, show that they occur in the inshore plankton from May to September, but never in large numbers. The two records in May show that they may breed a little earlier than Gurney suggested.

Nyctiphanes couchii (Bell) [Lebour, 1924, 1925]. Previous records of the larvae are from outside the Breakwater only. The present records show nauplii in small numbers in May and June, and calyptopis and early furcilia in January, March to June, and September to November. Though the numbers are small, these records distinctly indicate that breeding occurs occasionally close inshore.

REFERENCES TO DECAPOD LARVAE

BOUVIER, E. L., 1914*a*. Recherches sur le Développement post-embryonnaire de la Langouste commune (*Palinurus vulgaris*). *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 179–93.

—— 1914*b*. Observations nouvelles sur les *trachelifer*, larves luciféri formes de *Jaxea nocturna*. *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 194–206.

GURNEY, R., 1902. The metamorphosis of *Corystes cassivelaunus* (Pennant). *Quart. Journ. Micr. Sci.*, Vol. XLVI, pp. 461–78.

—— 1903. The metamorphoses of the Decapod Crustaceans *Aegeon* (*Crangon*) *fasciatus* Risso and *Aegeon* (*Crangon*) *trispinosus* (Hailstone.) *Proc. Zool. Soc. London*, 1903, Vol. II, pp. 24–30.

—— 1923. Some notes on *Leander longirostris* M. Edwards, and other British prawns. *Proc. Zool. Soc. London*, 1923, pp. 97–123.

—— 1924. The larval development of some British prawns (Palaemonidae). II. *Leander longirostris* and *Leander squilla*. *Proc. Zool. Soc. London*, 1924, pp. 961–82.

LEBOUR, M. V., 1924. The Euphausiidae in the neighbourhood of Plymouth and their importance as herring food. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 402–31.

—— 1925. The Euphausiidae in the neighbourhood of Plymouth. II. *Nyctiphanes couchii* and *Meganyctiphanes norvegica*. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 810–47.

—— 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity, with a description of the Larval stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 795–821.

—— 1928. The larval stages of the Plymouth Brachyura. *Proc. Zool. Soc. London*, 1928, pp. 473–560.

—— 1930*a*. The larvae of the Plymouth Galatheidae. I. *Munida banffica*, *Galathea strigosa* and *Galathea dispersa*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 175–87.

—— 1930*b*. The larval stages of *Caridion*, with a description of a new species, *C. steveni*. *Proc. Zool. Soc. London*, 1930, Part I, pp. 181–94.

—— 1931*a*. The larvae of the Plymouth Galatheidae. II. *Galathea squamifera* and *Galathea intermedia*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 385–90.

—— 1931*b*. The larvae of the Plymouth Caridea. I. The larvae of the Crangonidae. II. The larvae of the Hippolytidae. *Proc. Zool. Soc. London*, 1931, pp. 1–9.

—— 1932. The larval stages of the Plymouth Caridea. IV. The Alpheidae. *Proc. Zool. Soc. London*, 1932, pp. 463–9.

—— 1936*a*. Notes on the Plymouth species of *Spirontocaris* (Crustacea). *Proc. Zool. Soc. London*, 1936, pp. 89–104.

—— 1936*b*. Notes on the Plymouth *Processa* (Crustacea). *Proc. Zool. Soc. London*, 1936, pp. 609–17.

—— 1940. The larvae of the Pandalidae. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 239–52.

—— 1943. The larvae of the genus *Porcellana* (Crustacea Decapoda) and related forms. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 721–37.

—— 1944*a*. The larval stages of *Portumnus* (Crustacea Brachyura) with notes on some other genera. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 7–15.

—— 1944*b*. Shrimps and prawns. *Sch. Sci. Rev.*, No. 96, pp. 209–16.

—— 1945. The lobster and its relatives. *Sch. Sci. Rev.*, No. 99, pp. 208–14.

SARS, G. O., 1875. Om Hummerens postembryonale Udvikling. *Christiania Vedenskabs-Selskabs Forhandlingar* for 1874, pp. 1–27.

—— 1889. Bidrag til Kundskaben om Decapodernes Forvandlinger. II. *Arch. Math. Naturv.*, Vol. XIII, pp. 133–201.

SARS, G. O., 1890. Bidrag til Kundskaben om Decapodernes Forvandlinger. III. Fam. Crangonidae. *Arch. Math. Naturv.*, Vol. XIV, pp. 132–95.

—— 1900. Account of the postembryonal development of *Pandalus borealis* Krøyer with remarks on the development of other Pandali, and descriptions of the adult *Pandalus borealis*. *Rep. Norweg. Fish. Invest.*, Vol. I, No. 3, pp. 1–45.

—— 1906. Postembryonal development of *Athanas nitescens* Leach. *Arch. Math. Naturv.*, Vol. XXVII, No. 10, 29 pp.

—— 1912. Account of the postembryonal development of *Hippolyte varians* Leach. *Arch. Math. Naturv.*, Vol. XXXII, No. 7, 25 pp.

WEBB, G., 1919. The development of the species of *Upogebia* from Plymouth Sound. *Journ. Mar. Biol. Assoc.*, Vol. XII, pp. 81–135.

—— 1921. The larvae of the Decapoda Macrura and Anomura of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XII, pp. 385–425.

WILLIAMSON, C., 1911. Report on the larval and later stages of *Portunus holsatus* Fab.; *P. puber* L.; *P. depurator* Leach; *Hyas areneus* (L.) etc. *Fish. Scotland Sci. Inv.* 1909, Vol. I (1911), pp. 1–20.

MOLLUSC LARVAE

Only a small proportion of mollusc larvae are recognizable in the plankton, but the number has greatly increased during the last ten years. For the first time record has been kept of the occurrence in the inshore plankton of known species. These are mostly gastropods, the bivalve larvae being so much alike, except in a few striking instances, that it is almost impossible to recognize the individual species. Both bivalve and gastropod larvae occur throughout the year in the inshore waters, but they are rarest in the winter months and, usually, most abundant in spring and summer. A large number of bivalve larvae, however, occur in the autumn. The plankton is frequently characterized by one species, such as, for instance, the larva of *Mytilus edulis* in spring, or *Heteranomia squamula* in late summer and autumn. Of the gastropods, Rissoids are usually the commonest, but the species of these have not been identified further, although closer investigations can distinguish several genera and species.

Monthly occurrences are shown in Table III.

GASTROPODA

Many species are included under unidentified gastropod larvae which occur throughout the year, being most plentiful in the present material from June to September. Winter forms include the species of *Patella*, chiefly *P. vulgata*, *Patina pellucida*, *Trivia arctica* and *Littorina neritoides*. *L. littorea*, usually commonest in February and March, occurs throughout the year, *Trivia monacha* from April to September only, *Nassarius incrassatus* and *N. reticulatus* from March or April till October. Apparently none of the Turrids breed before May and are seldom seen in autumn. *Limacina retroversa* is recorded here from May to November, but is much the commonest in summer.

Patella spp. (chiefly *P. vulgata* L.) [Smith, 1935; Lebour, 1937*b*]. *Patella* larvae occur from September to April; none has been seen in the intervening months. There is only one record each for April and September, and much the largest numbers occur from November to February, maxima in December and January. The largest numbers seen were in December 1942.

TABLE III. MOLLUSC LARVAE

Larvae present Month ...	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Gastropod larvae *indet.*	×	×	×	×	×	×	×	×	×	×	×	×
Patella vulgata	×	×	×	×	.	.	.	.	×	×	×	×
Patina pellucida	.	×	.	.	.	.	.	×	×	.	×	×
Littorina littorea egg capsules	×	×	×	×	×	×	×	×	×	×	×	×
Littorina littorea larva	×	×	.	×	×	×	×	×	×	×	×	×
Littorina neritoides egg capsules	×	×	×	×	.	.	.	.	.	×	.	×
Rissoid larvae	×	×	×	×	×	×	×	×	×	×	×	×
Tornus subcarinatus	.	.	.	.	.	.	.	.	.	.	×	×
Trivia arctica	×	×	×	×	×	.	.	.	.	.	.	.
Trivia monacha	.	.	.	×	×	×	×	×	×	.	.	.
Lamellaria perspicua	×	×	×	×	×	×	×	×	×	×	×	×
Simnia patula	.	.	.	.	.	×	×	×	×	.	.	.
Natica catena	.	.	×	×	×	×	×	×	×	×	.	.
?*Bittium reticulatum*	.	.	.	.	.	.	×	×	.	.	.	.
Triphora perversa	.	.	.	.	.	.	×	×	×	×	.	.
Cerithiopsis tubercularis	×	.	.	.	.	×	×	×	×	×	.	.
C. barleei	.	.	.	.	.	.	.	×	.	.	.	.
Odostomia sp.	.	.	.	.	.	.	.	.	×	.	.	.
Balcis sp.	.	.	.	.	.	.	.	.	×	.	.	.
Caecum sp.	×	.	.	.	.	.	×	×	×	×	×	×
Nassarius reticulatus	.	.	×	×	×	×	×	×	×	×	.	.
Nassarius incrassatus	.	.	.	×	×	×	×	×	×	×	.	.
?*Haedropleura septangularis*	.	.	.	.	×	×	×	×	×	.	.	.
Mangelia nebula	.	.	.	.	.	.	×	×	×	×	×	.
Comarmondia gracilis	.	.	.	.	×	×	×	×	×	.	.	.
Philbertia linearis	.	.	.	.	.	×	×	×	×	×	.	.
Tectibranch larva *indet.*	×	×	×	×	×	×	×	×	×	×	×	×
Eolid larva	×	×	×	×	×	×	×	×	×	×	×	×
Limacina retroversa	.	.	.	.	×	×	×	×	×	×	×	.
Clione sp.	.	×	×	×	×	.	.	.	.	.	.	.
Doto larva	.	.	.	.	.	×	×	×	×	.	.	.
Chiton egg	.	×	×	×	×	×	×	×	×	×	×	.
Bivalve larvae *indet.*	×	×	×	×	×	×	×	×	×	×	×	×
Anomia (or relative)	×	×	.	.	×	×	×	×	×	×	×	×
Mytilus (or relative)	×	×	.	×	×	×	×	×	.	×	×	.
Pecten (or relative)	×	×	×	×	×	×	×	×	×	×	×	×
Lima hians	×	.	×	.	.	×	×	×	×	×	×	×
Kellia suborbicularis	×	×	×	×	×	×	×	×	×	×	×	×
?*Mysella* sp.	.	×	.	.	.	.	.	×	×	×	.	.
Ensis sp. (or relative)	×	×	×	×	×	×	×	×	×	×	×	.
Hiatella arctica	.	×	×	×	×	×	×	×	×	×	×	.
?*Teredo* sp.	.	.	.	.	.	.	.	×	.	×	.	.

Patina pellucida (L.) [Lebour, 1937*b*]. The larvae occur in the present records in August, September, November, December and February, but never in large numbers.

Littorina littorea (L.) [Lebour, 1937*b*]. The egg capsules occur very commonly in the inshore plankton, being present all the year. Although

February and March appear to be the chief breeding season (Moore, 1937), and maximum numbers occurred in March, they were sometimes plentiful from January to June, and from August to December. Indeed it is difficult to indicate any distinct breeding season. The larvae were frequently abundant in almost any month.

Littorina neritoides (L.) [Linke, 1935; Lebour, 1935*b*, 1937*b*]. Previous records of the spawning periods (Lysaght, 1941) were from September to April. The present records of the egg capsules are from December to April and in October. It is thus distinctly a winter and early spring breeder. Lysaght connected the main spawning with the high tides at fortnightly intervals.

Rissoid larvae [Lebour, 1934*a*, 1936, 1937*b*]. These are chiefly *Rissoa parva* (da Costa). Several other species are included but have not been distinguished. They occur throughout the year, often in large numbers, in the inshore plankton. These are fewest in December and January, most plentiful from April to December.

Tornus subcarinatus (Montagu) [Lebour, 1936]. The larvae were previously recorded from the plankton in summer (Lebour, 1936). The present records show them occurring only in November and December and then very rarely.

Trivia arctica (Montagu) [Lebour, 1933*a*, 1935*a*]. The larvae occur in the present inshore plankton records from January to May only. They have previously been recorded autumn to early spring but never in summer. May is rather exceptionally late.

Trivia monacha (da Costa) [Lebour, 1931*b*, 1933*a*, 1935*a*, 1937*b*]. This is known to be a late spring and summer breeder. The present records show it occurring from April to September. Thus the larva may overlap *T. arctica* in April and May but never occurs in the winter.

Lamellaria perspicua (L.) [Lebour, 1935*a*] was present throughout the year, but never in large numbers. It occurred most commonly in June and July; and only once in February.

Simnia patula (Pennant) [Lebour, 1932*a*, 1937*b*]. This usually occurs in outside waters. It is a summer breeder, recorded here from the inshore waters from June to September, fairly plentiful once in August 1942.

Natica (*Lunatia*) *catena* (da Costa) [Lebour, 1936, 1937*b*]. A summer breeder, previously recorded in late spring and summer. The present records show it from March to October in the inshore waters, commonest in June and July.

?Bittium reticulatum (da Costa) [Lebour, 1936]. Larvae which are probably this species have previously been recorded as common in spring and summer. The present records show it in July and August only.

Triphora perversa (L.) [Lebour, 1933*b*] is usually present commonly in the outside water although occasionally occurring inside, in spring, summer and autumn. The present records show it from July to October but never in numbers.

Cerithiopsis tubercularis (Montagu) [Lebour, 1933*b*]. Previously recorded as common in both inshore and outside plankton in spring, summer and autumn but usually outside. The present records show it in inshore waters from June to October, but not in large numbers.

Cerithiopsis barleei Jeffreys [Lebour, 1933*b*] was previously recorded in spring, summer and autumn. Here it is recorded, in the inshore waters, only in August.

Odostomia sp. (or relative) [Lebour, 1937*b*] and *Balcis* sp. [Lebour, 1935*c*] were each only seen once, in September.

Caecum sp., probably *imperforatum* (Kunmacher) [Lebour, 1936]. Previous records show that it is common in the summer and autumn plankton. The present records show it present from July to January, largest numbers in November.

Nassarius reticulatus (L.) [Lebour, 1931*a*] was previously recorded throughout the year but especially in spring and summer. The present records show it to be present from March to October, largest numbers from March to June.

Nassarius incrassatus (Ström) [Lebour, 1931*a*]. Larvae have been found in the plankton (usually outside the Breakwater) throughout the year but especially in spring and summer. The present records show them in the inshore plankton from April to October. They are not so common as *N. reticulatus* in these records, being most abundant from May to August.

?Haedropleura septangularis (Montagu) [Lebour, 1936]. The larvae probably belonging to this species are fairly common in the inshore plankton from May to September but never in numbers, July being the maximum month.

Mangelia nebula (Montagu) [Lebour, 1934*b*]. Breeding is known to take place in summer and larvae are usually common both in inshore and outside, shallow-water, plankton. The present records show it present, in small numbers only, from July to November.

Philbertia (*Comarmondia*) *gracilis* (Montagu) [Lebour, 1933*c*, 1934*b*]. The larvae are fairly common in outside waters in spring and summer. The present records show it from May to September, most frequent in July and August.

Philbertia linearis (Montagu) [Lebour, 1934*b*]. Previous records show it to be fairly common in spring and summer, both inshore and outside. The present records show it from June to October, fairly commonly, most abundant in July.

Tectibranch larva *indet*. These are present throughout the year, often in numbers, especially in autumn and winter.

Limacina retroversa (Fleming) [Lebour, 1932*b*]. Although this is an oceanic mollusc it is frequently common in the inshore plankton, in the adult, young or larval stage. The present records show it from May to November but never in the other months. In 1940 they were very abundant with the maximum in August and September. In 1942 they only began in July, the maximum being

in September, when they were very numerous. In 1943 they were only seen in July and August and were never abundant; in 1944 they began in May, were common in July and disappeared after August; and in 1945 they began in July when they were numerous, still more so in August, and disappeared after October. In all the samples the young stages were more numerous than adults, and larvae were frequently present, showing that breeding must have taken place close inshore.

Clione sp. This is a dark brown species, not identified. It occurred in the young stage singly or in very small numbers in February to May in the present inshore samples.

Eolid larva *indet.* (Pelseneer, 1911). Eolid larvae occur in the inshore plankton throughout the year, especially in summer, and most numerous in June.

Doto sp. larva. This larva with a huge velum and spiral shell occurs from June to September, usually singly, but fairly frequently, in the inshore waters.

Chiton eggs. These occur singly or in small numbers, in the inshore plankton from February to November.

Lamellibranchiata

Bivalve larvae *indet.* occur throughout the year in the present samples, frequently in large numbers. It has already been shown (Lebour, 1938*b*) that a large outburst of these larvae usually occurs in late summer or autumn, and this also occurs in the present records from inshore. These are usually few in January, but in 1944 and 1945 they were fairly common, as well as in February 1943 and 1944. The largest numbers however nearly always occur in September. In early spring the larva of *Mytilus edulis* nearly always predominates.

Anomia (or relative) [Lebour, 1938*b*]. The larvae of this group occur almost throughout the year in the present samples, only March and April excepted. They usually form a large part of the late summer or early autumn outburst and they are probably *Heteranomia squamula* (L.). This species may breed throughout the year although the height is in late summer and early autumn. In the present records it was specially numerous from August to October.

Mytilus (or relative). *M. edulis* breeds, as is stated above, chiefly in spring. Nearly all the records in spring and early summer probably refer to this species, but its relatives are so like it in the larval stages that it is not possible to be sure of this. The largest numbers occur in May, but except in March, September and December, they are recorded in every month.

Pecten (or relative). These occur throughout the year in the present records but the species are unrecognizable and they are seldom abundant. Largest numbers were in September and October.

Lima hians Gm. [Lebour, 1937*a*]. This remarkable larva has already been shown to occur most frequently in the plankton in late summer and early

autumn. It is found in both inside and outside plankton. The present inshore records show it present in January, and March, and from June to December, but it is much more abundant from September to November, the largest numbers occurring in October and November.

A different species of *Lima* larva, almost certainly *L. loscombi* Sowerby (Fig. 1), which is the only other species in the district, was seen once in September 1942, shell 0·40 mm. across. It is interesting because the velum is very large, much larger than in *L. hians*, and is indented in the centre of each lobe, thus approximating to a four-lobed velum—a very rare feature in the Lamellibranchs.

Kellia suborbicularis (Montagu) [Lebour, 1938*a*] breeds throughout the year, and the larvae are common in the plankton, but especially in summer and autumn. Most numerous in August and September, this larva is one of the largest and most conspicuous of the Lamellibranchs.

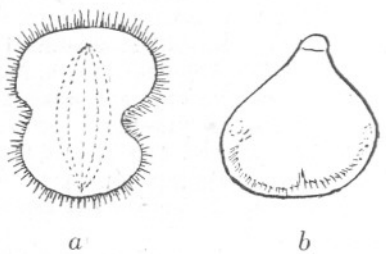

Fig. 1. Veliger of *Lima* sp., probably *Lima loscombi*. Shell 0·40 mm. across. *a*, Veliger swimming *b*, lateral view of shell.

Mysella sp. larva [Lebour, 1938*b*]. These occurred in the inshore plankton in February and from August to October, but not in such large numbers as they were found in outside waters in previous records. They were most numerous in September.

Ensis sp. or relative [Lebour, 1938*b*]. It is difficult to distinguish the species in the young stages, although *Cultellum pellucidus* can usually be recognized after the smallest stages by the red pigment behind the siphon. As a rule the larva of *Ensis siliqua* (L.) is common in the early spring months, characterizing the plankton, *Cultellus pellucidus* breeding later, usually in autumn and winter. Collectively the larvae of all the relatives of *Ensis* occur in the present inshore plankton throughout the year, except December, largest numbers in November 1941 and January 1942 (probably *Cultellus pellucidus*) and in March 1945 (probably *Ensis siliqua*).

Hiatella arctica (L.) [Lebour, 1938*b*] was present in the inshore plankton in every month except December and January, especially abundant in late summer and autumn, the largest numbers in September and October.

Teredo larva [Lebour, 1938*b*]. These were rarely found in the present samples. Larvae, almost certainly *Teredo navalis* var., occurred singly in August and October. It was found (Lebour, 1946) that this species carried active larvae throughout the year.

REFERENCES TO MOLLUSC LARVAE

LEBOUR, M. V., 1931*a*. The larval stages of *Nassarius reticulatus* and *Nassarius incrassatus*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 797–817.

—— 1931*b*. The larval stages of *Trivia europea*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 819–31.

—— 1932*a*. The larval stages of *Simnia patula*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 107–15.

—— 1932*b*. *Limacina retroversa* in Plymouth waters. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 123–9.

—— 1933*a*. The British species of *Trivia: T. arctica* and *T. monacha*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 477–84.

—— 1933*b*. The life-histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 491–8.

—— 1933*c*. The eggs and larvae of *Philbertia gracilis* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 507–10.

—— 1934*a*. Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth Rissoidae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 523–39.

—— 1934*b*. The eggs and larvae of some British Turridae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 541–54.

—— 1935*a*. The Echinospira larvae (Mollusca) of Plymouth. *Proc. Zool. Soc. London*, 1935, pp. 163–74.

—— 1935*b*. The breeding of *Littorina neritoides*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 373–8.

—— 1935*c*. The larval stages of *Balcis alba* and *B. devians*. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 65–9.

—— 1936. Notes on the eggs and larvae of some Plymouth Prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 547–65.

—— 1937*a*. Larval and post-larval *Lima* from Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 705–10.

—— 1937*b*. The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 105–66.

—— 1938*a*. The life history of *Kellia suborbicularis*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 447–51.

—— 1938*b*. Notes on the breeding of some Lamellibranchs from Plymouth and their larvae. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 119–44.

—— 1946. The species of *Teredo* from Plymouth waters. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 381–9.

LINKE, O., 1935. Der Laich von *Littorina* (*Melaraphe*) *neritoides* L. *Zool. Anz.*, Bd. 112, Heft 3–4, pp. 57–62.

LYSAGHT, A. M., 1941. The biology and trematode parasites of the Gastropod *Littorina neritoides* (L.) on the Plymouth Breakwater. *Journ. Mar. Biol. Assoc.*, Vol. XXV, pp. 41–67.

MOORE, H. B., 1937. The Biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life, and mortality. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 721–42.

PELSENEER, P., 1911. Recherches sur l'embryologie des Gastropodes. *Mem. Acad. R. de Belg.*, 2e. Ser., T. III, 167 pp.

SMITH, F. G. W., 1935. The development of *Patella vulgata*. *Phil. Trans. R. Soc. London*, ser. B, No. 520, Vol. 225, pp. 95–125.

ANNELID LARVAE

Monthly occurrences are shown in Table IV.

TABLE IV. ANNELID LARVAE

Larvae present Month ...	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Polygordius lacteus	.	×	.	×	×	×	×	×	.	.	.	.
P. appendiculatus	.	.	.	.	.	×	.	.	.	.	.	.
Polynoid larva	.	.	×	×	.	.	×	×	.	×	.	.
Tomopteris helgolandicus (juv.)	.	.	.	.	.	.	×	×	×	×	×	.
Syllid larva	.	.	.	.	.	×	×	.	.	.	.	.
Autolytus sp. ♂	×	.	×	×	×	×	×	×	×	×	×	×
Autolytus sp. ♀ with eggs	×	×	×	×	×	×	×	×	×	×	×	.
Nereid larvae	×	×	.	.	×	.	.	.	×	×	×	×
Nereid eggs	×	.	×	×	.	.	.	.	×	×	×	×
Spionid larvae and eggs	×	×	×	×	.	×	×	×	.	×	×	×
Nerine larva	.	×	×	.	.	.	.	.	.	.	.	.
Magelona papillicornis	×	.	×	×	×	×	×	×	×	×	×	×
Magelona sp. (? *cincta*)	.	.	.	×	×	×	×	×	×	×	.	.
Magelona sp.	.	.	.	.	×	×	×	×	×	×	.	.
Poecilochaetus serpens	.	×	×	×	×	×	×	×	×	×	×	.
Chaetopterus larva	.	.	.	.	.	.	.	×	×	×	×	.
Arenicola larva	.	.	×	×	×	.	.	.	.	.	×	.
Owenia larva	.	.	.	.	.	.	×	.	.	.	.	.
Pectinaria sp. (?*koreni*)	.	.	.	×	×	×	×	×	.	.	.	×
Lanice conchilega	.	×	×	×	×	×	×	×	×	×	×	×
Loimia medusa	×	×	×	×	×	×	.	.	.	.	.	.
Annelid larva *indet.*	×	×	×	×	×	×	×	×	×	×	×	×

ARCHIANNELIDA

Polygordius lacteus Schneider [Woltereck, 1902]. The larvae are not common in the inshore plankton, but occur from April to August and in February, being most abundant in August.

Polygordius appendiculatus Fraipont [Woltereck, 1925] occurred once, on 16 August 1940. The presence of this larva in the inshore plankton is interesting as it is the first time this species has been recorded from Plymouth, and Woltereck predicted that it would occur. It agrees exactly with the figures of Woltereck, who distinguishes it from that of *P. lacteus* by its smaller size and black spots round the periphery, *P. lacteus* being colourless.

POLYCHAETA

Many polychaete larvae occur in the inshore plankton and may be found in any month, the largest numbers in summer, but they are also very numerous in spring. The commonest identified species are *Loimia medusa*, *Lanice conchilega*, *Magelona papillicornis* and *Poecilochaetus serpens*. Various Syllids [Okada, 1930], Nereids, Spionids, and Sabellarians [Wilson, 1929] are sometimes very abundant.

Polynoid larva *indet.* [Johnstone, Scott & Chadwick, 1924] occurred in March, April, July, August and October, but not in large numbers.

Tomopteris helgolandicus Greef [Apstein, 1900]. Young of this worm, not larvae, occurred in the inshore plankton rarely. It usually is to be found outside. Single specimens were seen from July to November.

Syllid larvae *indet.* [Johnstone, Scott & Chadwick, 1924] were recognized in the inshore plankton in June and July; but not abundant.

Autolytus sp. (adult ♂) [Johnstone, Scott & Chadwick, 1924] occurred in every month except February but usually singly.

Autolytus (♀ with eggs) occurred in every month except December, usually in summer, nearly always singly. Sometimes the larvae were hatching from the eggs.

Nereid eggs and larvae *indet.* [Wilson, 1932*a*]. These occurred in the inshore plankton in any month except June and August, the largest numbers in September and November.

Spionid larvae and eggs *indet.* [Wilson, 1928*b*] occurred in the inshore plankton from October to April and June to August the largest numbers in March and April.

Nerine larva? was found rarely in the inshore plankton in February and March.

Magelona papillicornis Fr. Müller [Johnstone, Scott & Chadwick, 1924]. This is one of the commonest larvae of the inshore plankton, recorded in every month except February. It is much the commonest in late spring and summer, particularly May to July, and was once abundant in October.

Magelona, *?cincta* (Ehlers) was not so plentiful as *M. papillicornis*, but occurred in the inshore plankton from April to October, abundant in May, July and August.

Magelona sp. This third species, unidentified as yet, occurs in the inshore plankton from May to October, but is never numerous.

Poecilochaetus serpens Allen [Allen, 1904] occurs in the inshore plankton from February to November, previous records being only in the summer months ('not uncommon' according to Allen). It is more numerous, however, in spring and summer. The largest numbers seen were in May.

Chaetopterus larva *indet.* [Johnstone, Scott & Chadwick, 1924] was found from August to November in the inshore plankton, never in large numbers.

Arenicola larva *indet.* [Ashworth, 1912] was occasionally seen in the inshore plankton from March to May and in November. It was never numerous.

Owenia larva [Wilson, 1932*b*] was found once only in the inshore plankton, in July.

Pectinaria larva (*?koreni*) [Gravely, 1909; Wilson, 1936] occurred in the inshore plankton from April to August and in December, never in large numbers, but was fairly frequent in July 1942.

Lanice conchilega (Pallas) [Johnstone, Scott & Chadwick, 1924], one of the commonest annelid larvae in the inshore plankton, occurred in every month except January; commonest from April to October, rare in the other months.

Loimia medusa (Savigny) [Wilson, 1928*a*] was common in the inshore plankton from January to June, most frequent from March to May.

Annelid larvae *indet.* were in the inshore plankton in every month chiefly in spring and summer.

REFERENCES TO ANNELID LARVAE

ALLEN, E. J., 1904. The anatomy of *Poecilochaetus*, Claparède. *Q. Journ. Micr. Sci.*, Vol. XLVIII, pp. 79–151.

APSTEIN, C., 1900. Die Alciopiden und Tomopteriden der Plankton Expedition. *Plankton Exped.*, Bd. 2, pp. 1–61. Kiel.

ASHWORTH, J. H., 1912. *Catalogue of the Chaetopoda in the British Museum (Natural History)*. A. Polychaeta. Part I. Arenicolidae. Pp. 1–175.

GRAVELY, F. H., 1909. Polychaet Larvae. *Liverpool M.B.C. Memoirs*, Vol. XIX, 79 pp.

JOHNSTONE, SCOTT & CHADWICK, 1924. *The Marine Plankton.* Liverpool University Press. 194 pp.

OKADA, Yô K., 1930. A remark on the constitution of larval Syllids. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 479–87.

WILSON, D. P., 1928*a*. The post-larval development of *Loimia medusa* Sav. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 129–49.

—— 1928*b*. The larvae of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 567–603.

—— 1929. The larvae of the British Sabellarians. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 221–69.

—— 1932*a*. The development of *Nereis pelagica* Linnaeus. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 203–17.

—— 1932*b*. On the Mitraria larva of *Owenia fusiformis* Della Chiaje. *Phil. Trans. R. Soc. London*, Ser. B, Vol. 221, pp. 231–334.

—— 1936. Notes on the early stages of two Polychaetes, *Nepthys hombergi* Lamarck and *Pectinaria Koreni* Malingren. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 305–10.

WOLTERECK, R., 1902. Trochophora-Studien. I. Ueber die Histologie der Larve und die Entstehung des Annelids bei den *Polygordius*-Arten der Nordsee. *Zoologica*, Bd. XIII, Heft 34, pp. 1–71.

—— 1925. Neue und alte Beobachtungen zur Metamorphose der Endolarve von Polygordius (mit einem Zusatz, der die letzten Mitteilungen Dr Söderströms betrifft). *Zool. Anz.*, Bd. LXV, Heft 1–2, pp. 49–60.

OTHER PLANKTON LARVAE

Monthly occurrences of larvae from miscellaneous groups are shown in Table V.

Turbellaria

Müller's larva, probably *Cycloporus papillosus* Lang [Lang, 1884]. This larva has not been identified, but it is very likely to be the same species which Orton recorded in the Plymouth Fauna List as probably this species, having hatched it from the egg (19 August 1912). It occurs fairly frequently from July to October in the inshore plankton, but has not been seen in other months.

TABLE V. MISCELLANEOUS LARVAE

Larvae present Month ...	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Müller's larva	.	.	.	.	.	.	×	×	×	×	.	.
Pilidium	.	.	×	×	×	×	.	×	×	×	×	.
Cyphonautes	×	×	×	×	×	×	×	×	×	×	×	×
Tornaria	.	.	.	.	.	×	×	×	.	.	.	.
Actinotrocha	.	.	.	×	×	×	×	×	.	.	.	×
Echinopluteus (unidentified)	.	.	×	×	×	×	×	×	×	×	×	.
Ophiopluteus (*Ophiothrix*)	.	×	×	×	×	×	×	×	×	×	×	.
Ophiopluteus (ophiuroid)	.	.	.	.	.	.	×	×	×	×	.	.
Bipinnaria of *Asterias*	.	.	.	.	.	×	×	.	.	.	.	.
Auricularia (unidentified)	.	.	×	×	×	×	×	.	.	.	×	.
Luidia larva	.	.	.	.	.	.	×	.	.	.	.	.

Nemertinea

Pilidium larva, unidentified, probably belonging to *Lineus* sp. [Macbride, 1914] or *Cerebratulus* sp. [Sedgwick, 1898]. Two or three different species occurred in the inshore plankton from March to November (excepting July) but nearly always singly, never in numbers.

Bryozoa

Cyphonautes larva unidentified [Johnstone, Scott & Chadwick, 1924] probably *Membranipora* sp. Two different species, and occasionally a third, occur very commonly in the inshore plankton in any month. Largest numbers occurred in May 1943, but they may be abundant in any month.

Enteropneusta

Tornaria larva of *Balanoglossus* [Bourne, 1889], previously recorded as abundant in the Sound in summer. The present inshore records show it occurring only occasionally in small numbers or singly from June to August.

Phoronidea

Actinotrocha larva of *Phoronis* [Johnstone, Scott & Chadwick, 1924, erroneously designated *Balanoglossus*] occurs in the inshore plankton (probably two species) from April to August and in December, most frequent from May to July.

Echinodermata

By far the commonest larvae of the Echinoderms in the inshore plankton is the Ophiopluteus of *Ophiothrix fragilis*; next come Echinoplutei unidentified. Others occur much less frequently.

Ophiopluteus of *Ophiothrix fragilis* (Abildgaard) [Johnstone, Scott & Chadwick, 1924] occurs from February to November but most commonly from June to September, sometimes in large numbers.

Ophiopluteus of ophiuroid unidentified [Mortensen, 1927] occurs occasionally in the inshore plankton from July to October, never in large numbers, commonest in August.

Echinopluteus unidentified [Mortensen, 1927], probably chiefly *Echinocardium* and *Echinocyamus*, occurs in the inshore plankton from May to November, chiefly in summer, commonest July and August.

Auricularia larva of Holothurian unidentified [Mortensen, 1927] occurs rarely in the inshore plankton from March to July, never in numbers.

Bipinnaria larva of *Asterias* [Mortensen, 1927] occurs very rarely in the inshore plankton in June and July.

Bipinnaria larva of *Luidia* [Mortensen, 1927] occurred only once in July 1944. It is usually entirely confined to the outside waters.

OTHER REFERENCES

BOURNE, G. C., 1889. On a Tornaria found in British Seas. *Journ. Mar. Biol. Assoc.*, Vol. I, pp. 63–8.

CUNNINGHAM, J. T., 1892. On a species of *Siphonophore* observed at Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. II, pp. 212–15.

JOHNSTONE, SCOTT & CHADWICK, 1924. *The Marine Plankton.* Liverpool University Press. 194 pp.

LANG, A., 1884. Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna und Flora des Golfes von Neapel*, Bd. XI, pp. 1–688.

LEBOUR, M. V., 1947. An interesting young *Velella* in the Plymouth plankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 548–50.

MACBRIDE, E. W., 1914. *Text Book of Embryology.* Vol. I. *Invertebrata.* London.

MORTENSEN, T., 1927. *Handbook of the Echinoderms of the British Isles.* 471 pp.

RUSSELL, F. S., 1934. On the occurrence of the Siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 555–8.

—— 1938. On the development of *Muggiaea atlantica* Cunningham. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 441–6.

SEDGWICK, A., 1898. *A Student's Text-Book of Zoology.* Vol. I. *Protozoa to Chaetognatha.* London.

AN INTERESTING YOUNG *VELELLA* IN THE PLYMOUTH PLANKTON

By Marie V. Lebour, D.Sc.

From the Plymouth Laboratory

(Text-fig. 1)

On 2 February 1943, after some very fierce south-westerly storms, a curious object was found in the inshore plankton which proved to be the 'float' of a very young *Velella* in the Rataria stage. In order to be certain of its identity some small complete Velellas were compared. These were kindly sent by Miss Delap of Valencia, to whom I am much indebted. They ranged from 1·5 to 2 mm. across and were very similar to the young forms described and figured by Huxley (1858), who identified them with the *Rataria* of Eschscholz (1829). In this stage the float is growing and may already have the crest, a soft, much higher structure, projecting above it. In order to see the float clearly one of the Irish specimens, 2 mm. across, was macerated in 10% caustic potash, the float separating out and proving to be exactly similar to the Plymouth specimen.

The peculiar structure of this float and the fact that the available figures of the *Rataria* of similar size show only the external features make a short note desirable, for in the existing figures one cannot be certain of the exact extent and position of the float. So difficult was it to decipher that, although it seemed very probable that we had the float of a *Velella*, it was not possible at first to be certain.

The float (Fig. 1) which was obtained at Plymouth measured 2·4 by 1·6 mm., was of an oval shape in surface view, divided obliquely by a high ridge (the crest), and indented at right angles to this. A clear central portion is surrounded by concentric lamellae, pierced by a series of apertures in the region of the crest. Examined sideways the crest was seen to be pinched off from the upper portion, and a central inner cone was attached to the clear central portion. A very small amount of the soft parts of the animal remained, chiefly as dried up tentacles round the inner cone. On comparing the float from the Irish specimen the two corresponded exactly and the position of the float in the whole animal is clear. The covering of the crest is prolonged dorsally into a soft upper crest with canals running down it as in Huxley's figures. The inner cone of the float contains the 'liver' region, and this cone is the beginning of the floor of the float which becomes much flatter as it grows and as the space between is gradually closed up, the whole of the polyp portion with the tentacles lying within the cone. Thus eventually the float is composed

of the two layers as already known. Specimens from Ireland hardly more than 1 mm. across had a very much smaller float with no concentric lamellae, showing that the float must grow very quickly. The specimen which was macerated had its stomach full of harpacticid copepods, a common food, as already known, and there were also two nematodes, probably parasitic.

The extremely interesting life history of *Velella* has been well interpreted by Woltereck (1904), who found the earliest larva (*Conaria*) in the deep waters of the Mediterranean, having the red colour usually found in such deep water animals. He followed the changes from this *Conaria* from deep waters up to

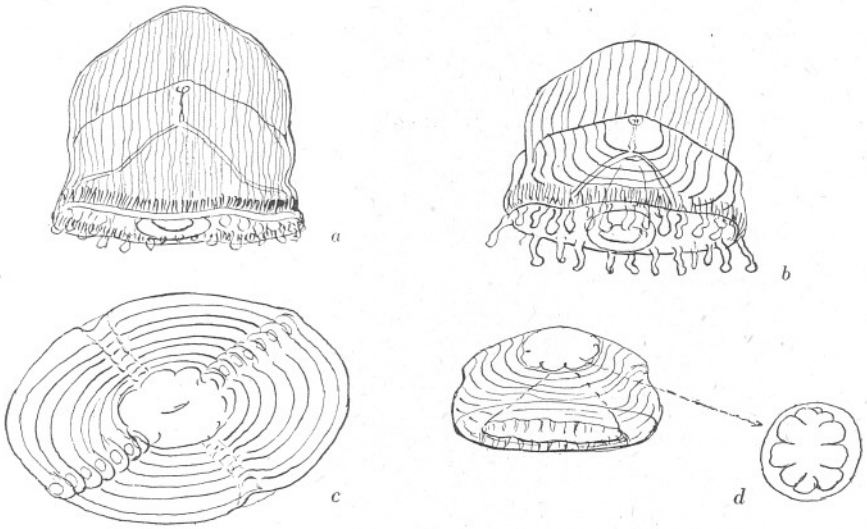

Fig. 1. Young *Velella* and float. *a*, 2 mm. across, untreated (from Miss Delap, Valencia Island, 1904). *b*, 2 mm. across, partly treated with caustic potash to show float (from Miss Delap, Valencia Island, 1904). *c*, float of *Velella* from Plymouth (4 February 1943), 2·4 mm. across from above. *d*, the same from the side.

the surface-living purple *Rataria*—a truly wonderful metamorphosis. Swarms of *Velella* occur occasionally near our coasts after violent storms. In Plymouth they have been known to occur in March, October, June and September, and always after storms (see *Plymouth Marine Fauna*, 1931). Russell & Kemp (1932) attribute these invasions either to an indication of wind drift of surface water, or an increase of flow in Atlantic water. Even the presence of this one small float of *Velella* is of interest in this connexion, for it must mean that somewhere near this organism was present in abundance. The fact that such a very young float was found so close inshore in the Plymouth plankton is also of great interest, considering that the young usually occur in much more open waters.

REFERENCES

ESCHSCHOLZ, 1829. *System der Acelephen, eine ausführliche Beschreibung aller Medusen-artigen Strahlthiere.* (Not seen.)

HUXLEY, T. H., 1858. *The Oceanic Hydrozoa.* Ray Society, pp. 1–141.

RUSSELL, F. S. & KEMP, S., 1932. Pelagic Animals off the South-West Coasts of the British Isles. *Nature*, Vol. 130, p. 664.

WOLTERECK, R., 1904. Ueber die Entwicklung der *Velella* aus einer in der Tiefe vorkommenden Larve. *Zool. Jahrb.*, Supp. VII, Festschrift A. Weismann, pp. 347–72.

ON THE FERTILITY OF MARINE CLADOCERA WITH A NOTE ON THE FORMATION OF THE RESTING EGG IN *EVADNE NORDMANNI* LOVÉN AND *PODON INTERMEDIUS* LILLJEBORG

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(Text-figs. 1–5)

CONTENTS

INTRODUCTION

The present paper is the second in a series dealing with the reproductive capacity of marine Crustacea, the first being concerned with the fecundity of some gammarids (Cheng, 1942).

Relatively little is known of the reproductive capacity of marine Cladocera. Lilljeborg (1900) in a taxonomic study on the Cladocera of Sweden recorded the size of broods in various marine species. Rammer (1933) made a comparison of the fertility of *Evadne nordmanni* Lovén in different regions, showing that it is, on the whole, highest in the warmer water. Jorgensen (1933), who carried out an investigation into the life cycle of *E. nordmanni* off the Northumbrian coast of England, made a few remarks on its reproductive capacity. In the present investigation a statistical study was made of the fertility of various species of marine Cladocera together with a note on the formation of the resting egg[1] in *E. nordmanni* and *Podon intermedius* Lilljeborg.

It is a great pleasure to express my gratitude to the late Director of the Marine Biological Laboratory at Plymouth, Dr S. Kemp, F.R.S., for providing

[1] It is also called 'winter' egg, which is rather misleading, as it can be produced in the summer as well. The word 'resting' is more appropriate, because the egg is incapable of developing immediately after fertilization; it requires a certain period of 'rest'.

me with facilities and to members of the staff for their kind help in various ways. I wish to thank Prof. A. C. Hardy, F.R.S., for putting his Clyde samples at my disposal.

Material and Method

The material was collected partly off Plymouth during the summer of 1938, but largely from the Clyde Sea-Area by Prof. Hardy in the summers of 1941 and 1942 in an investigation on the yield of zooplankton. The Clyde samples were taken by the Plankton Indicator[1] at a depth of 10 m. in 1941 and by a 50 cm. diameter tow-net with 200 meshes to the inch at a depth of 18 m. in the following year.

The method of studying fertility was as follows. A number of adult parthenogenetic females were picked out at random. After measuring the total length of each (from the anterior margin of the head to the posterior end of the caudal furca) by means of an ocular micrometer, all the embryos in the brood-pouch were taken out and counted. The total number of parthenogenetic females of various species thus examined for the two areas is shown in Table 1.

When working at Plymouth in the summer of 1938, the writer was able to make some observations upon the formation of the resting egg in living specimens of *Evadne nordmanni* and *Podon intermedius*. The different stages of the formation were drawn with the aid of a camera lucida.

Notes on the Species

Four species[2] occurred in the Clyde Sea-Area material: *Evadne nordmanni*, *Podon intermedius*, *P. polyphemoides* (Leuckart) and *P. leuckarti* G. O. Sars, all of which have been recorded for this region by Scott (1905). Only two species were present in the Plymouth samples: *Evadne nordmanni* and *Podon intermedius*. According to the Plymouth Marine Fauna list published in 1931, *P. leuckarti* occurs also in this region, but *P. polyphemoides* does not. The three species of *Podon*, though very much alike in appearance, can easily be distinguished from each other not only by the number of setae on the exopodite of the first trunk-limb (*P. leuckarti* 1, *P. intermedius* 2, *P. polyphemoides* 3), but also by the mean length of the body (Table 1).

Evadne nordmanni is, by far, the commonest species of Cladocera in the Clyde Sea-Area, attaining its maximum in August. Of the three species of *Podon*, *Podon intermedius* and *P. polyphemoides* are more common in our samples than *P. leuckarti*, but this is most likely due to the fact that the last-named is a typical surface form (Apstein, 1910) and our samples were collected at a depth of either 10 or 18 m. As a rule, these species of *Podon* reach their maximum abundance later than *Evadne nordmanni*, i.e. in September.

[1] For its construction and method of use, see Hardy (1936).

[2] For the geographical distribution of the four species, see Cleve (1900), Gibitz (1922), Rammer (1931) and Stephensen (1938).

TABLE I. MEAN BODY LENGTH (IN MM.) AND FERTILITY (IN NO. OF EMBRYOS PER BROOD) OF VARIOUS SPECIES FOUND IN THE CLYDE SEA-AREA AND MEAN FERTILITY OF *EVADNE NORDMANNI* AND *PODON INTERMEDIUS* OFF PLYMOUTH (IN BRACKETS).

		Body length		Fertility	
Species	No. of animals	Mean ± S.E.	Standard deviation	Mean ± S.E.	Standard deviation
P. leuckarti	32	0·67 ± 0·01	0·06 ± 0·01	2·6 ± 0·19	1·08 ± 0·13
P. intermedius	224 (198)	0·99 ± 0·005	0·08 ± 0·004	3·0 ± 0·08 (3·5 ± 0·11)	1·14 ± 0·05 (1·56 ± 0·08)
P. polyphemoides	199	0·39 ± 0·003	0·04 ± 0·002	4·7 ± 0·10	1·38 ± 0·07
E. nordmanni	753 (269)	0·45 ± 0·002	0·05 ± 0·001	4·4 ± 0·06 (3·2 ± 0·13)	1·77 ± 0·04 (2·11 ± 0·09)

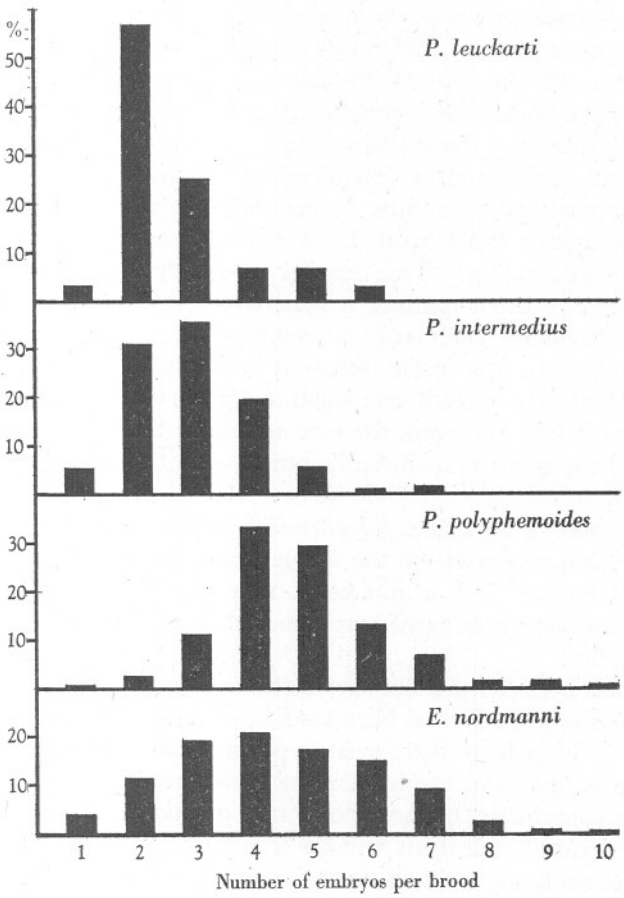

Fig. 1. Histograms showing the percentage frequency distribution of the fertility of various species found in the Clyde Sea-Area.

Fertility of Various Species

From Table 1 it will be seen that the mean fertility varies with different species: *Podon leuckarti* 2·6, *P. intermedius* 3·0, *P. polyphemoides* 4·7 and *Evadne nordmanni* 4·4; although the specific difference is by no means large. The mean value of *Podon leuckarti* is, however, less reliable than that of the others because of the small number of animals obtained. It is noteworthy that the mean fertility of *Evadne nordmanni* appears to be lower in the Plymouth region than in the Clyde Sea-Area (Table 1). Such discrepancy may be accounted for by the fact that the Plymouth samples were taken much earlier, i.e. in May. In Fig. 1 is shown the range and mode of the fertility of various species, the latter being as follows: *Podon leuckarti* 2, *P. intermedius* 3, *P. polyphemoides* 4 and *Evadne nordmanni* 4.

Relatively little is known of the reproductive capacity of marine Cladocera in other European waters. Lilljeborg (1900) recorded the size of broods of various species off the coast of Sweden as follows: *Evadne nordmanni* 7–8 embryos in older females, *E. spinifera* P. E. Müller 6–7, *Podon polyphemoides* 2–4, *P. intermedius* 2–5 (sometimes more), *P. leuckarti* mostly 2; but as he gives no record of the numbers examined, we cannot compare the fertility in Swedish waters with that in ours. Jorgensen (1933) made some observations on the reproductive capacity of *Evadne nordmanni* off the Northumbrian coast of England, stating: 'The number of embryos in a batch may vary considerably. The usual number is generally 6–8 or 9; while at times the majority of specimens carry only 2–5 embryos.... The greatest number of embryos, i.e. 12–14 has been observed only in the very large form of *E. nordmanni*.' In the present investigation a great variation in the fertility of this species was also observed, the size of broods being probably controlled by the age of the mother, food, temperature, etc.; as suggested by Allen & Banta (1929).

It is noteworthy that *Podon polyphemoides*, though smaller than the other species of *Podon*, possesses, on the whole, the highest reproductive capacity (Table I and Fig. 1). It is of interest to note that Sexton (1928) and Cheng (1942) found among gammarid amphipods that the smaller species had the higher fecundity.

The relation between the size or weight and the reproductive capacity of the individuals of a species has been studied in various groups of animals (see Cheng, 1942). In general, there exists a positive correlation between the two. In other words, the older the female, the more productive it is. The present investigation shows that the same holds true of *Evadne nordmanni* and *Podon intermedius*. From Table II it will be seen that the mean fertility of large females is generally higher than that of smaller ones, although the difference between the two extreme size-groups is very small, i.e. less than two eggs per brood.

TABLE II. MEAN FERTILITY OF VARIOUS SIZE GROUPS (IN μ) OF *EVADNE NORDMANNI* AND *PODON INTERMEDIUS* TAKEN FROM THE CLYDE SEA-AREA.

E. nordmanni			*P. intermedius*		
Size groups	No. of animals	Mean fertility	Size groups	No. of animals	Mean fertility
300–400	42	2·7	800–900	34	2·7
400–500	489	3·4	900–1000	91	2·6
500–600	159	4·2	1000–1100	75	3·0
			1100–1200	22	4·4

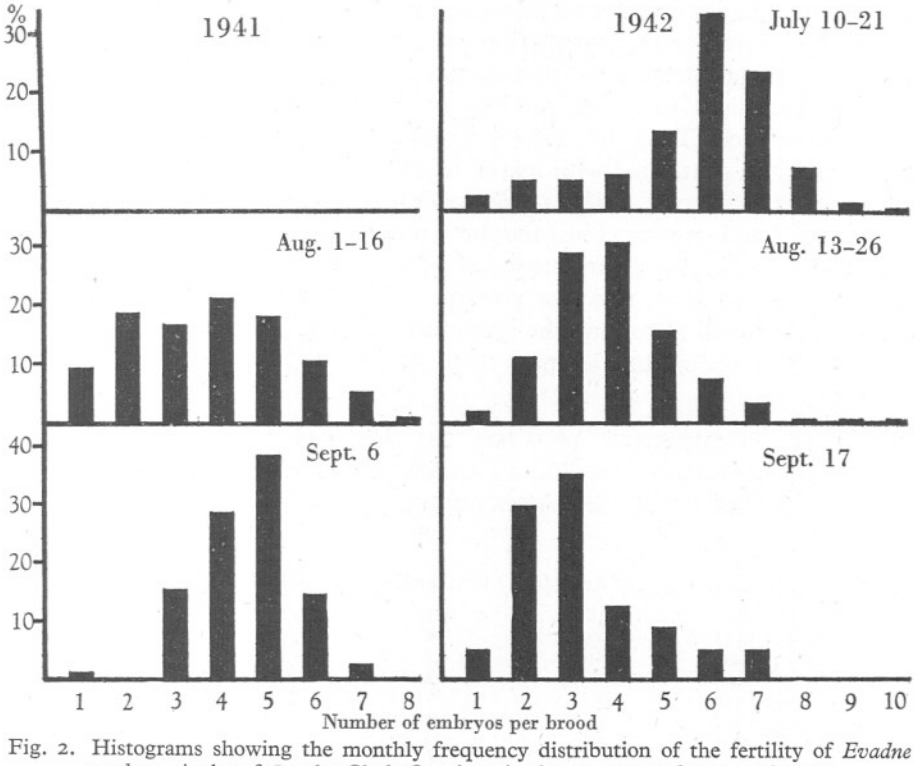

Fig. 2. Histograms showing the monthly frequency distribution of the fertility of *Evadne nordmanni* taken from the Clyde Sea-Area in the summers of 1941 and 1942.

TABLE III. MEAN FERTILITY AND PERCENTAGE OF SEXUAL INDIVIDUALS (♂, ♀) OF *EVADNE NORDMANNI* TAKEN FROM THE CLYDE SEA-AREA DURING THE SUMMER MONTHS OF 1941 AND 1942.

		Fertility		
Month and year	No. of animals	Mean	Standard deviation	% of sexual individuals
1–16 Aug. 1941	167	$3·7 \pm 0·13$	$1·69 \pm 0·09$	13·3
6 Sept. 1941	84	$4·5 \pm 0·12$	$1·06 \pm 0·08$	6·9
10–21 July 1942	184	$5·8 \pm 0·13$	$1·80 \pm 0·09$	1·0
13–26 Aug. 1942	261	$3·9 \pm 0·09$	$1·40 \pm 0·06$	3·4
17 Sept. 1942	57	$3·3 \pm 0·20$	$1·49 \pm 0·14$	7·1

Owing to the limitation of material, it is impossible to undertake a detailed investigation on the seasonal variation in reproductive capacity. It is of interest, however, to compare the fertility of *Evadne nordmanni*[1] month by month during the periods 1 August–6 September, 1941 and 10 July–17 September, 1942. It will be seen from Table III and Fig. 2 that during the latter year the fertility appears to fall off towards the end of summer, the mean value of July being nearly twice as high as that of September. But the reverse holds true of 1941, the mean fertility of September being higher than that of August. In order to find out whether such seasonal variation in reproductive capacity is due to the corresponding fluctuations in the abundance of phytoplankton in the surrounding waters, a comparison was made between the mean fertility of *E. nordmanni* and the mean number of diatoms taken by the same net. It is evident from Table IV that no correlation exists between the two. This finding may be contrasted with that of Marshall (1937) who observed that the fecundity of a copepod, *Oithona helgolandica*, reaches its first maximum at the end of April and its second in June; both maxima appear to be correlated with the period of high diatom production. Unfortunately, owing to the lack of data on water temperature, it is not possible to study the relation between this important external factor and the reproductive capacity of *Evadne nordmanni*. The latter, according to Rammer (1933), is greatest in water of higher temperature.

TABLE IV. COMPARISON BETWEEN THE MEAN FERTILITY OF *EVADNE NORDMANNI* AND THE MEAN NUMBER OF DIATOMS TAKEN BY THE SAME NET IN THE CLYDE SEA-AREA DURING THE SUMMER MONTHS OF 1941 AND 1942

Date of collection	No. of animals	Mean fertility	No. of hauls	Mean number of diatoms
1 Aug. 1941	61	4·7	5	59,974
16 Aug. 1941	106	3·2	6	42,530
6 Sept. 1941	84	4·5	9	2,367
21 July 1942	156	6·4	7	5,550
13 Aug. 1942	147	4·1	3	9,867
26 Aug. 1942	114	3·7	7	19,552
17 Sept. 1942	57	3·3	6	16,450

During the summer months of 1942, a marked reduction in the fertility of *E. nordmanni* took place after July. This occurred at the time when the production of sexual individuals was steadily increasing, as shown in Table III. It is evident that there exists an inverse relationship between the reproductive capacity of parthenogenetic females and the intensity of sexual reproduction. The same holds true of 1941: the percentage of sexual individuals in August was nearly twice as high as that in September, whilst the mean fertility of the latter month was higher than that of the former. This finding is in accord with that of Berg (1931) and Uéno (1934) who observed in nature that the size of

[1] Owing to the small number of animals obtained, it is not possible to make a similar study on other species.

broods produced by the parthenogenetic females of fresh-water daphnids tends to decrease after the sexual reproduction has set in. According to the hypothesis put forward by Berg (1934), the diminution in the size of broods is regarded as a manifestation of a state of depression during the transition from parthenogenesis to sexual reproduction brought about by unfavourable external conditions such as poor nutrition and low temperature.

Formation of the resting Egg in *Evadne nordmanni* and *Podon intermedius*

Two kinds of eggs are produced by Cladocera, a thin-walled parthenogenetic egg and a thick-walled resting egg. The latter is larger, fewer in number, full of yolk spherules and incapable of developing without fertilization. The individual developed from a fertilized resting egg after a certain period of quiescence is invariably a parthenogenetic female. As a rule, the production of resting eggs is at its highest when parthenogenesis has reached its lowest ebb.

Sexual reproduction of *Evadne nordmanni* has already been studied by Jorgensen (1933) who gives a fairly complete account of the formation of the resting egg. The following notes give more details of this process and also describe that in *Podon intermedius*. All observations were made upon living specimens obtained off Plymouth in the summer of 1938.

Fig. 3 shows the various stages of formation of a resting egg in *Evadne nordmanni*. It will be seen that at the beginning the four oocytes are more or less alike in appearance (*A*). Later (*B* and *C*) the third cell (counted from the anterior end of the ovary) begins to outgrow the others. It continues to grow in size until becoming the large resting egg full of yolk spherules, whilst the other three remain somewhat unchanged and finally disappear, being probably absorbed by the egg; as shown by Allen & Banta (1929) in a fresh-water cladoceran, *Moina macrocopa*. They write: 'Only one sexual egg normally matures in each ovary at a clutch. During growth it absorbs three nurse cells.' The egg then migrates into the brood-pouch filled already with nurse cells which, according to Jorgensen (1933), are produced by the proliferation of cells lining the wall of the brood-pouch and not being, as supposed by Claus (1877), originally oocytes formed at the same time as the one giving rise to the resting egg. After reaching its maximum size, a thick chitinous wall is formed around it.

It is worthy of note that on one occasion a slender tubular structure containing cells of various size was observed in direct connexion with the posterior end of the tetrad (Fig. 3, I). It is very easily overlooked because of its minute size. Judging from its contents and position, it is most likely the germarium and the cells inside are oogonia. But Jorgensen (1933) failed to find it, stating: 'No germarium is visible, the ovarian wall being closely apposed to the edges of the tetrad.' This repays further investigation.

In the great majority of sexual females of *Evadne nordmanni* only one resting egg is present in the brood-pouch (Fig. 3, G). But, occasionally, two

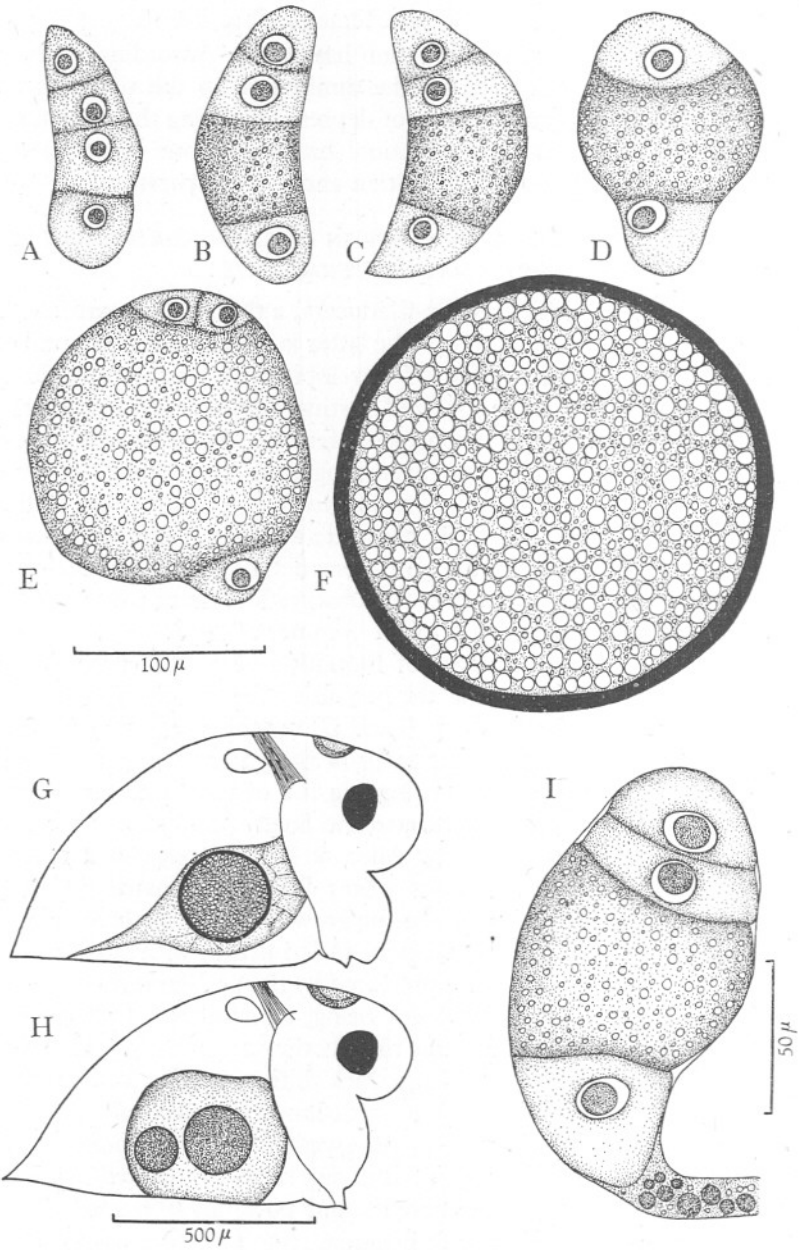

Fig. 3. Formation of a resting egg in *Evadne nordmanni*: A–E, a series of tetrad stages showing the gradual enlargement of the third oocyte to become the resting egg. F, a mature resting egg with a thick chitinous wall. G, a sexual female with a mature resting egg in the brood-pouch. H, a sexual female with two resting eggs of unequal size in the brood-pouch. I, a tetrad stage with a germarium attached to its posterior end.

were found, one being usually smaller than the other (Fig. 3, H). Such sexual females with two resting eggs were encountered more frequently in the Plymouth than in the Clyde samples. Their occurrence in this species has been recorded by Lilljeborg (1900) and Jorgensen (1933).

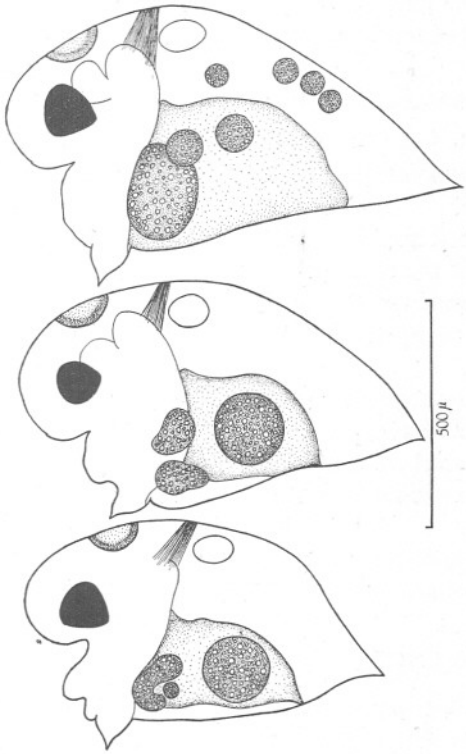

Fig. 4.

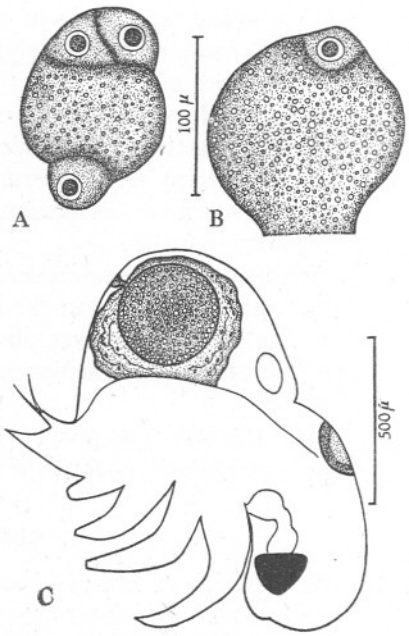

Fig. 5.

Fig. 4. Three sexual females of *Evadne nordmanni* with several irregular masses of yolk-laden protoplasm scattered in the shell-cavity. Note the large resting egg in the brood-pouch.

Fig. 5. Formation of a resting egg in *Podon intermedius*: A and B, two relatively late tetrad stages with the third oocyte enlarging to become the resting egg. C, a sexual female with a mature resting egg in the brood-pouch.

In the Plymouth samples there occurred some sexual females of *E. nordmanni* in the shell-cavity of which were found several irregular masses, usually rounded, of protoplasm full of yolk spherules (Fig. 4) which, in view of their contents, are probably formed by the disintegration of another resting egg. No such sexual females were, however, met with in the Clyde samples. So far as the writer is aware, this phenomenon has not, hitherto, been observed in either marine or fresh-water Cladocera.

Fig. 5 shows the formation of a resting egg in *Podon intermedius*. It will be seen that it commences too with the tetrad stage of which the third cell is destined to become the resting egg, whilst the other three serve as nurse cells and are finally absorbed by the growing egg. Unfortunately, owing to the lack of sufficient material, it is not possible to study it in such detail as in *Evadne nordmanni*. However, judging from the few stages available, the whole picture of the formation of the resting egg appears to be essentially similar to that of the latter species.

Summary

A statistical study was made of the fertility of *Evadne nordmanni*, *Podon intermedius*, *P. leuckarti* and *P. polyphemoides* in the Clyde Sea-Area and of the former two species off Plymouth.

The mean fertility of parthenogenetic females varies with different species. This is not correlated with the size of the species.

Within the species, *Evadne nordmanni* and *Podon intermedius*, there exists, in general, a positive correlation between the size and the fertility of parthenogenetic females.

The fertility of *Evadne nordmanni* is subject to seasonal variation. This is not correlated with fluctuations in the abundance of diatoms.

An inverse relationship was observed in *Evadne nordmanni* between the reproductive capacity of parthenogenetic females and the intensity of sexual reproduction.

A brief account was given of the formation of the resting egg in *Evadne nordmanni* and *Podon intermedius*.

References

Allen, E. & Banta, A. M., 1929. Growth and maturation in the parthenogenetic and sexual eggs of *Moina macrocopa*. *Journ. Morph.*, Vol. xlviii, pp. 123–51.

Apstein, C., 1910. Cladocera. *Bull. Trimestr. Explor. Mer, Copenhagen*, Pt. 1, pp. 39–51.

Berg, K., 1931. Studies on the genus *Daphnia* with special reference to the mode of reproduction. *Vidensk. Medd. F. Dan. Naturh. Foren.*, Vol. xcii, 212 pp.

—— 1934. Cyclic reproduction, sex determination and depression in the Cladocera. *Biol. Rev.*, Vol. ix, pp. 139–74.

Cheng, C., 1942. On the fecundity of some gammarids. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 467–75.

Claus, C., 1877. Zur Kenntnis des Baues und der Organisation des Polyphemiden. *Denkschr. K. Akad. Wiss. Wien, Math.-Naturw. Kl.*, Bd. xxxvii, pp. 137–60.

Cleve, P. T., 1900. The seasonal distribution of Atlantic plankton organisms. *Goteborgs Vetensk. Handl.*, Vol. iii, 369 pp.

Gibitz, A., 1922. Verbreitung und Abstammung mariner Cladoceren. *Verhandl. Zool. Bot. Gesel. Wien*, Bd. lxxi, pp. 85–105.

Hardy, A. C., 1936. The ecological relations between the herring and the plankton investigated with the Plankton Indicator. Part I. The object, plan and methods of the investigation. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 147–76.

JORGENSEN, O. M., 1933. On the marine Cladocera from the Northumbrian plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 177–226.

LILLJEBORG, W., 1900. Cladocera Sueciae. *Nova Acta Reg. Soc. Sci. Ups.*, Ser. 3, Vol. XIX, 701 pp.

MARSHALL, S. M., 1937. In Director's *Ann. Rep. Scot. Mar. Biol. Assoc.*, 1937–8, p. 9.

RAMMER, W., 1931. Mittelungen über marine Cladoceren. *Biol. Zentr.*, Bd. LI, pp. 618–33.

—— 1933. Die Cladoceren der 'Meteor'-Expedition. In *Wiss. Erg. Deutsch. Atlantischen Exped. Forsch. Vermess. 'Meteor'*, 1925–7, Bd. XII, pp. 111–21.

SCOTT, T., 1905. A report on the free-swimming Crustacea found in the Firth of Clyde, 1901–1902. *Proc. Roy. Soc. Edinb.*, Vol. XXV, pp. 792–805.

SEXTON, E. W., 1928. On the rearing and breeding of *Gammarus* in laboratory conditions. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 33–55.

STEPHENSEN, K., 1938. Marine Ostracoda and Cladocera. *The Zoology of Iceland*, Vol. III, Pt. 32, 19 pp.

UÉNO, M., 1934. The fresh-water Branchiopoda of Japan. III. Genus *Daphnia* of Japan. *Mem. Coll. Sci., Kyoto*, Vol. IX.

MANGANESE AND THE GROWTH OF PHYTOPLANKTON

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Hydrographer at the Plymouth Laboratory

(Text-figs. 1–2)

CONTENTS

Introduction

Several marine plants grow at very different rates when kept in sea water collected from different positions and depths, after the waters have been heated to kill the naturally occurring organisms and have been enriched with phosphate, nitrate, silicate and iron. Instances have been recorded where a water, treated in this manner, has proved completely infertile towards one or other species of diatom introduced into it.

There is also evidence that in the sea, in nature, different bodies of water may support less, or more, rapid growth of phytoplankton for reasons other than their content of available phosphorus, nitrogen and silica. Hart (1941) records that the plant life in the Scotia Sea, fed by a current which has washed outlying islands of the Antarctic continent and passed over a submarine ridge, is twice as great as elsewhere in corresponding latitudes. He attributes this heavier development of plant life to some constituent in the water derived from land drainage.

As yet there is no further direct evidence that, in nature, trace elements other than combined nitrogen and phosphorus affect the rate of phytoplankton growth, nor that the minute quantities of organic matter in solution play a part in regulating the growth of one or other species, but experimental evidence is suggestive.

Some of this experimental evidence may be epitomized. It is generally recognized that for a vigorous growth of diatoms in culture it is necessary to add iron, either as an iron salt, as a trace of ferric hydroxide, or of the ferric phosphate precipitate formed on adding the Allen-Miquel nutrient solutions, or as an integral part of some stimulating addition such as soil or yeast or algal extract.

The following experiments proved instructive: samples of inshore waters, relatively rich in iron compared with water further out to sea and containing the natural community of phytoplankton organisms, were collected during the spring of 1946 and enriched with nitrate and phosphate, some with iron citrate also. They were kept aerated in a north window. Growth of the mixed communities of planktonic diatoms was more vigorous and the final crop greatest in the flasks to which iron citrate had been added. The natural inshore sea waters contained insufficient available iron for maximum growth rate or for a maximum crop. That iron is not the only minor constituent sometimes lacking in sea waters, other than sources of available phosphorus and nitrogen, is shown by diatom growth experiments in Japanese and English Channel waters. Matudiara (1939) found considerable differences in the proliferation of the diatoms *Nitzschia closterium* and *Skeletonema costatum* when grown in samples of water taken from different depths and positions in the sea, after the waters had been heated and enriched with nitrate, phosphate, silicate and iron. Harvey (1939) found differences in the growth of *Ditylium brightwelli* in different waters which had been heated and enriched with nitrate, phosphate, iron, silicate and manganese also. A further instance of the different capability of sea waters to support plant growth other than owing to their nitrogen-phosphate-iron content, has been supplied by de Valera (1940), who found that the spore-ling of the sea weed, *Enteromorpha*, would grow more rapidly in water taken from the algal zone than in water collected from further out to sea. Later Suneson (1943) showed that extracts of algae, or even contact with algae, would render enriched sea water capable of supporting more rapid growth of *Enteromorpha* and of *Ulva*.

These differences between one sea water and another are not always, or wholly, due to variable concentrations of inorganic constituents essential for plant life. Allen (1914) found that an addition of organic substances, occurring in *Ulva* extract or in natural sea water, was essential for the growth of the diatom *Thalassiosira gravida* in artificial sea water. The writer (1939), in a series of experiments with *Ditylium brightwelli*, found that at least two organic substances or groups of substances were necessary for continued growth. One of these, which could be extracted from either sea water, soil or algal extracts, was probably a sulphur containing organic acid and could be replaced by several organic compounds containing divalent sulphur—cystine, methionine, thiamin, impure biotin and (in later unpublished experiments) by sodium sulphide. The other could be replaced by alanine. However, this was only a

first step towards finding the organic essentials for optimum growth, because relatively large quantities, several milligrams per litre, of the pure chemicals had to be used, more than ever likely to occur in a natural fully 'fertile' sea water. These experiments on organic growth stimulants also indicated that variability of trace elements, other than iron and manganese, in different sea waters may perhaps play some part in regulating the rate of diatom growth. Later Levring (1945) has shown that it is only the extracts of some species of seaweeds which stimulate diatom growth, not others; he, Kylin (1941–5), and Algeus (1946) have further added to the list of pure organic substances which stimulate the growth of marine plants.

In nature the ever-varying standing crop of phytoplankton, the primary food of marine animals, is a momentary balance resulting from the rate the plants have been multiplying and the rate they have been eaten. In most seas, other than the nutrient rich Antarctic, the low concentrations of available nitrogen and phosphorus impose a brake on the rate of multiplication since these nutrients are usually in insufficient concentration for most rapid growth.

There can be little doubt that low concentrations of available iron often act in the same way.

It now seems probable that shortage of another trace element, manganese, may at times exacerbate these natural brakes upon the rate of multiplication of at least some species of phytoplankton.

Experiments with *Chlamydomonas* sp. and with *Coscinodiscus excentricus*

A marine *Chlamydomonas*, isolated from Oslo Fiord by Mrs Foyn, has been in culture since 1928, for many years in an artificial sea water made from laboratory reagents.

When subcultured into sea water, obtained from the entrance to Plymouth Sound at high water in the late summer of 1945, which had been enriched with nitrate, phosphate and iron citrate, this flagellate made poor growth, the cells becoming small. On further subculture growth almost ceased. Other samples of inshore water obtained at intervals during the autumn proved similarly infertile.

On the other hand, when cultured in samples of water obtained some 15 miles offshore in late August and early November, the flagellate grew well.

It was found that very small additions of manganese, well within the range of 1–10 mg. Mn/m.^{3} found by analysis of Pacific and Baltic waters, rendered these infertile autumn inshore waters fertile. Heavy crops of full-sized flagellate cells would then grow in it after enrichment.

Experiments were made with inshore and offshore water collected in August, enriched with equal quantities of nitrate, phosphate and iron, and inseminated with equal numbers of the diatom *Coscinodiscus excentricus*.

A final crop of 181 diatoms/c.c. was produced in the inshore water. The addition of manganese in these experiments gave rise to a crop of 220 diatoms/c.c. In the offshore water 559 diatoms/c.c. were produced, with added manganese 606. Lack of this element did not account for the relative infertility of the inshore water.

A similar experiment was made with waters collected in November. In the inshore water 392 diatoms/c.c. were produced and the addition of Mn raised the crop to 493 per c.c. In the offshore water, likewise sterilized by heat and enriched in identical manner, only 122 diatoms/c.c. were produced and the addition of manganese did not increase the production.

While the addition of manganese had only a minor effect on the growth of *Coscinodiscus* in these experiments, no water, which was infertile to *Chlamydomonas* after enrichment, failed to produce a large crop of this flagellate after addition of manganese.

Effect of added Manganese on the Growth of *Chlamydomonas*

Water collected at the entrance to Plymouth Sound in early October was filtered, heated to kill any organisms which had passed the filter, and enriched with 8000 mg. N as nitrate, 400 mg. P as phosphate and 80 mg. Fe/m.^{3} as citrate. The water was then inseminated with *Chlamydomonas*, which had been grown in a similar infertile water and was showing the effects of manganese starvation—the cells had multiplied slowly and many were less than normal size. Roughly, 3 cells/mm.^{3} were added. The water was filled into a series of small flasks, manganous chloride added, and the flasks placed below a fluorescent strip light.

Fig. 1*a* shows the crop which was produced after 9, 11, 15 and 22 days of continuous illumination.

As little as 0·1 mg. Mn/m.^{3} had a significant effect during the early stages of growth; neither the effect of this nor of 0·25 mg./m.^{3} persisted long enough to permit a considerable crop to develop. However, the addition of 0·5 mg./m.^{3} was sufficient to allow the utilization of more than half the large quantity of phosphate in the enriched sea water.

The final crop obtained due to the addition of 0·1 and 0·25 mg. Mn/m.^{3} is less than one-fifth or one-half, respectively, of the crop due to the addition of 0·5 mg. Mn/m.^{3} There would appear to be a limiting concentration below which manganese is not fully made use of—in this instance rather less than 0·5 mg./m.^{3} plus that which was in the water initially and the minute amount added with, and in, the cells used to inoculate. Two later experiments with an infertile inshore water showed that the addition of 0·5 and even of 1·0 mg./m.^{3} did not provide sufficient to allow a considerable crop to develop, although larger quantities led to heavy crops.

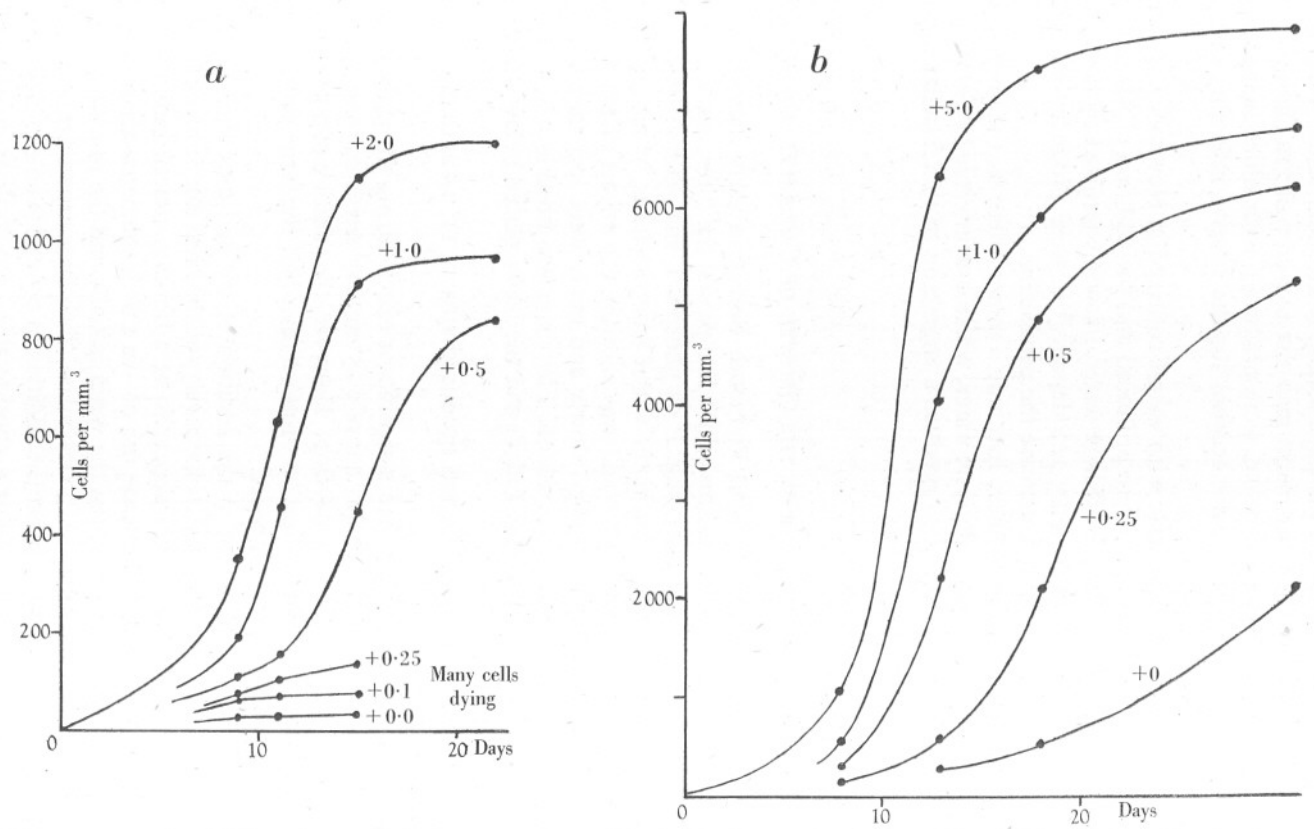

Fig. 1. *a*, growth of *Chlamydomonas* in inshore sea water enriched with nitrate, phosphate, and iron, with additions of 0·1, 0·25, 0·5, 1·0 and 2·0 mg. Mn/m.^{3} *b*, growth of *Chlorella* in same medium, with additions of 0·25, 0·5, 1·0 and 5·0 mg. Mn/m.^{3}

Hence these experiments provide no absolute value of the minimum concentration necessary for prolific growth, but they do show that the addition of as little as 0·5 mg./m.^{3} may just tip the scale.

In these and subsequent experiments the water used had been filtered, either through a Berkfeld candle long in use for filtering sea water or through filter-paper, and the waters had been heated, usually to 70–90° C., in order to kill organisms which had passed the filter. It was, therefore, desirable to find out if this filtration robbed the waters of any of their naturally occurring manganese by adsorption, and to find whether heating affected the fertility of the water towards *Chlamydomonas*. Samples of the same water were (*a*) passed through the Berkfeld candle, (*b*) passed through a filter-paper. These and also the same water unfiltered were heated, enriched and inseminated with manganese-starved *Chlamydomonas*. Similar growth took place in all three waters and the growth was increased to the same extent by additions of the same small quantity of manganese. The experiments gave no reason to suppose that any manganese initially present in the raw waters was adsorbed on either filter. In a subsequent experiment it was observed that an unfiltered water containing much plankton and detritus gave less increased growths with added manganese than when the particulate organic matter had been removed by filtration before the manganese chloride was added. The adsorption upon organic detritus of manganese at the great dilutions which occur in the sea was later investigated (p. 575).

In order to find whether the preliminary heating before enrichment in any way affected the fertility of the water, it was necessary to free a sample from included organisms. A Seitz filter had proved effective for this purpose (Schreiber, 1929) but experiment showed that even after being well washed the asbestos pad gave off a trace of manganese into the water, rendering a heated inshore water more fertile towards *Chlamydomonas*. A sample of inshore water was, therefore, rough filtered and divided into two parts. One portion was passed through a Seitz filter, the other portion heated to 95° C. and cooled. Part of this heated water was passed through the Seitz filter; both this and the remainder and the unheated Seitz filtered water were enriched to the same extent with nutrient salts and iron, and 40 mg. Mn/m.^{3} added to all three. This heavy addition of manganese was made in order to smooth out any differences due to manganese derived from passage through the Seitz filter. Identical growths of *Chlamydomonas* were obtained in all three waters—unheated, heated, and both heated and Seitz filtered. The experiment provided no grounds for supposing that the preliminary heat treatment affected the fertility of the water, provided the enrichment with iron was made after heating and cooling (Harvey, 1937) as was done in all the experiments. In many of the experiments the plants were illuminated continuously, a condition which does not occur in nature. An inshore water was therefore enriched, inseminated and kept under different conditions of illumination.

The experiment (Table I) gave no indication that results brought about under continuous illumination would not occur under natural conditions of alternate light and darkness. It also showed that addition of manganese was equally effective in increasing growth in bright light as in the relatively dim light of October days. This was of interest since experiments (unpublished) with the diatom *Ditylium* had suggested, but not proved, that addition of this element had marked effect on growth in a particular sea water in dim light but less effect in bright light; subsequently Emerson & Lewis (1939) found that manganese deficiency affects photosynthesis in weak light.

In these experiments manganese was added as a divalent manganous salt. It is not known in what form the element occurs naturally in sea water, so the effect on *Chlamydomonas* was tried of adding heptavalent manganese. This, permanganate, is reduced in sea water and the product formed is likely to be

TABLE I. EXPERIMENT 2–29 OCTOBER

Filtered inshore water enriched with 1000 mg. nitrate-N, 50 mg. phosphate-P and 20 mg. Fe, inseminated with *Chlamydomonas*

	Cells/mm.³ on day					
	3	6	10	14	18	25
In north window:						
Without addition	1	—	6	19	24	Cells dead
With 5 mg./m.³ Mn	9	—	42	106	127	115
In continuous illumination:						
Without addition	10	—	17	8	Cells dead	
With 5 mg./m.³ Mn	90	135	145	132	71	
In continuous illumination at about 1/20 intensity:						
Without addition	4	10	6	4	Cells dead	
With 5 mg./m.³ Mn	21	90	113	127	100	

of as high a valency as the manganese occurring naturally in solution. The addition of the same quantity of the element in either the di- or the heptavalent form caused equal increases in growth, from which it is inferred that adding manganous manganese was not in any way different from increasing the manganese occurring naturally in the sea.

The effect of low concentration of manganese on the size of this flagellate is shown in the experiment of 10–17 October. *Chlamydomonas* from a reasonably vigorous culture which had not been unduly starved of manganese was used to inseminate an infertile sea water enriched with 6000 mg. nitrate-N, 300 mg. phosphate-P and 20 mg. Fe as citrate per m.³ This was distributed in flasks to which varying amounts of manganous chloride were added. On the seventh day of continuous illumination measurements were made of the average diameter of the cells (Table II).

It has been observed by A. Kylin (1943, 1945) that the addition of a heavy dose of manganese to sea water, 250 mg. Mn/m.³, stimulated the growth of sporelings of *Ulva lactuca* when nitrogen was supplied as nitrate, but not when supplied as ammonium. A vigorous culture of *Chlamydomonas*, which had

been washed with inshore water by centrifuging and which was not manganese starved, was used to inseminate an inshore water enriched with phosphate, iron and with either nitrate or ammonium chloride. A substantial increase in growth rate was observed where 40 mg. Mn/m.³ had been added. In this experiment (19 September–30 October), sufficient Mn had been introduced

TABLE II. EXPERIMENT 10–17 OCTOBER

Mn added (mg./m.³)	Cells/mm.³, on day 5	Cells/mm.³, on day 7	Mean diameter (μ)
0	49	100	6
1	230	840	$8\frac{1}{2}$
2	415	890	$9\frac{1}{2}$
5	376	940	$9\frac{1}{2}$

in the cells of the inoculum for an almost full crop to develop without further addition of this element. The results are shown in Table III. It appears that manganese increases the growth rate of this plant whether nitrogen is supplied in either form and that, in this respect, the flagellate differs from *Ulva*. Noack & Pirson (1939) have also found that *Chlorella* responds to manganese with nitrogen supplied in either form.

TABLE III. EXPERIMENT 19 SEPTEMBER–30 OCTOBER

Enrichment			Addition	Cells/mm.³ after day								
mg./m.³N	mg./m.³P	mg./m.³Fe	mg./m.³Mn	0	6	9	12	15	19	22	27	41
1000 (as nitrate)	50	40	0	10	71	133	156	156	169	151	130	85
1000 (as nitrate)	50	40	20	10	159	145	182	188	174	152	156	68
500 (as nitrate)	25	40	0	10	61	77	93	105	—	100	65	55
500 (as nitrate)	25	40	20	10	—	92	101	118	—	94	96	49
1000 (as ammonium)	50	40	0	10	71	123	170	154	—	—	—	—
1000 (as ammonium)	50	40	20	10	185	144	182	153	—	—	—	—
500 (as ammonium)	25	40	0	10	65	90	90	104	—	—	—	—
500 (as ammonium)	25	40	20	10	108	95	107	122	—	—	—	—

EFFECT OF OTHER MICROELEMENTS ON THE GROWTH OF *CHLAMYDOMONAS*

In previous experiments (Harvey, 1939) it was observed that the addition of trace elements to sea water enriched with iron and manganese increased the growth of the diatom *Ditylium brightwelli*; the addition of coal ash dissolved in hydrochloric acid, considered likely to contain a representative collection of metals necessary for plant growth, was effective, but no attempt was made to ascertain the salts in this mixture which stimulated growth.

Riley (1943) has observed that the addition of a gallium salt stimulated the growth of the diatom *Nitzschia closterium* in nutrient-deficient sea water but not when an ample supply of nitrate and phosphate was present.

Amongst the growing list of microelements which are either essential or stimulants for higher plants, several occur in sea water at less than 1 mg./m.^{3}, and a number of trace elements are concentrated by marine algae to the extent of several grams per ton.

It was, therefore, of interest to find whether the addition of such elements to sea water, enriched with nitrate, phosphate, iron and manganese, would enhance the growth rate of *Chlamydomonas*. Using inshore sea water collected during the winter of 1945–6, no increased division rate of the flagellate was caused by the addition of 2 mg./m.^{3} of Ni, Ga, Co, Zr, Mo, La, V, Ge, plus 10 mg./m.^{3} of Zn and Cu. Nor was any increase in growth rate caused by the addition of the ash of *Ulva lactuca* dissolved in hydrochloric acid, although this did bring about a greater final crop, apparently due to its phosphate content.

Hence it may be concluded that the inshore sea waters contained sufficient micronutrients for optimum growth rate, with the exception of available P, N, Fe and Mn.

Experiments with diatoms (Harvey, 1937; Levring, 1945) have shown that the addition of divalent sulphur in the form of cystine increases the growth rate of these plants, and subsequent experiments showed that addition of sulphide had a similar effect. Experiments with *Chlamydomonas* showed no increased growth rate due to the addition of 1 mg. divalent sulphur/litre in the form of either cystine or sodium sulphide.

Effect of Manganese on the Growth of other Flagellates

I am indebted to Dr M. W. Parke for cultures of two brown Chrysomonads and a red Cryptomonad. These flagellates had been obtained from the Irish Sea and cultured in sea water enriched with phosphate, nitrate and soil extract.

On subculturing into an inshore water enriched with phosphate, nitrate and iron citrate, the growth was slow and limited. These subcultures were kept in flasks in a north window on a rotating table in order that each should obtain the same illumination, together with flasks to which had been added 5 mg. Mn/m.^{3} and which had been inseminated with the same quantity of the flagellates. In these latter the growth was more rapid and the final crop greater. They responded to the increase in manganese as did *Chlamydomonas*.

Effect of Manganese on the Growth of *Chlorella*

A culture of a marine species of *Chlorella*, in enriched sea water with soil extract for which I am also indebted to Dr Parke, was subcultured in the same way. There was no increase in growth rate or final crop due to added manganese; however, at the third subculture both the rate of growth and final crop

were greatly increased by added manganese. The parent cells grown with soil extract were sufficiently rich in manganese to allow many divisions to take place before the low concentration of this element in the inshore water affected their growth.

This third subculture without added manganese, being of cells to some degree starved of this element, was used to inseminate inshore water to which varying quantities of manganese had been added after enrichment with nitrate, phosphate and iron. The flasks were kept under a strip-light as in previous experiments; each contained 33 cells/mm.^{3} at the start and counts were made at intervals. Data are shown in Table IV and in Fig. 1*b*.

TABLE IV. EXPERIMENT 20 DECEMBER–21 JANUARY

Manganese added mg./m.^{3}	*Chlorella* cells/mm.^{3} on day				
	1	8	13	18	31
0·0	33	185	268	517	2125*
0·25	33	—	595	2100	5240
0·5	33	291	2220	4860	6250
1·0	33	520	4040	5910	6850
5·0	33	1080	6340	7440	7850

* Many small, also misshapen and empty cells.

An examination of these population densities leads to two observations. If the increase in number of *Chlorella* cells after 13 or after 18 days is divided by the quantity of manganese added, this proportional increase is seen to be greatest where 0·5 mg. Mn/m.^{3} was added; a similar observation was made in the previous experiment with *Chlamydomonas*. If the growth rate is examined, this is seen to increase after the earlier period of illumination where 0·25–1 mg. Mn/m.^{3} had been added. Thus a lag period is indicated before the manganese exerts its full effect.

ADSORPTION AND ABSORPTION OF MANGANESE BY *CHLORELLA*

An experiment was designed to see whether *Chlorella* cells would at once adsorb a material quantity of manganese ions on their surface, from water containing a low concentration of the element, and *retain* or absorb sufficient of these ions, not allowing them to be de-adsorbed, when transferred to an infertile inshore water—sufficient to permit an increased growth rate. Equal volumes of a culture of manganese-starved cells were dosed with 5 mg. Mn/m.^{3} and centrifuged at once, after 10 min. and after 18 hr., the liquid poured off and the cells transferred to infertile inshore water which had been enriched.

As control an equal volume of the culture, without prior treatment with manganese, was centrifuged and transferred to the inshore water. Growth was perceptibly increased by the shortest period of contact with 5 mg. Mn/m.^{3}, increased still more by contact for rather more than 10 min., and very markedly increased by contact for 18 hr.

It is significant that such short contact with manganese ions at such great dilution should allow an effective quantity to be retained by the plants. Presumably manganese was not only adsorbed on the surface but actually passed into the interior of the cells during the short period of contact with the manganese-enriched sea water.

Reference to published work on photosynthesis by freshwater species of *Chlorella* indicate that manganese penetrates the cell rapidly when added to the water. Pirson (1937) had found that when a relatively large quantity—55 mg. Mn/m.^{3}—was added to a culture of manganese-starved cells, it at once —'augenblick'—increased the rate of photosynthesis. Emerson & Lewis (1939) found that manganese played a major part in maintaining or restoring maximum photosynthetic activity and that 'under some circumstances it may have an effect within a short period after it is supplied'. The quantity added is not stated, but it seems usual in working with freshwater organisms to add much more than the minute amounts occurring in the sea or concerned with in the present investigation.

The next experiment was designed to see whether the growth of a considerable crop of *Chlorella* would abstract a material proportion of manganese added to sea water. A crop was grown in enriched water to which 5 mg. Mn/m.^{3} had been added. This was gently centrifuged and the centrifugate, containing some *Chlorella* cells, was further enriched with nutrient salts and iron. This nitrogen-phosphate-iron enriched centrifugate was divided, and 1 mg. Mn/m.^{3} added to one part. After illumination an obvious and marked increase in the second crop of *Chlorella* was seen in the flasks to which this 1 mg./m.^{3} had been added. In an ancillary experiment no such difference was apparent between the growth of these cells in enriched inshore water dosed with 5 and 6 mg. Mn/m.^{3} The result suggests that the first crop of *Chlorella* had abstracted a material proportion of the 5 mg. Mn/m.^{3} added at the beginning of the experiment. This is in conformity with Thompson and Wilson's observation that the concentration of manganese in the sea is less when phytoplankton is abundant.

The Lag Period of Manganese-starved *Chlorella*

Several observations were made concerning the lag or pause before growth starts when cells, which have nearly ceased growth owing to lack of manganese, are subcultured. The experiment shown in Fig. 2*a* indicates a lag of approximately 2 days irrespective of the manganese content of the water into which the cells were subcultured, although its addition greatly increased the subsequent growth rate of the cells. The experiment also indicates that, where cells growing rapidly in water with ample manganese are subcultured into inshore water, growth starts almost at once.

With the aim of finding whether storage in the dark after adding manganese would reduce the lag period, a nitrogen-phosphate-iron enriched water was inseminated with *Chlorella*; to one portion 5 mg. Mn/m.^{3} were added, both

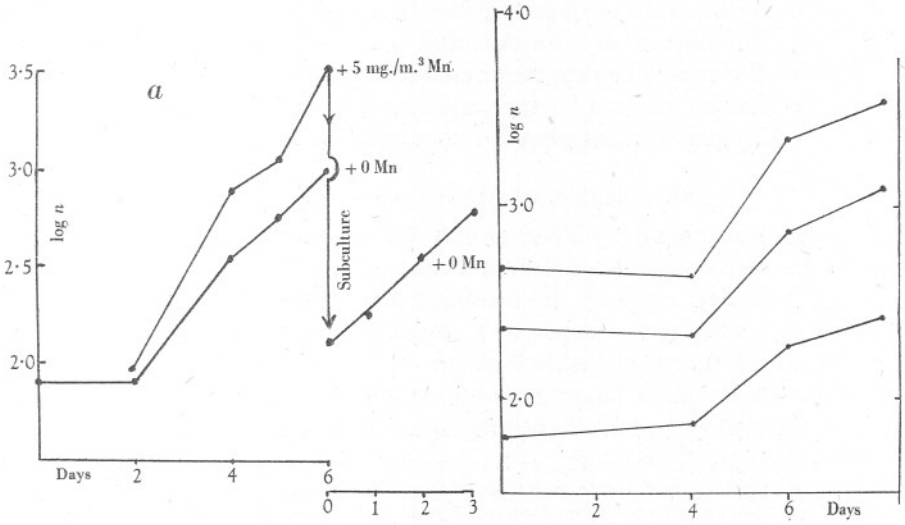

Fig. 2. Growth of manganese-starved *Chlorella*. *a*, the lag period and subsequent growth when transferred to sea water enriched with nitrate, phosphate and iron, without and with added manganese; the latter subcultured on the sixth day into enriched sea water. *b*, the effect of varying the quantity of inoculum on the lag period and subsequent growth rate. The number of cells per mm.^{3} (*n*) is shown on a logarithmic scale.

portions were kept in the dark for 4 days; then the same quantity, 5 mg./m.^{3}, of manganese was added to the second portion, and both were illuminated. No difference was found in the lag period, which lasted less than 24 hr., or in the subsequent growth rate of the *Chlorella* (Table V).

TABLE V. GROWTH OF *CHLORELLA* (CELLS/MM.^{3}) AFTER STORAGE IN DARK

	Stored in the dark with 5 mg. Mn/m.^{3}	Stored in the dark prior to addition of Mn (Cells/mm.^{3})
At start of insolation	152 ± 12	149 ± 12
After 24 hours	180 ± 13	173 ± 12
,, 48 ,,	362 ± 17	378 ± 22
,, 72 ,,	928 ± 56	835 ± 45
,, 96 ,,	1400 ± 80	1320 ± 80

When bacteria are subcultured into fresh nutritive media, the lag period before logarithmic growth commences is reduced by increasing the size of the inoculum or by adding filtered medium from the parent culture. Experiment

showed that it is otherwise with *Chlorella*; increasing the inoculum (Fig. 2*b*) had no obvious effect upon the length of the lag period.[1]

These observations indicate that the lag was a resting stage induced by starvation of a necessary cell constituent, on this occasion manganese. Recovery from this resting stage requires both a supply of manganese which is very rapidly collected by the cells and light for internal changes to take place within the cells. The time required for recovery, the lag period, appeared to be little if at all affected by the time required by the cells to collect and absorb a sufficiency of manganese for continued growth.

Occurrence of Manganese in the Sea

Direct chemical analysis by Thompson & Wilson (1935) has shown a variable content of dissolved manganese in ocean waters of the Pacific, ranging between 1 and 10 mg./m.[3] In the plankton-rich waters of the San Juan Channel they obtained evidence of a seasonal variation, less being found in solution during spring and early summer.

Noddack & Noddack (1940) found 4 mg. Mn/m.[3] in water collected off the coast of Sweden by means of spectrographic analysis.

[1] In the experiment shown in Fig. 2*b* it is seen that after expiration of the lag period the growth rate is greater where larger quantities of inoculum were added. A further experiment was made in which centrifugate from a parent culture was added to subcultures. This addition increased the growth rate. A similar observation has been made with the diatom *Nitzschia closterium*. This evidence, although limited, suggests that the products of metabolism which dissolve from the cells into the water stimulate vegetative reproduction of *Chlorella* and *Nitzschia*, a somewhat unique diatom whose ready growth in culture is less susceptible to adverse conditions than most planktonic forms.

In contrast to these observations, Levring (1945) has found that water from an old culture of the diatom *Skeletonema costatum* appeared to contain substances inhibitory to the growth of this species, just as bacteria excrete inhibitory metabolic products which limit their growth in rich media long before the nutrients are exhausted.

The effect of metabolites discharged into the water from the same species and from other creatures—both plants and animals—upon the growth of phytoplankton organisms should repay further study. The classic experiment of Allen showed that the growth of diatoms in enriched sea water, collected inshore or from an aquarium, was often improved if the water was previously treated with charcoal or hydrogen peroxide or chlorine. This suggests the presence of inhibitory substances in the water which were adsorbed, oxidized or chlorinated respectively. Furthermore, the improved growths obtained by the use of Allen-Miquel solution, which produces a heavy precipitate in the water, compared with simple nitrogen-phosphate-iron enrichment suggests that inhibitory substances may be carried down in the precipitate which is mostly removed before insemination with the diatom to be cultured. Matudiara (1939) observed that the great differences in growth of *Skeletonema* in waters collected from different depths, and similarly enriched, was still apparent if the waters were treated with Allen-Miquel solution in place of simple enrichment, but he found that greater growths of the *Skeletonema* occurred after Allen-Miquel treatment of the water than after simple enrichment. These observations confirm those of Allen and show that either inhibitory substances did not wholly cause the differences between one water and another, or, alternatively, were not entirely adsorbed from the water and carried down in the precipitate. As for the nature of these imaginary inhibitory substances, fungi are known to occur in the sea on algae (ZoBell 1946, pp. 131–5) and not uncommonly on fish in aquaria; the writer has observed that algal extracts, set aside to undergo bacterial breakdown, become poisonous to diatoms if moulds develop on them.

Thompson & Wilson record that waters rich in phytoplankton contained less dissolved manganese, and they found that the ash of mixed plankton organisms, mainly diatoms, was singularly rich in this element, containing as much as 0·07%. Correns (1941), quoted by Pettersson (1945), has also found that the shells of three species of Foraminifera taken from oceanic deposits contained between 0·01 and 0·02%. On the other hand Cooper (1939) found that two plankton animals, *Pleurobrachia* and *Sagitta*, contained insignificant quantities of manganese.

From the foregoing experiments with autotrophic flagellates and *Chlorella* it is clear that manganese plays a role in plankton growth as expected by Thompson & Wilson, and that phytoplankton collects a large proportion of the small quantity ever present in solution. In addition to being absorbed as an essential constituent, it is likely to be adsorbed on cell surfaces—a purely physical occurrence which would further deplete the sea of dissolved manganese. Experiment shows that this takes place.

Adsorption of Manganese on Organic Detritus

The following experiments were made to determine whether dead animal and vegetable matter would adsorb any material proportion of the very small quantity of manganese occurring in sea water.

Organic detritus was prepared by heating a tow-net catch of mixed diatoms and zooplankton, to kill the organisms, filtering and washing with filtered sea water. An inshore water was enriched with nitrate and phosphate and divided into 250 c.c. portions with: (*a*) the addition of organic detritus prepared as above; (*b*) the addition of an equal quantity of this organic detritus and also 1 mg. Mn/m.^{3}; (*c*) no addition, to act as control. After standing for 24 hr. all three were filtered, heated to 70° C., cooled, enriched equally with iron citrate, inseminated with the same quantity of a *Chlamydomonas* culture and distributed into small flasks. One flask of each of the three waters was dosed with 1 mg. Mn/m.^{3} and all illuminated under a strip-light. Counts of the *Chlamydomonas* were made after 6 and 11 days.

	Chlamydomonas per mm.^{3} on day	
	6	11
Control (no pretreatment)	45	126
Pretreated with detritus	35	44
Pretreated with detritus and manganese	45	100

The same waters to which 1 mg. Mn/m.^{3} had been added 24 hr. after pretreatment with detritus and immediately before illumination.

Control	81	283
Pretreated with detritus	45	103
Pretreated with detritus and manganese	63	247

The experiment shows that contact with the detritus rendered the water less fertile and the inference is drawn that it has done so by adsorbing manganese. It would further appear that where 1 mg. Mn/m.^{3} had been added at the same time as the detritus, all this added quantity had been taken up by the dead plant and animal cells.

An experiment was then made with marine bacteria, grown in sea water enriched with a trace of organic matter, killed by heat, and washed with several changes of filtered inshore water. A small addition of these bacterial corpses was made to an enriched inshore water to which 1 mg. Mn/m.^{3} and *Chlamydomonas* had been added. It reduced their growth rate. This experiment is inconclusive since some inhibitory substance might have leached into the culture from the washed corpses. A similar experiment was therefore made in which washed dead bacteria were added not only to water with small (1 and 2 mg./m.^{3}) additions of manganese, but also to water with relatively heavy additions (5 and 100 mg./m.^{3}). It was thought that the abstraction by the corpses of a small proportion of the manganese in the latter would not materially reduce the growth of *Chlamydomonas*, whereas any inhibitory or poisonous substances leached out from them would reduce growth. The result of the experiment was that the addition of dead washed bacteria reduced growth in waters to which 1 and 2 mg. Mn had been added, but made no difference to the growth where 5 and 100 mg./m.^{3} had been added.

Another observation also points to the same conclusion, that very small amounts of manganese are adsorbed from sea water on some organic surfaces. The addition of glucose was found to increase the growth of *Chlamydomonas* in inshore water, but if an ample supply of manganese was added to the water glucose had no effect on the growth rate for several days. Later, however, as bacteria developed in the culture with glucose and manganese, the growth rate of the flagellate became materially less than in the control without the added sugar.

Adsorption of Manganese on Inorganic Detritus

Pettersson (1945) has investigated the possibility that manganese may be adsorbed on windborne inorganic dust after falling into the sea far from land, where manganese rich mud is continuously deposited on the bottom. His calculations indicate that some 15 mg. MnO are deposited annually below each square metre of the open ocean in depths averaging some 5000 m.

Samples of powdered pumice and of volcanic ash were shaken with sea water to which a manganese salt had been added. Subsequent analysis showed no marked accumulation of manganese in the powders, and provided no evidence that windborne dust was likely to carry down with it any considerable quantity of manganese into the deep-sea deposits.

Pettersson draws attention to the presence of kaolinite and halloysite of terrestrial origin in these deep-sea deposits; this suggested using *Chlamydomonas* and *Chlorella* as analysts in order to find whether shaking inshore water,

to which only 1 mg. Mn/m.^{3} had been added, with kaolin would remove any substantial part of this addition and thereby reduce the growth rate of these plants in the water. The experiments showed no marked reduction in growth rate, indicating that the kaolin had not adsorbed any substantial part of the manganese in the water.

It would appear, therefore, that manganese dissolved in ocean waters is probably not adsorbed on inorganic detritus, although it is readily adsorbed on living and recently dead organisms. As these sink and are broken down by bacterial attack and autolysis, taking perhaps two years before they finally reach the bottom, the manganese may or may not be de-adsorbed and pass back into solution. If it is de-adsorbed we would expect the surface layers beyond the influence of land drainage to be robbed of manganese; there is lack of observation showing the distribution of manganese in the ocean far from land.

Summary

Inshore water collected near Plymouth during the late summer and autumn of 1945, after enrichment with nitrate, phosphate and iron, did not support continued growth of a species of *Chlamydomonas*, of *Chlorella*, of a Cryptomonad and of two species of Chrysomonads.

The addition of 0·5–2·0 mg. $Mn^{\cdot\cdot}$ or Mn^{v}/m.^{3} allowed vigorous growth and the production of heavy crops. The effect on *Chlamydomonas* of adding as little as 0·1 mg./m.^{3} was apparent.

The growth of *Coscinodiscus excentricus* varied in waters collected from inshore and from offshore which had been similarly enriched with N, P and Fe. The addition of manganese had only a minor effect.

The addition of other microelements to inshore waters enriched with N, P, Fe and Mn did not affect growth rate of *Chlamydomonas*.

Manganese starvation led to the production of small *Chlamydomonas* cells.

Manganese starvation caused a resting condition or lag period in *Chlorella*. A supply of manganese alone was insufficient for recovery; a period of illumination was also required for internal changes to take place before logarithmic growth was resumed.

The addition of manganese was effective when either nitrate or ammonium was supplied as source of nitrogen, in dim, bright, continuous, or discontinuous illumination.

Metabolic products which leached out of the cells into the water during the growth of both *Chlorella* sp. and of *Nitzschia closterium* acted as a growth stimulant.

Manganese at great dilution is rapidly 'collected' from solution by *Chlorella*. During growth this alga abstracts a material proportion from water containing 5 mg. Mn/m.^{3}

Using *Chlamydomonas* as 'analyst', it was found that added organic detritus, or the corpses of marine bacteria, adsorbed a material proportion of the manganese in sea water containing 1–2 mg. Mn/m.[3]

REFERENCES

ALGEUS, S., 1946. *Untersuchungen über die Ernährungsphysiologie der Chlorophyceen.* Lund.

ALLEN, E. J., 1914. On the culture of the plankton diatom *Thalassiosira gravida* Cleve, in artificial sea water. *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 417–39.

ALLEN, E. J. & NELSON, E. W., 1910. On the artificial culture of marine plankton organisms. *Quart. Journ. Micr. Sci.*, Vol. LV, pp. 361–431.

COOPER, L. H. N., 1939. Phosphorus, nitrogen, iron and manganese in marine zooplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 387–90.

CORRENS, W., 1941. *Nachr. Akad. Wiss. Göttingen, Math.-Phys. Klasse*, Bd. 5, p. 119. (Quoted by Pettersson, 1945.)

EMERSON, R. & LEWIS, C., 1939. The quantum efficiency of photosynthesis. *Carnegie Inst. Year Book*, Vol. XXXIX, pp. 154–8.

HART, T. J., 1941. Phytoplankton periodicity in Antarctic surface waters. *Discovery Rep.*, No. 21, pp. 261–356.

HARVEY, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 205–19.

—— 1939. Substances controlling the growth of a diatom. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 499–520.

KYLIN, H., 1941. Biologische Analyse des Meerwassers. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 11, No. 21.

—— 1942. Über den Einfluss von Glucose, Ascorbinsäure und Heteroauxin auf die Keimlinge von *Ulva* und *Enteromorpha*. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 12, No. 12.

—— 1943. Über die Ernährung von *Ulva lactuca*. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 13, No. 21.

—— 1945. Weitere Angaben über die Ernährung von *Ulva lactuca*. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 15, No. 3.

LEVRING, T., 1945. Some culture experiments with marine plankton diatoms. *Göteborgs Kungl. vetenskaps och Vitterhets samhälles Handlingar* (6), Ser. B, Bd. 3, No. 12, 18 pp.

—— 1946. Some culture experiments with *Ulva* and artificial sea water. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 16, No. 7.

MATUDIARA, T., 1939. The physiological property of sea water considered from the effect upon the growth of diatom, with special reference to its vertical and seasonal change. *Bull. Jap. Soc. Sci. Fish.*, Vol. VIII, pp. 187–93.

NOACK, K. & PIRSON, A., 1939. Die Wirkung von Eisen und Mangan auf die Stichstoff-assimilation von *Chlorellen*. *Ber. dtsch. bot. Ges.*, Bd. 57, p. 422.

NODDACK, I. & NODDACK, W., 1940. Die Häufigkeiten der Schwermetalle in Meerestieren. *Archiv für Zoologie*, Bd. 32, No. 1, p. 1.

PETTERSSON, H., 1945. Iron and manganese on the ocean floor. *Göteborgs Kungl. vetenskaps och Vitterhets samhälles Handlingar* (6), Ser. B, Bd. 3, No. 8, 37 pp.

PIRSON, A., 1937. Ernährungs- und stoffwechselphysiologische Untersuchungen an *Fontinalis* und *Chlorella*. *Z. Bot.*, Bd. 31, pp. 193–267.

RILEY, G. A., 1943. Physiological aspects of spring diatom flowerings. *Bull. Bingham Oceanogr. Coll.*, Vol. VIII, Art. 4, 53 pp.

SCHREIBER, E., 1929. Die Methoden einer physiologischen Meerwasseranalyse. *Rapp. Cons. Explor. Mer*, T. 53, pp. 75–9.

SUNESON, S., 1942. Über wachstumsfördernde Wirkung von Algenextrakten auf *Ulva* und *Enteromorpha*. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 12, No. 16.

—— 1943. Weitere Untersuchungen über wachstumsfördernde Wirkung von Algenextrakten auf *Ulva lactuca*. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 13, No. 20.

THOMPSON, T. G. & WILSON, T., 1935. The occurrence and determination of manganese in sea water. *Journ. Amer. Chem. Soc.*, Vol. LVII, pp. 233–6.

DE VALERA, M., 1940. Note on difference in growth of *Enteromorpha* species in various culture media. *Fysiogr. Sällsk. Forhandl. Lund*, Bd. 10.

ZOBELL, C. E. 1946. *Marine Microbiology*. Watham, Mass., U.S.A.

THE INORGANIC CONSTITUTION OF MOLLUSCAN BLOOD AND MUSCLE

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CONTENTS

Introduction

A good many papers have been published in recent years leading to the conclusion that mammalian tissues can be viewed as composed of separate phases, corresponding approximately to cells and intercellular spaces, which differ in their inorganic composition. The technique has been to analyse the tissue as a whole and, by comparison with serum analyses, to calculate the space occupied by the cells and their constitution. Direct histological work provides additional evidence on the proportion of a tissue accounted for as cells.

It appeared desirable to extend this type of work to another phylum, and the Mollusca were selected because of possible future opportunities to compare related terrestrial, aquatic and marine forms, such as are found among the Gastropoda. The Mollusca also show an excellent fossil record, so that they might be expected to provide opportunity to test out the idea that land animals carry with them some record of the constitution of the ocean at the time they left it. We have not yet had an opportunity to extend our analyses to those gastropods that have left the sea, but the present results on marine forms provide a basis for such a study. The single fresh-water species used was a clam, and it did not exhibit any peculiarities that could be said to reflect the presumed composition of the ocean in earlier times.

Samples for Analysis

Specimens of *Anodonta* were brought to Plymouth and maintained there in fresh water. *Pecten*, *Aplysia*, *Buccinum*, *Eledone*, *Eusepia*, and *Loligo forbesi* were taken near Plymouth and maintained in aquarium water, which was sea water to which had been added 25% extra calcium. *Mactra*, *Busycon* and *Loligo pealii* were collected near Woods Hole and maintained in sea water there.

To obtain blood from *Anodonta* or *Mactra* a hole was cut in the shell (*Anodonta*) or the hinge muscle was sliced to allow the clam to open (*Mactra*) and a cannula ligatured into one end of the exposed heart. The animals being kept under water, the heart continued to beat until up to 25 ml. of blood (*Anodonta*) or 60 ml. (*Mactra*) were pumped out. As the blood pressure was low the flow was assisted by making the collecting tube serve as a siphon. With *Pecten* the procedure was to remove an individual from water and, when the shell gaped naturally, to keep it open by inserting a cork. The animal was then held hinge uppermost and the sea water inside drained and blotted away. The blood bulged into sinuses by the hinge muscle and edges of the mantle between the eyes, so that an incision could be made with fine scissors, allowing 6–8 ml. of blood to flow out at once.

Aplysia blood was obtained simply by opening the dorsal body wall, care being taken not to contaminate the sample with mucus. To secure *Buccinum* and *Busycon* blood samples, a cord was tied under the operculum, a little of the shell chipped away, and the foot pulled out somewhat. Adherent sea water was dried off and a cut made under the foot with a razor blade, which permitted 25 ml. of blood to gush out from the pedal sinus of *Busycon*, or 6–8 ml. from *Buccinum*.

With cephalopods the animal was first nailed to a board through its tentacles with the ventral side up (*Eusepia*, *Loligo*) or the dorsal side up (*Eledone*). The mantle was then slit open exposing a prominent blood vessel (vena cava in *Eusepia* and *Loligo*; aorta in *Eledone*). Into this a cannula was ligatured and connected to a collecting flask. The board and flask were immersed in a tank, the system being completely closed except for a tube extending from the flask above the surface, through which a gentle suction could be applied to start the blood flow. The flask was at a lower level than the animal, so that the collecting tube could act as a siphon. If the operation were completed quickly the *Eledone* or *Eusepia* soon began to respire and pumped 50 ml. or more of blood into the flask. Specimens of *Loligo forbesi* failed to yield sufficient blood for analysis, either by the above technique or others tried. With *Loligo pealii* up to 10 ml. of blood could be obtained from a specimen before respiratory movements ceased. Dr Z. M. Bacq kindly showed us how to carry out several of the foregoing techniques.

For tissue analyses the main hinge muscle was taken from Pelecypoda, foot muscle from Gastropoda, and mantle muscle from Cephalopoda. The muscle was freed from any other tissue and in the gastropod foot, the pedal sinus was exposed and drained before the tissue was analysed. In *Aplysia* the foot muscle was so spongy that it was difficult to cut away surface tissue cleanly or to blot up adherent water in a uniform manner; the physical appearance suggested that intercellular space occupied a large proportion of the muscle, an idea borne out by the analyses.

Treatment of Samples

To estimate water content a known volume of blood, or weight of muscle, was dried at 100° C. For determination of base the samples taken at Plymouth were ashed at 400° C. and dissolved in acid. In Woods Hole they were extracted with boiling water in a Soxhlet apparatus and the protein precipitated with trichloracetic acid or uranium acetate (the latter not very satisfactory).

Sodium was estimated by the method of Ball & Sadusk (1936). The method followed for potassium was that of Kramer (1920). For magnesium the method used was that of Greenberg *et al.* (1932, 1935). Calcium was precipitated as oxalate, and finally estimated either by the gasometric method given in Peters & van Slyke (1932, p. 425), or according to Larson & Greenberg (1938). A specially ashed sample was used for each chloride determination, following van Slyke (1923–4). Special ashing with the Benedict-Denis reagent was also resorted to for some of the sulphate tests, others being done on the Soxhlet extracts. The sulphate in the extracts was titrated with barium chloride using either sodium rhodizonate (Robertson & Webb, 1939) or tetrahydroxyquinone (Sheen & Kahler, 1936) as an indicator. We have also tried the benzidine method of Fiske (1921). Results on blood sulphur were fair, but those on muscle are not good enough to publish.

The muscle samples were weighed, hence the analytical results came out directly as per cent by weight. Blood samples however, were taken by volume so that the results in the first instance appeared as g./100 ml. blood, that is as per cent w/v. In order to express the blood results gravimetrically they were multiplied by the factor 0·974, which is the volume occupied by 1 g. of sea water at 17·5° C. Thus all figures in Table I are in per cent by weight. (No factor was applied to *Anodonta* blood which was found to have practically the same density as distilled water.)

The ultimate analytical standard was a sample of Copenhagen sea water of known chlorinity, from the laboratory of Prof. Knudsen. From the chloride the concentration of the other ions was calculated, assuming the relative strengths as given in Dittmar's classical figures. The sample was subjected to repeated analyses and appropriate factors derived for our reagents, which were used in subsequent blood and muscle tests.

Previous Analyses

In Table I there have been included some analyses from the literature which appear to be directly comparable with our own. Values have, where necessary, been recalculated to make them read per cent by weight, using for marine blood, the factor given above. A word might be said about some analyses not quoted in the table.

Table I. Mineral Constitution of Molluscan Blood and Muscle

All values are in g./100 g. Where no reference is given on the right, the analyses are our own

	Blood							Muscle						
	Water	Na	K	Ca	Mg	Cl	SO_4	Water	Na	K	Ca	Mg	Cl	Reference
Plymouth sea water *	97·4	1·097	0·0388	0·0428	0·134	1·967	0·274	—	—	—	—	—	—	—
Plymouth aquarium water	—	—	—	0·0531	—	—	—	—	—	—	—	—	—	—
Woods Hole sea water	97·4	—	—	—	0·109	1·86	0·286	—	—	—	—	—	—	—
Pelecypoda:														
Mactra solidissima	—	—	—	—	0·110	1·77	0·266	—	—	—	—	0·0249	0·243	—
Mytilus edulis	—	1·009	0·0341	0·0448	0·115*	1·87	—	—	—	—	—	—	—	Bethe & Berger (1931), *Krogh (1939)
M. edulis	—	—	—	—	—	—	—	—	0·110	0·369	0·1020	0·0210	—	Bialaszewicz & Kupfer (1936)
Ostrea circumpicta	95·9	1·160	0·0353	0·0414	0·149	2·05	0·275	—	—	—	—	—	—	Kumano (1929)
Pecten maximus	96·4	1·094	0·0514	0·0540	0·105	1·92	0·282	80·7	0·112	0·439	0·0112	0·0081	0·190	—
Pinna nobilis	—	—	0·0630	0·0590	0·140	2·20	0·285	—	—	—	—	—	—	Bialaszewicz (1933)
Gastropoda:														
Aplysia punctata	—	1·130	0·0382	0·0535	0·119	1·92	0·282	85·5	0·751	0·187	0·0670	0·2320	1·34	—
Buccinum undatum	—	0·952	0·0301	0·0427	0·102	—	0·249	—	0·144	0·325	0·0315	0·0860	0·431	—
B. undatum	—	—	—	—	—	1·88	—	—	—	—	—	—	—	Duval (1925)
Busycon canaliculata	—	—	—	—	0·103	1·68	0·285	—	—	—	—	0·0647	0·306	—
Doris tuberculata	—	1·149	0·0572	0·0491	0·135	1·84	—	—	—	—	—	—	—	Bethe & Berger (1931)
Cephalopoda:														
Eledone cirrosa	—	0·979	0·0473	0·0467	0·139	1·68	0·414	—	0·186	0·403	0·0146	0·0310	0·325	—
Eusepia officinalis	95·5	1·048	0·0450	0·0480	0·125	1·85	0·277	80·4	0·198	0·398	0·0083	0·0085	0·360	—
E. officinalis	—	—	—	—	—	—	—	—	0·180	0·775	0·0335	0·0561	—	Bialaszewicz & Kupfer (1936)
Loligo forbesi	—	—	—	0·0390	—	1·94	0·271	83·9	0·156	0·383	0·0051	—	0·221	—
L. pealii	—	—	—	—	0·100	1·67	—	—	—	—	—	0·0146	0·223	—
L. pealii	—	0·815	0·0650	—	—	1·66	—	77·6	0·123	0·444	—	—	0·252	Manery (1939)
L. vulgaris	—	—	—	—	—	—	—	—	0·155	0·742	0·0260	0·0480	—	Bialaszewicz & Kupfer (1936)
Pelecypoda, fresh-water:														
Anodonta cygnea	99·8	0·0356	0·00155	0·0212	0·00086	0·0370	0·0147	84·9	0·0119	0·0413	0·0215	0·00597	0·0370	—

Griffiths (1891, 1892) made estimations on the blood of a dozen molluscs, together with many other invertebrates. His figures provide the first demonstration that the blood is in a general way similar in composition to sea water.

There are several analyses of chloride in blood by Duval (1925) which are very like our own. The one on *Buccinum* is quoted in Table I.

Myers (1920) reports an extraordinary concentration of calcium in the blood of *Schizotherus nuttalli*. In view of his method of collection the purity of the sample is open to doubt. He states that 'the exposed body of the clam was superficially cut in several places and then gently macerated. The liquid collected was filtered through loose cotton.'

McCance & Shipp (1933–4) give values for the four bases in the muscle of *Cardium edule*. The results fall clearly between our figures for blood and muscle. They state 'that the magnesium, sodium and water tend to vary together', and that 'the potassium concentration in the various organs of these invertebrates runs parallel not with the water but with the dry matter'. It is a fair deduction, in the light of our results, that McCance & Shipp were dealing with muscle containing a good deal of adherent blood or sea water.

Singh (1937–8) has done sodium, potassium and chloride in *Mytilus* blood and muscle, the results on muscle, like those of McCance & Shipp, falling between our blood and muscle values, probably for the same reason.

Blood of Marine Forms

On averaging the results of Table I and taking the scatter into account, the following conclusions may be drawn. The concentrations of sodium and potassium in pelecypod and gastropod blood cannot be shown to differ from those of sea water; in the Cephalopoda sodium appears to be a little lower and potassium a little higher than in sea water. In all three classes calcium is higher and magnesium lower than in the sea. It is known (Collip, 1920) that bivalves, on being kept in the air as between tides, show a marked rise in blood calcium, and sometimes a slighter rise of magnesium. It is likely in such instances that an accumulation of carbonic and lactic acids reacts with calcium from the shell (Dugal, 1939; Culbreth, 1941). Blood chloride in the Pelecypoda cannot be shown to differ in concentration from that of the sea; in the other two groups, especially Cephalopoda, it is hypotonic to sea water. Krogh (1939, p. 56) has a table leading to the same conclusion. As regards sulphate no concentration differences between outer and inner media are seen. In summary, the cephalopods show regulatory powers with respect to five of the six ions under consideration, the gastropods three, and the bivalves two.

Muscle of Marine Forms

The quantities of the ions in muscle are quite different from those in blood and appear to follow the same pattern in the three classes. The concentration ratios of muscle to blood are approximately: sodium 1/10 to 1/5, potassium

10/1 according to our results, but 20/1 in cephalopod muscle according to Bialaszewicz & Kupfer (1936), calcium 1/4 to 3/4, magnesium 1/10 to 2/3, chloride 1/10 to 1/5. The above estimate leaves *Aplysia* out of account, for the analyses suggest that in this genus there is a great deal of blood mixed in with the cells, while the foot appears on dissection as a loose network of fibres quite different from the compact muscle mass obtained from other molluscs.

Expressed as milliequivalents per kg. of water, the decrease in sodium from blood to muscle amounts to about 400, to which are added smaller losses of calcium and magnesium. Against this the gain in potassium is only about 100. It follows that in so far as these bases are concerned, muscle will be markedly hypotonic to blood. Isotonicity is apparently brought about by small organic molecules such as taurin (Kelly, cited by Krogh, 1939, p. 57).

The marked differences between blood and muscle salts suggest that muscle might be considered in two phases, an intercellular blood space containing all the sodium chloride, and a cell space. The intercellular space, i, is obtained, as a per cent of the whole muscle by the formula

$$i = \frac{\%\ \text{Na (or Cl) in muscle} \times 100}{\%\ \text{Na (or Cl) in blood}},$$

application of which to several genera is given in the left-hand columns of Table II. The averages are 18·1 % intercellular space for gastropod-cephalopod blood and 10·9 % for pelecypod space. Singh (1937–8) gives higher results of 20–30 % for *Mytilus*, but his specimens were out of water for some hours prior to analysis, which might account for a difference.

TABLE II. PER CENT OF MUSCLE OCCUPIED BY INTERCELLULAR SPACE AND CONCENTRATION OF IONS WITHIN THE CELLS

Genus	Intercellular space %. Calculated from		Constitution of cells, % of wet weight (Na and Cl being taken as zero)		
	Na	Cl	K	Ca	Mg
Mactra	—	13·7	—	—	0·011
Mytilus	10·0	—	0·41	0·11	0·010
Pecten	10·2	9·8	0·48	0·0064	−0·003
Buccinum	15·1	22·9	0·39	0·38	0·083
Busycon	—	18·2	—	—	0·056
Eledone	19·0	19·4	0·39	−0·090	0·005
Eusepia	18·0	19·4	0·48	−0·007	−0·018
Loligo	17·8	13·2	0·45	−0·002	−0·004

By making use of the intercellular space value derived as above described, one is able to estimate the quantities of potassium, calcium and magnesium in the cells themselves by use of the formula

$$i \times \%\ \text{of ion in blood} + (100 - i)\, x = 100 \times \%\ \text{of ion in whole muscle},$$

where i is the intercellular space and x is the per cent of the ion in muscle cells. The application of the formula gives values which are set down in the right-hand columns of Table II. Pelecypod and cephalopod cells appear to be alike

and to contain, within the limits of error, K 0·44%, Ca none, Mg none. The Gastropoda, on the inadequate evidence presented, have K as in other groups, together with appreciable amounts of Ca and Mg. It may be that the difference between the groups is due to the presence of inactive precipitates of calcium and magnesium in gastropods, such as McCance & Masters (1937) report in *Archidoris*. We are thus led to the general conclusion that, of the ions under consideration, the cells themselves may contain only potassium.

The analyses of Bialaszewicz & Kupfer (1936) on cephalopod muscle give values for potassium, calcium and magnesium that are two or three times as high as ours (Table I) and which lead, on calculation, to the conclusion that considerable amounts of all three substances are present in the cells. The contradiction between their results and ours cannot be explained at present.

The Fresh-water Clam

Table I has analyses of *Anodonta* blood and muscle, whose values in general are much lower than those of marine forms; in fact fresh-water clams are said to have a lower proportion of solids in their blood than any other animal. A comparison of *Anodonta* blood with marine fluids is facilitated if sodium be assigned a value of 100 and other ions calculated in proportion. This is done in Table III which shows that *Anodonta* blood is characterized by a large quantity of calcium and a lack of sufficient chloride to neutralize the sodium.

Table III. *Anodonta* Blood Compared to Sea Water, in Each Assigning Sodium a Value of 100

Figures in brackets are those of de Waele (1930)

Ion	Sea water	*Anodonta* blood
Na	100	100
K	4	4 (7)
Ca	4	59
Mg	12	2 (6)
Cl	180	104
SO_4	25	41

Investigation would doubtless reveal enough bicarbonate to account for most of the excess base. The figures in brackets are those of de Waele (1930), which have been included only in places where his results differ materially from ours. An analysis of sodium and calcium in the blood of four genera of fresh-water clams by Ellis *et al.* (1930) is in general agreement with our results.

Turning to muscle, one may treat the values in Table I as was done for marine forms, i.e. assume two phases, cells and blood, which differ in constitution, and attempt to find the space occupied by each. The only element that can be used for such a computation is sodium, since it is the only ion found in higher concentration in blood than in muscle. From Table I we obtain

$$\text{Na space} = \frac{0{\cdot}0119 \times 100}{0{\cdot}356} = 33\%.$$

From this the constitution of a muscle cell may be obtained as already described, and works out as follows in per cent: Na none (assumed), K 0·061, Ca 0·022, Mg 0·0085, Cl 0·037. Potassium is clearly the dominant ion but other base is present as well, and there is a considerable quantity of chloride. Expressed in other terms, the above base sums up to 3·4 milliequivalents, while the chloride amounts to only 1·0 milliequivalent, so that unless most of the base is osmotically inactive, some additional acid must be present, probably largely bicarbonate. As might be expected the cells are markedly hypotonic to those of marine forms, the dominant ion, potassium, being only one-seventh as concentrated.

Summary

Estimations of sodium, potassium, calcium, magnesium, chloride and sulphate have been made on the blood and muscle of marine molluscs and of the fresh-water clam, *Anodonta*.

On comparing marine blood with sea water it appears that the cephalopods show a regulatory power (i.e. difference between blood and sea water) with respect to all ions tested except sulphate. The gastropods have a regulatory power for calcium, magnesium and chloride; the pelecypods for calcium and magnesium.

Calcium is always higher in blood than in sea water, while magnesium is lower. Chloride, where it differs, is lower.

If muscle is considered as two phases, cells and intercellular blood space, then from whole muscle and blood analyses it is possible to calculate the spaces between the cells, which work out at 11% for pelecypods and 18% for the other two groups. Further calculation gives the constitution of the cells themselves, leading to the conclusion that, of the ions under consideration, only K is present in the Pelecypoda and Cephalopoda, while the Gastropoda may have some Ca and Mg as well as K.

As expected the fresh-water clam contains little inorganic material. In relative proportions its blood is characterized by more calcium and less magnesium and chloride than that of marine forms. In muscle cells potassium dominates but other ions are present as well.

This work was carried out at the Laboratory of the Marine Biological Association, Plymouth, in the summers of 1936 and 1937, and at the Oceanographic Institution, Woods Hole, in 1939. It is a pleasure to express our thanks to the Directors and Staffs of these establishments for accommodation, facilities and advice during the progress of the investigation.

REFERENCES

BALL, E. G. & SADUSK, J. F., Jr., 1936. A study of the estimation of sodium in blood serum. *Journ. Biol. Chem.*, Vol. 113, pp. 661–74.

BETHE, A. & BERGER, E., 1931. Variationen im Mineralbestand verschiedener Blutarten. *Pflügers Arch. ges. Physiol.*, Bd. 227, pp. 571–84.

BIALASZEWICZ, K., 1933. Contribution à l'étude de la composition minérale des liquides nourriciers chez les animaux marins. *Arch. Internat. Physiol.*, T. 36, pp. 41–53.

BIALASZEWICZ, K. & KUPFER, CH., 1936. De la composition minérale des muscles des animaux marins. *Arch. Internat. Physiol.*, T. 42, pp. 398–404.

COLLIP, J. B., 1920. Studies on molluscan celomic fluid. Effect of change in environment on the carbon dioxide content of the celomic fluid. Anaerobic respiration in *Mya arenaria*. *Journ. Biol. Chem.*, Vol. 45, pp. 23–49.

CULBRETH, S. E., 1941. The role of tissues in the anaerobic metabolism of the mussel, *Anodonta hallenbeckii* Lea. *Biol. Bull.*, Vol. 80, pp. 79–85.

DUGAL, L-P., 1939. The use of calcareous shell to buffer the product of anaerobic glycolysis in *Venus mercenaria*. *Journ. Cell. Comp. Physiol.*, Vol. 13, pp. 235–51.

DUVAL, M., 1925. Recherches physico-chimiques et physiologiques sur le milieu intérieur des animaux aquatiques. Modifications sous l'influence du milieu extérieur. *Ann. Inst. Océanograph.*, T. 2, pp. 232–407.

ELLIS, M. M., MERRICK, A. D. & ELLIS, M. D., 1930 (1931). The blood of North American fresh-water mussels under normal and adverse conditions. *Bull. U.S. Bur. Fisheries*, Vol. 46, pp. 509–42.

FISKE, C. H., 1921. The determination of inorganic sulfate, total sulfate, and total sulfur in urine by the benzidine method. *Journ. Biol. Chem.*, Vol. 47, pp. 59–68.

GREENBERG, D. M., ANDERSON, C. & TUFTS, E. V., 1935. A note on a closed titration flask for use in the bromometric determination of magnesium with 8-hydroxyquinoline. *Journ. Biol. Chem.*, Vol. 111, pp. 561–5.

GREENBERG, D. M. & MACKEY, M. A., 1932. The determination of magnesium in blood with 8-hydroxyquinoline. *Journ. Biol. Chem.*, Vol. 96, pp. 419–29.

GRIFFITHS, A. B., 1891. On the blood of the Invertebrata. *Proc. Roy. Soc. Edin.*, Vol. 18, pp. 288–94.

—— 1892. On the blood of the Invertebrata. *Proc. Roy. Soc. Edin.*, Vol. 19, pp. 116–30.

KRAMER, B., 1920. Direct quantitative determination of potassium and sodium in small quantities of blood. *Journ. Biol. Chem.*, Vol. 41, pp. 263–74.

KROGH, A., 1939. *Osmotic Regulation in Aquatic Animals*. Cambridge.

KUMANO, M., 1929. Chemical analysis on the pericardial fluid and the blood of *Ostrea circumpicta* Pils. *Sci. Rep. Tôhoku Imp. Univ.*, Ser. IV, Vol. 4, pp. 281–4.

LARSON, C. E. & GREENBERG, D. M., 1938. The analysis of calcium in blood and other biological material by titration with ceric sulphate. *Journ. Biol. Chem.*, Vol. 123, pp. 199–201.

MCCANCE, R. A. & MASTERS, M., 1937. The chemical composition and the acid-base balance of *Archidoris britannica*. *Journ. Mar. Biol. Assoc.*, Vol. 22, pp. 273–9.

MCCANCE, R. A. & SHIPP, H. L., 1933–4. The magnesium and other inorganic constituents of some marine invertebrates. *Journ. Mar. Biol. Assoc.*, Vol. 19, pp. 293–6.

MANERY, J. F., 1939. Electrolytes in squid blood and muscle. *Journ. Cell. Comp. Physiol.*, Vol. 14, pp. 365–9.

MYERS, R. G., 1920. A chemical study of the blood of several invertebrate animals. *Journ. Biol. Chem.*, Vol. 41, pp. 119–35.

PETERS, J. P. & VAN SLYKE, D. D., 1932. *Quantitative Clinical Chemistry. Vol. II. Methods*. Baltimore.

ROBERTSON, J. D. & WEBB, D. A., 1939. The micro-estimation of sodium, potassium, calcium, magnesium, chloride, and sulphate in sea water and the body fluids of marine animals. *Journ. Exp. Biol.*, Vol. 16, pp. 155–77.

SHEEN, R. T. & KAHLER, H. L., 1936. Direct titration of sulfates. Further studies with tetrahydroxyquinone as an internal indicator. *Indust. Eng. Chem., Anal. Ed.*, Vol. 8, pp. 127–30.

SINGH, I., 1937–8. Factors affecting the sodium, potassium and total base content of the anterior retractor of the byssus of *Mytilus edulis*. *Journ. Physiol.*, Vol. 91, pp. 398–412.

VAN SLYKE, D. D., 1923–4. The determination of chlorides in blood and tissues. *Journ. Biol. Chem.*, Vol. 58, pp. 523–9.

DE WAELE, A., 1930. Le sang d'*Anodonta cygnea* et la formation de la coquille. *Mem. Acad. roy. Belg. Cl. Sci.*, Ser. 2, T. 10, pp. 1–52 with five plates.

THE LIFE HISTORY OF *PATINA PELLUCIDA* (L.).

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(Text-figs. 1–6)

An opportunity to examine specimens of *Patina* in large numbers presented itself when Dr M. W. Parke and Miss E. Clay, B.Sc., who have been carrying out special research on algae at the Plymouth Marine Laboratory, offered to let us have all the limpets which they collected during their periodical examinations of *Laminaria* at Wembury, south Devon, and on the west coast of Scotland. The value of the specimens was enhanced by the fact that they were accompanied by notes on the locality of collection, the precise habitat of each mollusc and by the date of collection. This has permitted us to work out the life history of *Patina* with greater accuracy than has been possible before, and to come to some conclusions regarding the specific nature of populations of this limpet. We would express our great indebtedness to Dr Parke and Miss Clay for the material they so willingly supplied and for help provided on many occasions, as well as to Birkbeck College for a grant of £10 towards the cost of publication.

As is well known *Patina* is a small limpet found growing on *Laminaria* spp. and occasionally on other weeds such as *Fucus*, whilst the youngest stages are also to be found on the rocks and stones of the shore. It occurs in two distinct facies of which one is a characteristic inhabitant of the fronds of *Laminaria*, and the other is restricted to caves which it excavates for itself on the base of the holdfast, directly under the stipe, or on the outside of the lowest part of the latter. The taxonomic relationships of these two forms have been a matter of argument and have been decided in different ways by different authorities: Forbes & Hanley (1853) and Jeffreys (1865) both place the two types in the one species *pellucida*, but the more recent lists of Winckworth (1932) and Eales (1939) regard them as separate species, and call the form from the frond *pellucida* and that out of the holdfasts *laevis*, using for this the name first employed by Pennant (1777).

The differences between the two forms of *Patina* are not merely of habitat, but extend to the shell and animal as well, the points of contrast of the shells of the two types, however, being much more pronounced than those affecting the soft parts. With regard to the latter the most marked difference is in the coloration, animals from fronds being invariably more pigmented than those from the holdfasts, probably because of their greater exposure to light. This,

in its turn, depends in part upon the most conspicuous difference in the shell of the two (Fig. 1). In *pellucida* the shell is invariably smooth, rather regularly oval in outline (breadth/length = 0·688, S.D. = 0·139, range 0·56–0·85), rather low and stream-lined when seen in profile (height/length = 0·273, S.D. = 0·057, range 0·13–0·60), and of a clear horn colour and texture, sufficiently transparent to allow of the general disposition of most of the viscera being made out and for such things as the pigmented margin of the attachment of the shell muscle to be quite a conspicuous feature of the appearance of the animal when alive.

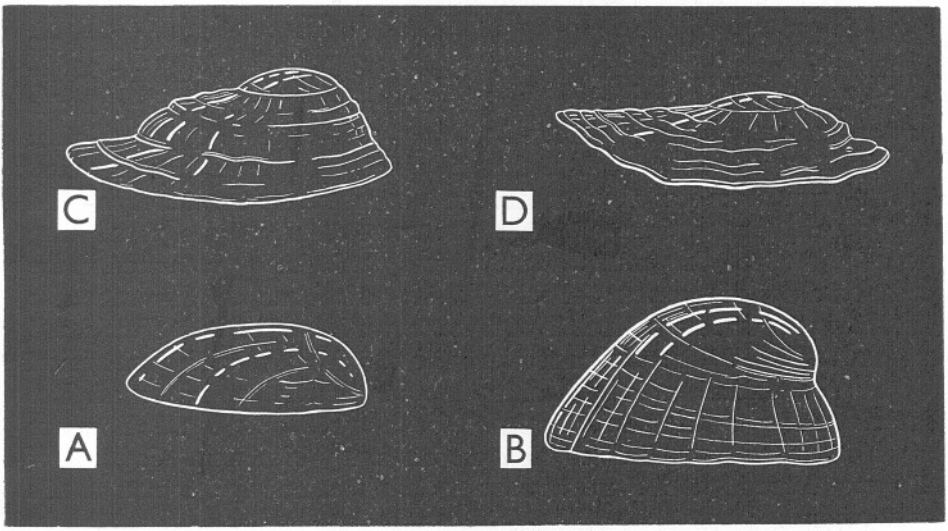

Fig. 1. Silhouettes of four types of shells. × about 6. A, young *pellucida* from frond of *Laminaria*; B, old *pellucida* from frond of *Laminaria*; C, D, two shapes of *laevis* from holdfast of *Laminaria*.

The apex of the shell is placed close to the anterior margin, which it overhangs almost vertically, and the mouth of the shell has a lip lying all in one plane, as might be expected in an animal which lives on a flat surface such as the frond of *Laminaria*. Two black or brown marks overlying accumulations of pigment in the underlying mantle are generally pronounced, one a spot near the apex of the shell, the second a streak running in an antero-posterior direction and placed about its centre. The beautiful blue-green rays, which are rather variable in number, ranging from 2 to 8, are very prominent against the brown background provided by the rest of the shell and this is usually without epizoic growths of any kind.

In *laevis*, which grows mainly on the holdfast of the weed, the shell is of much more variable shape and two silhouettes of frequent occurrence are shown in Fig. 1 C, D. It is usually more nearly circular in outline than is

pellucida (breadth/length = 0·818, S.D. = 0·183, range 0·45–0·95) and is frequently higher for a given length than is that variety (height/length = 0·344, S.D. = 0·083, range 0·17–0·57), the apex of the shell is more nearly central, though never absolutely so, and the mouth is never an opening with a plane lip, but would fit against a concave surface such as is offered by the hemispherical caves in which the creature lives. The most marked difference affects the substance of the shell, which is thick and obviously calcareous in composition and of a pale brown or greenish brown ground colour against which the blue-green rays are often very inconspicuous, whereas reddish brown lines, alternating with the green ones, are much more obvious, especially in the anterior half of the shell and towards the margins: these red lines are apparently not usually present in *pellucida* at all, having been observed only once. The number of blue-green lines is often much greater than in *pellucida* and may rise to as many as forty-six. The growth of these shells has often clearly been more irregular than that of *pellucida* and, while circular striae, lines of growth, are here a regular occurrence in contrast to the almost polished surface of *pellucida* there are often also great steps and ledges marking irregular growth. One such change is always particularly pronounced in the neighbourhood of the apex of the shell. This area is found, on examination, to be formed of a small smooth shell, with the proportions of that of *pellucida*, and with radiating blue lines but no red ones; beyond this the shell has the typical appearance of *laevis* and the transition line between the two is marked. The internal dark spots of *pellucida* are here faint or even absent, but the nacreous layer is on the other hand much more brilliantly iridescent. Growths of Polyzoa, Serpulid worms and small barnacles are extremely common on this type of shell.

So far as the soft parts of the animals are concerned it is not easy to find any but trifling differences between the two types. The mantle of *pellucida* has invariably the squarish blot of jet-black pigment in the roof of the pallial cavity and the longitudinal streak over the posterior half of the visceral hump which underlie corresponding pigmented regions of the shell, whilst these marks are at most very poorly developed in *laevis*. The other external characteristics appear to be identical in the two kinds of animals, though we have a suspicion that the branchial leaflets of the frond-dwelling type are relatively smaller than those of the animals living inside the holdfasts, a point which may be correlated readily enough with the greater exposure to which they are subject. The general arrangement of the viscera is the same in both, though the proportions of the parts vary with the proportions of the shell. In addition, the elaborate coiling of the intestinal region of the gut is modified so as to allow of proper packing within the available space: this is clearly seen in Fig. 2. If the coiling of the two types be analysed it will be found that in both the general plan is the same, but that the exact disposition of the coils varies so as to give in the one a lay-out elongated in one direction and in the other in a

direction at right angles to that. This is achieved mainly by the altering of the two coils which are numbered 3 and 6 in the figure; in *pellucida* coil 3 is flung in an anterior direction, whilst in *laevis* it remains alongside the others; and coil 6, which forms a small, slightly isolated loop in *pellucida*, is in the other type a narrow transverse coil, again more nearly parallel to the others. It will be noticed, too, that the exact stratification of the coils differs: for example, the stretch of oesophagus running back to the stomach of *pellucida* is the most ventral of all the parts shown, whereas in *laevis* no less than three loops pass between it and the foot. These differences, however, are clearly not of great moment and are no more than might be anticipated in animals of such varying shape. Slight variation is, in fact, found amongst the different shapes of the thick-shelled *laevis*.

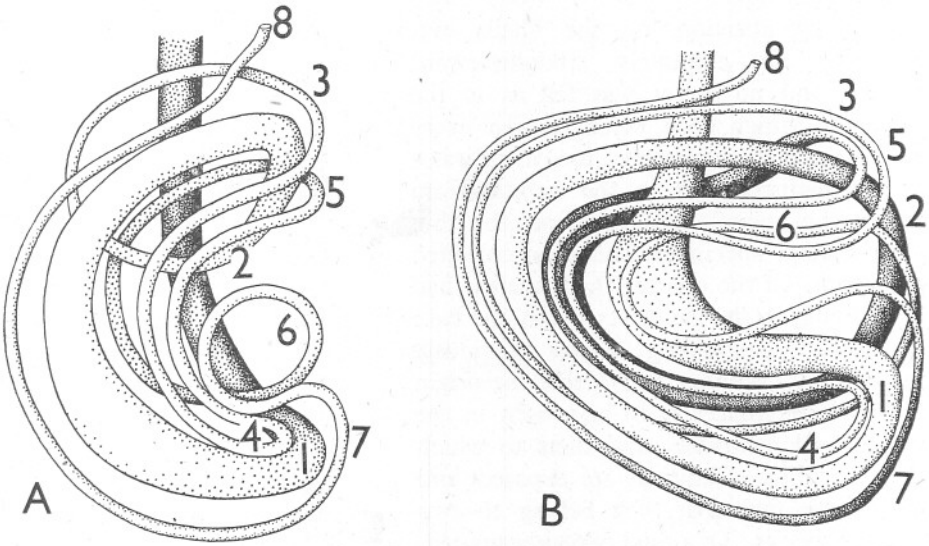

Fig. 2. Diagrams showing the coiling of the gut; A, of *pellucida*; B, of *laevis*. 1–7, coils; 1, the stomach; 8, the anus. × about 10.

The radula (Fig. 3) has apparently the same arrangement in both thick- and thin-shelled varieties and bears a close similarity to that of *Patella*. The central tooth is minute, the outermost lateral has three denticles, and there are regularly three (in one example observed, four) uncoloured marginals beyond that. A comparison of the wear shown by the most anterior teeth in both habitats indicated a clearly greater degree in those animals found in the holdfasts. These are patently feeding on the tissue of the stipe of the weed which they undercut: their diet, living where they do, must be one of more or less undiluted *Laminaria*. The animals living on the fronds, however, whilst obviously from the appearance of the weed using that for at least part of their nourishment, are also, from the contents of their gut, ingesting vast quantities

of other material in much the same way as their relative *Patella*. It is quite probable that the intake of diatoms and similar food from the soft and slimy surface of the *Laminaria* is a method of feeding which is less destructive of the radular teeth than the direct feeding on the weed, which seems to be the main method followed in the holdfast.

The animals seem to be ripe from lengths of about 5 mm. upwards, so far as can be estimated from an examination of preserved specimens.

All the specimens were classified as either the 'thin' *pellucida* type or as of the 'thick' *laevis* type. They were then measured to the nearest tenth of a millimetre for length, breadth and height of the shell, the animals taken out, and the shell weighed after careful removal, under a binocular microscope, of any encrusting growth.

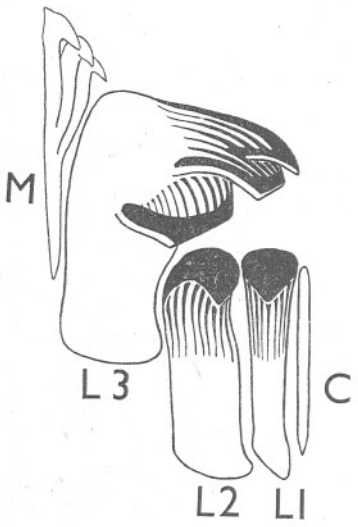

Fig. 3. One half-row of radular teeth, not yet in use, from *laevis*. C, central tooth; L_1, L_2, L_3, lateral teeth; M, marginal teeth.

The classification of the shells was normally an extremely straightforward matter, and no doubt was felt as to the group to which each belonged. In every one of these clear examples, too, there was a sharp distinction as to the habitat from which the animal had come: all the thin clear-shelled specimens had been collected on fronds, all the opaque thick-shelled had been living in the holdfasts or on the base of the stipe, suggesting, as was previously indicated by Boutan (1897), that the origin of these differences is to be sought in the varying microclimates and diets to which the two kinds of animals are exposed, and not to the fact that they belong to two distinct species. Of a total of 684 examined, 444 (=64·8%) were of the thin type, 199 (=29·5%) were of the thick type, whilst 41 (=5·8%) were sufficiently intermediate in their appearance for it to be impossible to decide which they were. Almost half of the latter animals were living in holes on the stipe, the rest living more or less evenly divided between frond and holdfast. In many instances, therefore, those animals of intermediate structure come from a habitat also intermediate in its characteristics, and so again support Boutan's view that exposure and habitat are the factors responsible for the differentiation of the two main types. These intermediate shells were not used for later work.

When the shells are sorted into classes according to their length and type, and when the numbers are examined, the results expressed in Fig. 4 are obtained. This gives several pieces of information. It shows that the pro-

portion of individuals of the thick type is least in the smallest sizes—though this is partly a reflection of the fact that it is most difficult to differentiate clearly between these two types when dealing with the most minute shells—and it suggests that there is only one type in the very smallest and youngest stages. It shows, too, that the proportion of thick shells rises as the age of the animals increases, until amongst the giant shells the thin type forms an unimportant percentage: this may obviously be linked with the much greater probability of frond-dwellers being damaged, swept away from their homes or eaten by predators, than the thick-shelled animals leading a more sheltered

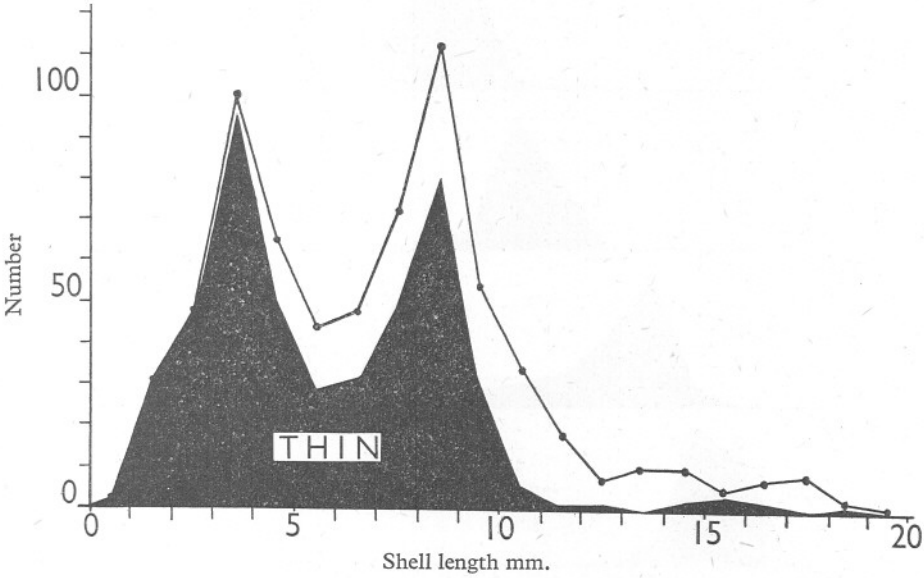

Fig. 4. Size-distribution curve of total number of *Patina* examined. The upper line gives the total number of animals for each length, the area shaded black the number of thin shells, the area left white therefore showing the number of thick shells.

existence in the holdfasts. The peaks in the curve mainly reflect the seasonal activities of the collectors, but they do indicate that the population of *Patina* must be made up of age classes, each derived from a single fall of spat.

To explore this question further the shells were next sorted according to the month in which they had been collected, and in this way a series of size-frequency curves which are shown in Fig. 5 was obtained. In each group of this series the modal class has been represented as 100 and the other points calculated as percentages. It is clear that the bulk of *Patina* in May measure 1·0–3·0 mm. in length and are presumably the comparatively recently settled spat of the same spring. No collections are available after May until September,

but here again the shape of the curve shows that the greater part of the population has then a size of 2·5–5·0 mm. length, a growth of 1·5–2·0 mm. over a

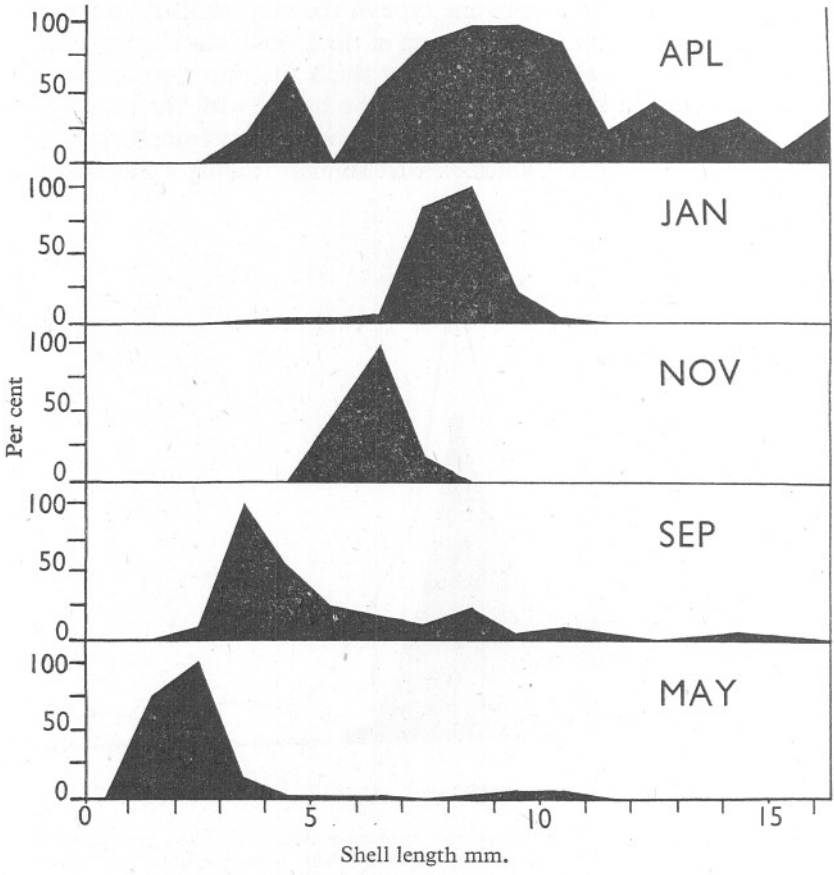

Fig. 5. Size-distribution curves for five months of the year: in each curve the modal point has been made 100.

period of four months. By November the modal point has risen to 6·5 mm. length, by January to 8–9 mm., and growth continues during the spring until by April of the next year the population has a modal length of 9–11 mm.

Month	Modal length (mm.)	Growth (mm.)
May	2·5	—
Sept.	3·5	1·0
Nov.	6·5	3·0
Jan.	8·5	2·0
Feb.	9·5	1·0
Apr.	10·0	0·5

From this it would appear that a population which is formed in the spring of one year by spatfall from the crop of planktonic larvae has reached a size of about 10 mm. length by the same month of the following year, growth being more or less rapid in summer, autumn and early winter months, but reduced to a lower level during the first months of the year. By comparing this with the size distribution over the whole population as shown in Fig. 4, it would seem that the first peak, at 3·5 mm., represents the collectors' haul in summer, the second peak, at 8·5 mm., their catch in early winter. The large reduction in numbers collected of shells of greater size, however, representing animals which must be over one year old, and which would therefore have been captured in May in numbers equal to those of the shells 3–4 mm. long, had they been there to catch, indicates that practically every specimen of *Patina* dies at an age of about 12 months and that only remnants of the original population survive into a second year. As was remarked above, these are nearly always limpets of the thick-shelled type which have found a sheltered haven in the holdfasts of the weed they inhabit. The rate of growth revealed by these figures for *Patina* is very noticeably less than those recorded by Orton (1928) for various molluscs, even for such a near relative as *Patella*, and is still considerably less than the lower figures obtained by Russell (1909) for that animal. It is however much more nearly comparable with those recorded by Moore for *Littorina* (1936*b*) and *Nucella* (1938).

Comparing the weights of shells of similar length belonging to the two types shows (Fig. 6) that the thick type put on weight more rapidly at all stages in the life history, but with increasing speed as they age, so that a shell of the thick type at a length of 9 mm. or more, will weigh at least twice as much as a thin shell of the same length.

If we now attempt to reconstruct the course of the life history of *Patina* from the data given above it appears as follows. The eggs are laid apparently during any month of the year (at Plymouth) according to Lebour (1937), but there is a spring period during which egg-laying reaches a maximum. We have ourselves found that animals are sexually mature from a length of about 5 mm. This they attain by about November, so that from then into the following spring the entire population will be actively reproducing. The veligers have a short planktonic life—only a few weeks (Lebour, personal communication)—and they then metamorphose and settle on whatever substratum is adjacent. These metamorphosed creatures are therefore likely to be found not merely on *Laminaria* but on other weeds and on rocks as well: it is probably the first group alone, however, that survives, the others dying for lack of proper food after longer or shorter periods, as it is only on *Laminaria* that individuals more than 3–4 mm. in length can be found. All of these newly settled spat are alike and it is not possible to classify them into thick- or thin-shelled varieties, indicating that their transformation into one or the other of these is a later phenomenon. Amongst those that settle on *Laminaria* the majority will fall on

the fronds and will proceed to feed on the surface of these, either on the substance of the weed itself or on the diatoms and similar minute material which may occur on the surface. If they persist in this habitat these limpets will grow, but will retain the thin shell characteristic of the newly metamorphosed animal, and because of the greater exposure of their soft parts to light on this account will become more highly pigmented, whilst because of their greater exposure to wave action their shell will develop into a rather low structure which reduces

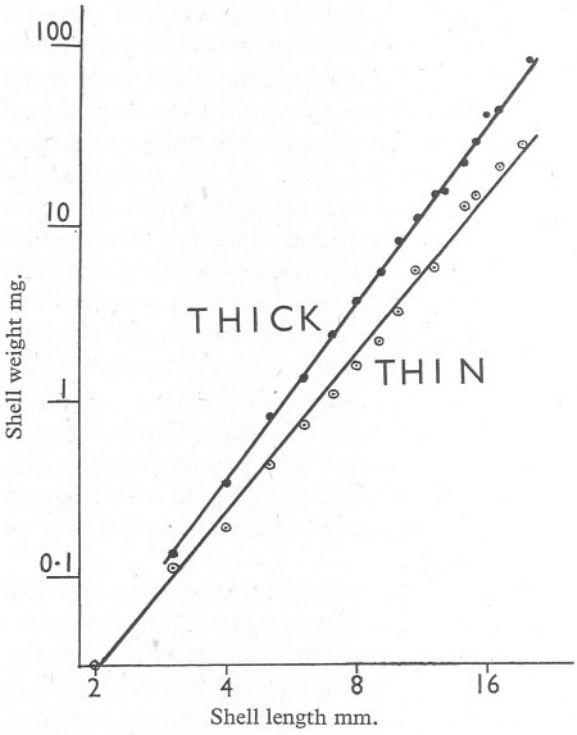

Fig. 6. Relation between length of shell and weight of shell. Plotted logarithmically.

the risk of their being swept away. This shell construction must be due, at least in part, to the nature of their diet; and to that too, as with *Nucella* (Moore, 1936*a*), the lack of brownish red rays in the shell. Some *Patina*, on the other hand, will settle on, or may be carried by water currents into, or may actively migrate into, the space inside the holdfast of *Laminaria*, and these will grow into the thick type with rounder shells, which fit into the more limited space available, and with higher shells because they are much more sheltered from wave action. The shells also, probably because of the different diet of the animals, become much more solidly calcified and have prominent reddish lines in addition to the usual blue. These thicker shells will give extra

protection to the soft parts against light and will so prevent the development of pigment. That the number of limpets which ultimately end in the holdfasts of *Laminaria* is greater than the number which originally fall there by chance as spat, and that it is augmented by an active migration of small individuals from the fronds, is indicated by the detailed structure of the shell of most animals of this type: the youngest part has the proportions, the colouring and the texture of the thin type and this changes abruptly at one point to those characteristic of the thick. An analysis of 150 shells of the thick type, selected at random, shows that the change in shell structure indicates a change of habitat at a length of 3 mm. for 16%, at a length of 4 mm. for 46%, of 5 mm. for 26·6%, at 6 mm. for 10%, and that only 1·2% migrate at a greater length. These lengths are reached during the first summer of the animal's life, and the bulk of the migratory movement is over by October–November. It would therefore appear quite definite that there is only the one species of *Patina*, to which the name *pellucida* must be applied, whilst *laevis* is not worthy of specific rank, but is an environmental form induced by the different conditions of food and exposure within the holdfast.

The next point to be considered is the relationship of *Patina* to the life cycle of the weeds upon which the animals are living. In this respect discussion will be limited to the two species of *Laminaria digitata* and *Cloustoni*, and is based on information provided very generously by Dr M. W. Parke and Miss E. Clay. *Laminaria digitata* has a long fruiting season, with maxima in spring and autumn. After the autumn fruiting is over the upper half of the frond gradually disintegrates and little by little breaks off, after which, in the first few months of the year a new growth occurs, mainly in February, March and April, leading to the production of a new frond for the next season of the plant's growth, though a certain amount of further breakdown occurs after the spring fruiting. If *Laminaria* fronds be examined in April, say, the young *Patina* which have just settled thereon are found scattered more or less at random over the surface of the weed upon which they are feeding. It is clear that if they maintain this random distribution over the surface of the frond during the spring breakaway a certain number of limpets will be cast away with the frond and lost: this presumably happens, but the number of limpets so lost will be minimal, as at that time of the year the majority of the animals found on this region of the frond are newly metamorphosed spat, and a much greater number of these will be lost by settling on rocky and other unsuitable substrates where prolonged life is not possible. As the autumn breakdown of the *Laminaria* is much greater than the spring disintegration the result would then be much more serious to the limpet population, especially as the animals are then preparing for their period of maximum reproduction. This loss, however, is prevented by a downward migration of the limpet which takes place in late autumn: it has the effect of concentrating the animals on the most basal part of the frond which will not be cast off and which will gradually elongate to

form the weed of the next season. Since the numbers of *Patina* do not seem to drop off markedly until the spring of the year after that in which they settle as spat, this downward migration is seen as an important reaction on the part of the animal. As it takes place about the time they are becoming sexually mature it is of very great importance as a means of securing a base on which the animal may survive the winter to participate in the spring reproductive maximum. To what, however, does the limpet react? The conclusion would seem inevitable that *Patina* must be feeding on the weed (and not merely relying on superficial detritus attached to it) to a sufficient extent to make it appreciate changes in the chemical composition of the plant tissue and to respond to changes in the amount of edible material present. Precisely what substance this affects seems to be indefinite, and it might be variation in any one of a series of stored products which causes the downward passage of the limpet—thus Hoffmann (1939) lists variation in the polysaccharide laminarin, in the sugar mannite, and in alginic acid from season to season, and Parke and Clay (*in litt.*) have found a difference between the amount of fucosan in the younger and older cells of the weed.

Laminaria Cloustoni fruits during the winter, and instead of a gradual disintegration of the frond thereafter, the whole structure is constricted off at its base from the new frond which starts growth in January. The old frond is carried up on the new growth and cast off in spring as 'Mayweed'. The limpets behave on *L. Cloustoni* in a similar manner to *L. digitata*—migrating downwards in late autumn—but in this species the movement stops when the animals have reached the basal part of the old frond, only a small number getting on to the extreme basal region from which the next year's growth is derived. It is difficult in these circumstances to see how the limpets are not frequently cast off with the remains of the old frond, but as this does not occur until late spring or early summer the breeding period will then be over and the animals are probably exhausted and moribund whatever happens.

Summary

Patina pellucida occurs in two facies with characteristics of habitat and structure, the latter affecting mainly the shell. One variety, *pellucida*, which lives on the fronds of *Laminaria*, has a smooth, elongated oval and low shell, which is transparent and brown in colour, with 2–8 blue rays radiating backwards from the summit which is placed at the anterior end; it is normally devoid of either epiphytic or epizoic growth. The soft parts are pigmented because of the translucency of the shell, the radular teeth only slightly worn, and the arrangement of the gut coils adapted to a long, narrow haemocoelic space.

The second variety, *laevis*, lives in caves in the holdfasts of *Laminaria*, and has a rough, round and usually high shell, though the proportions are more variable than in the variety *pellucida*. The shell is opaque and brown in colour, with 2–46 blue rays and also red-brown ones more or less regularly alternating

with them; it has a central summit and is frequently covered with growths of various sorts. The soft parts are not pigmented, the radular teeth are considerably worn, and the coiling of the gut modified to fit into the rounder haemocoel.

The life history may be summarized: the animals breed maximally in winter and spring, the planktonic larvae settling mainly in May as spat about 2 mm. in length. They grow so as to reach a length of about 5 mm. in the following autumn and 10 mm. after a year of sedentary life, becoming sexually mature at 5 mm. length. The majority of the animals die after a settled life of 12 months, but a few linger on into a second year: nearly all these belong to the variety *laevis*, living a sheltered life within the holdfast of the weed, not exposed like *pellucida* to the effects of wave action and storm.

When the larvae fall as spat all are at first alike, with the characteristics of *pellucida*. If they stay on the fronds these persist into the adult stage; if, however, they migrate into the holdfasts, the influence of the changed surroundings and diet evokes the characteristics of *laevis*; this migration occurs during the animal's first summer.

The idea that there are two species of *Patina* would thus appear to be wrong: there are two varieties of the nature of ecotypes.

The life history of the variety *pellucida* involves a downward migration on the fronds of *Laminaria*. When the species is *L. digitata* this migration brings the limpets on to the next season's frond and prevents them being cast off when the weed has fruited.

REFERENCES

BOUTAN, L., 1897. L'organe glandulaire périphérique de l'*Helcion pellucidum* (Lin.). *Arch. Zool. gén. exp.*, 3me série, T. 5, pp. 437–82.

EALES, N. B., 1939. *The Littoral Fauna of Great Britain*. Cambridge.

FORBES, E. & HANLEY, S., 1853. *A History of British Mollusca and their Shells*. London.

HOFFMANN, C., 1939. Die praktische Bedeutung der Meeres-algen. *Kieler Meeresforschungen*, Bd. 3, pp. 165–232.

JEFFREYS, J. G., 1865. *British Conchology*. London.

LEBOUR, M. V., 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journ. Mar. Biol. Assoc.*, Vol. 22, pp. 105–66.

MOORE, H. B., 1936*a*. The biology of *Purpura lapillus*. Part I. Shell variation in relation to environment. *Journ. Mar. Biol. Assoc.*, Vol. 21, pp. 61–89.

—— 1936*b*. The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *Journ. Mar. Biol. Assoc.*, Vol. 21, pp. 721–42.

—— 1938. The biology of *Purpura lapillus*. Part II. Growth. *Journ. Mar. Biol. Assoc.*, Vol. 23, pp. 57–66.

ORTON, J. H., 1928. Observations on *Patella vulgata*. Part II. Rate of growth of shell. *Journ. Mar. Biol. Assoc.*, Vol. 15, pp. 863–74.

PENNANT, T., 1777. *British Zoology*. London.

RUSSELL, E. S., 1909. The growth of the shell of *Patella vulgata*. *Proc. Zool. Soc. London*, 1909, pp. 235–53.

WINCKWORTH, R., 1932. The British marine Mollusca. *Journ. Conch.* Vol. 19, pp. 211–52.

A CERCARIA OF THE GENUS *HAPLOCLADUS* FROM *NUCULA NUCLEUS* (L.)

By W. J. Rees, D.Sc.

(Text-figs. 1–2)

The cercaria described here was found on 21 April 1936, in twelve out of sixteen specimens of *Nucula nucleus* (L.) from Cawsand Bay, Plymouth Sound. The parasite was found by Dr Marie V. Lebour, who kindly gave me the infested molluscs for examination. I have thought it advisable to publish these notes, incomplete as they are, as it may not be possible for me to obtain further specimens of infested *Nucula* for some time to come.

The trematode was found to parasitize the digestive gland and gonad. The cercariae develop in irregularly shaped parthenitae which each contain from two to ten larvae in various stages of development. The parthenitae measure 0·9–2·0 mm. in length.

The cercaria is very large and has a long, forked tail (Fig. 1). The measurements on the left of Table I were made with an ocular micrometer when the living cercariae were slightly flattened under the pressure of a cover-slip.

The body is elongate in outline, with a slight constriction just behind the oral sucker, and reaches its greatest diameter opposite the ventral sucker. The pre-acetabular region of the body is highly muscular and capable of much extension and contraction. Near the posterior border of the oral sucker there are two blunt processes, ventro-lateral in position. In section, the body is somewhat cylindrical, and consequently it is almost impossible to obtain true measurements from living cercariae because different individuals could not be subjected to the same pressure under a cover-glass. The measurements given on the right of Table I are of mature cercariae fixed in Bouin's fluid without pressure, and supplement those of living cercariae.

The tail is longer than the body and consists of a proximal, muscular portion which divides distally to form two contractile caudal furcae (Fig. 1). The oral sucker is well developed and has a slit-like mouth situated ventrally. It opens into the buccal cavity of the powerful oral sucker connecting with the pharynx. The oesophagus leads back in the median line and passes imperceptibly into the unbranched intestine. This passes to the right of the acetabulum and returns to the median line at the posterior end of the body, where it terminates. No anal pore opening into the excretory bladder was observed. The unbranched intestine is characteristic of trematodes of the genus *Haplocladus* Odhner, 1911.

The excretory bladder is Y-shaped, thin-walled and filled with excretory granules of irregular shape. The horns of the bladder reach as far forward as the

TABLE I. MEASUREMENTS (IN MM.) OF THE CERCARIA OF *HAPLOCLADUS* SP.

	Living (under pressure of cover-slip)	Fixed (without pressure)
Body: Length expanded	1·25	1·10
Length resting	0·55–0·70	0·75
Length contracted	0·50	—
Breadth resting	0·20–0·30	0·20
Tail: Length (to fork)	1·10–1·70	1·00
Breadth	0·15–0·17	—
Length of furca (resting)	0·60–0·75	0·15–0·40
Oral sucker: Diameter	0·12–0·15	0·08–0·09
Acetabulum: Diameter	0·08–0·10	0·07–0·075
Pharynx: Length	0·07–0·10	0·08–0·09
Breadth	0·05–0·09	0·05–0·055

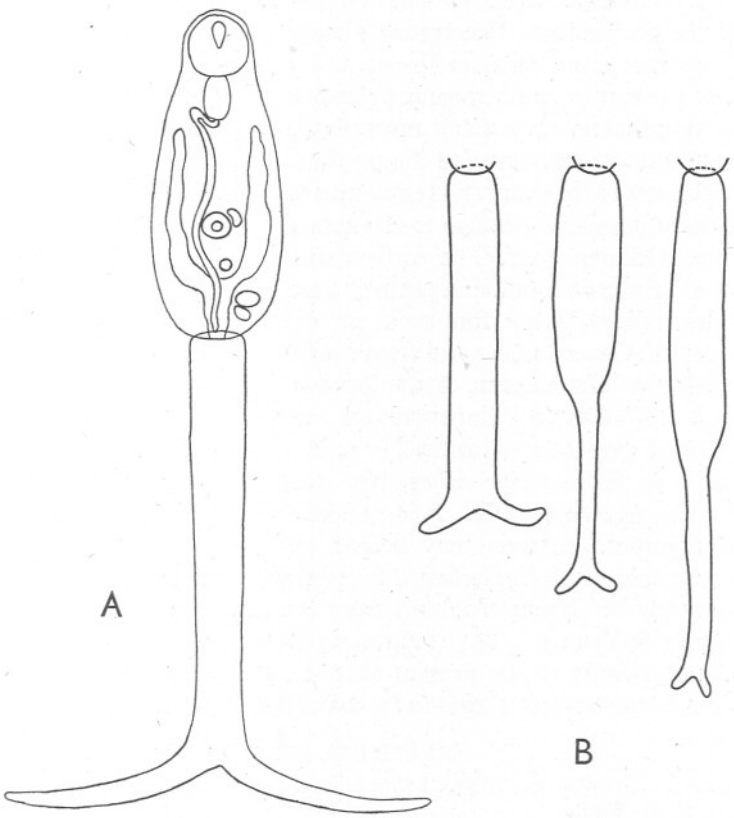

Fig. 1. Cercaria of *Haplocladus*. A, ventral view under slight pressure of cover-slip; Plymouth, 21 April 1936. B, different shapes assumed by the tail during 10 min.

posterior end of the pharynx (Fig. 2). Each main excretory duct opens into the horns of the bladder near their anterior end. The main excretory tubule, which is flagellated, passes postero-laterally for a short distance and then divides to form anterior and posterior collecting tubules. The position of a number (but not all) of the flame-cells was determined; these are indicated in Fig. 2, those of one side only being shown.

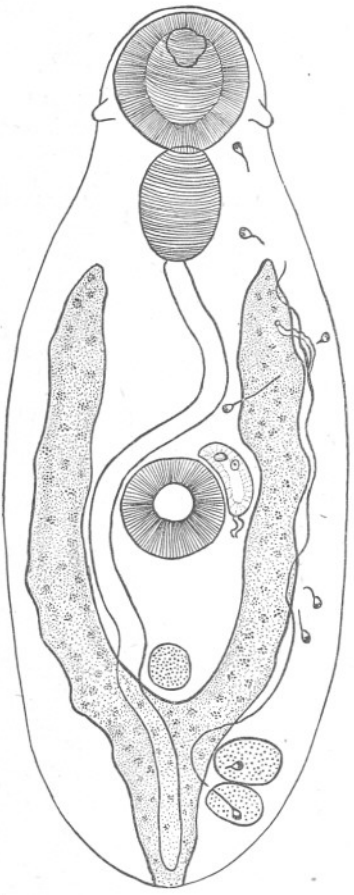

Fig. 2. Cercaria of *Haplocladus* species: detail of body, tail omitted.

The ovary appears as a small, round body midway between the acetabulum and the posterior end of the body. The two testes are situated one in front of the other, lateral to the excretory bladder and near the posterior end of the body. There is a well-developed cirrus-pouch situated close to and antero-lateral to the acetabulum. Penetration glands and cystogenous gland cells are absent, indicating that the metacercaria stage is probably very brief and that no encystment takes place.

The unbranched intestine and the position of the rudiments of the ovary and testes clearly indicate that the species belongs to the genus *Haplocladus* Odhner, 1911. The earliest and only record of a cercaria of this genus is that of Odhner (1911), who found it in an aquarium with *Nucula nucleus* and *Syndosmya* at Kristineberg. His account of the larva is insufficient to allow a comparison to be made with the present specimens. He refers his cercaria to *Haplocladus minor*, but did not prove this experimentally. It is possible that the Plymouth cercaria may belong to the common species of *Haplocladus*, *H. typicus* Odhner, which I have found in the intestine of *Caranx trachurus* from the same locality.

La Valette St George (1855) figures a *Cercaria dichotoma* which shows a remarkable similarity to the present species. Odhner is probably correct in regarding it as the larva of *Tergestia laticollis* (Rud.), which is closely related to *Haplocladus*.

REFERENCES

La Valette St George, A., 1855. Symbolae ad trematodum evolutionis historiam. Inaug. Diss., Berlin.

Odhner, T., 1911. Zum natürlichen System der digenen Trematoden. III. *Zool. Anz.*, Bd. xxxviii, pp. 99–117.

ON THE SEASONAL ABUNDANCE OF YOUNG FISH. VIII. THE YEAR 1946, JUNE TO DECEMBER

By F. S. Russell, F.R.S.
Director of the Plymouth Laboratory

(Text-figs. 1–3)

During the years 1930–9 a series of records was obtained on the abundance of pelagic young of teleostean fish occurring in standard half-hour oblique hauls made with the 2 m. stramin ringtrawl in the neighbourhood of the Eddystone. These results provided a record by which the composition of the young fish populations could be compared from year to year and any marked changes brought to notice. During the course of the observations there had been a striking reduction in abundance of young fish, and this had been correlated with the movements of water masses as indicated by certain plankton animals. The series of observations was brought to a conclusion in August 1939 on the outbreak of war. The earliest opportunity after the cessation of hostilities has been taken to continue these observations on young fish, and collecting was started in June 1946 when a research ship was once more available. There has thus been a gap of nearly seven years during which there has been no detailed information on the conditions in the waters off Plymouth. The 1946 collections were started too late to include the main period of abundance of young fish resulting from the spring spawners, but they afford evidence that as regards the summer spawners at any rate there is no significant change from the conditions existing in 1939. We cannot say what the conditions have been during the intervening years, but analyses of phosphorus content of the water during each of the winters in the period 1939–46 tend to show that conditions have remained much as they are at present, and that it is unlikely that there has been any large incursion of the rich water characterized by *Sagitta elegans* which supports a large population of young fish.

The dates on which collections were made are given in Table I, and the average monthly catches for each month from June to December 1946 are given in Table II; the fortnightly averages of all young fish less clupeids are shown in Fig. 1. A comparison of the average monthly figures with those given in the corresponding table in the report for 1939 (Russell, 1940) shows very close similarity. All species of summer spawning fish were very poorly represented, the only fish which were at any time at all numerous being *Callionymus*, *Ctenolabrus rupestris* and *Blennius gattorugine*. The high monthly average in July is due to these latter species which were abundant in the first two weeks of the month.

Records have at the same time been kept of the plankton animals in the catches (Figs. 2, 3). Throughout the period there has been a paucity of

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1946

All 2 miles east of Eddystone

June	July	Aug.	Sept.	Oct.	Nov.	Dec.
20	5	6	16	7	7	9
26	10	13	23	14	11	16
..	18	20	30	20	29	31
..	23	27	..	28	..	..
..	31	..	..	..	..	..

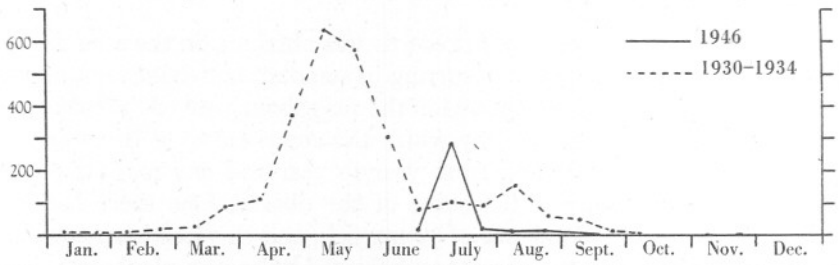

Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2 m. ringtrawl for each fortnight for all young fish, excluding clupeids, in 1946 (June to December) (——), and the same averaged over the period 1930–4 inclusive (-----).

plankton and a predominance of *Sagitta setosa*, itself present only in small numbers. In late summer and autumn there was a large increase in numbers of *Muggiaea* which is normal for that time of year. The predominant species was *M. atlantica*, but it is noteworthy that in five of the collections in August and September a very small number of *M. kochi* were found, generally less than 1%. This is the first time that the two species have been recorded together off Plymouth. Records kept by Dr Lebour during the war years have indicated that *M. atlantica* was present each year. This species has thus now been dominant at Plymouth since the winter of 1926[1] when it replaced *M. kochi*. A few *Liriope* were caught in October and November 1946.

The occurrence of indicator species close inshore during the war as recorded by Lebour (1947) are tabulated below, *Sagitta setosa* being the prevailing *Sagitta* species during the period.

	1940	1941	1942	1943	1944	1945
Muggiaea atlantica	Aug.–Oct.	June–Dec.	Jan., July–Dec.	Apr.–Oct.	May–June	June–Nov.
Salpa fusiformis	Aug.	—	—	—	—	—
Stephanomia bijuga	Aug.	—	—	—	—	—
Doliolum	—	—	Aug.	—	—	—
Sagitta elegans	—	Jan.–Feb.	—	May	—	Feb.–Apr.

Pilchard eggs have been abundant in 1946, the catches on the different dates being as follows: June 20 (5510), 26 (21,700); July 5 (3820), 10 (4420), 18 (3740), 23 (2440), 31 (40); August 6 (400); September 16 (14), 23 (228),

[1] In Figs. 4, 3 and 4 of the reports for the years 1937, 1938 and 1939 respectively, the year 1927 has inadvertently been substituted for 1926 in the legends. It was correctly given as 1926 in the legend of Fig. 3 of the report for the year 1936.

30 (7); October 7 (82), 14 (696), 20 (91), 28 (51); November 7 (830), 11 (25), 29 (20).

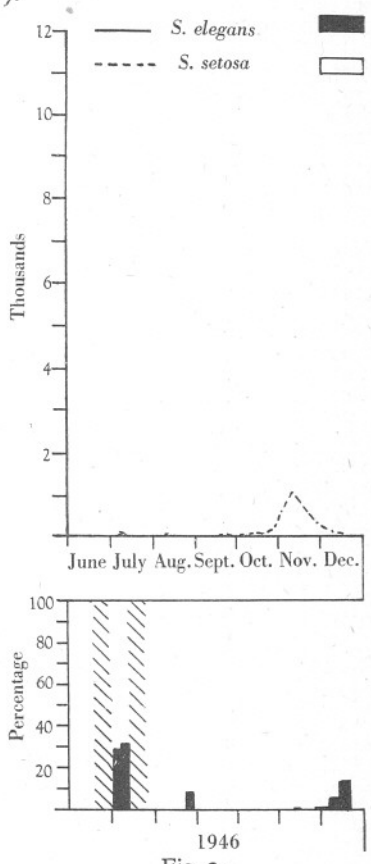

Fig. 2.

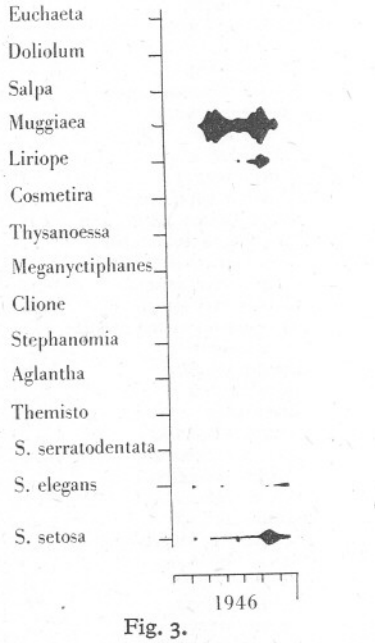

Fig. 3.

Fig. 2. Above, curves showing the actual abundance of *Sagitta elegans* (——) and *S. setosa* (-----) in half-hour oblique hauls with the 2 m. ringtrawl during the period June to December 1946. Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched.

Fig. 3. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the period June to December 1946. The *Muggiaea* species were practically entirely *M. atlantica*; a very small number of *M. kochi* occurred at times (see text).

It is noteworthy that in spite of the rest from fishing in the Channel during the war the numbers of pelagic young of summer spawners show no increase over those of the years just before the war.

REFERENCES

LEBOUR, MARIE, V., 1947. Notes on the inshore plankton of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 527–47.

RUSSELL, F. S., 1940. On the seasonal abundance of young fish. VII. The year 1939, January to August. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 265–70.

TABLE II. AVERAGE MONTHLY CATCHES OF POST-LARVAE PER HALF-HOUR

Oblique hauls with 2 m. ringtrawl, 1946

	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total young fish	35	190	39	..	2	6	2	274
Ditto, less Clupeids	12	125	12	..	+	2	+	152
All Clupeid spp.	24	64	27	..	1	4	2	122
Clupea harengus	..	..	..	..	..	..	..	..
Gadus pollachius	..	..	..	..	..	..	..	..
Gadus merlangus	..	1	..	..	..	..	..	1
Gadus minutus	..	2	..	..	..	..	..	2
Gadus luscus	..	..	..	..	..	+	..	+
Gadus callarius	..	..	..	..	..	..	..	..
Onos spp.	..	2	1	..	..	..	..	3
Molva molva	..	..	..	..	..	..	..	..
Merluccius merluccius	..	+	+	..	..	1	+	2
Raniceps raninus	..	..	..	..	..	..	..	..
Capros aper	..	..	..	..	..	..	..	..
Zeus faber	..	..	..	..	..	..	..	..
Arnoglossus sp.	1	1	1	..	..	..	..	3
Rhombus maximus	..	..	1	..	..	..	..	1
Scophthalmus norvegicus	1	2	..	..	..	..	..	3
Zeugopterus punctatus	..	..	..	..	..	..	..	..
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..
Pleuronectes limanda	..	..	..	..	..	..	..	..
Pleuronectes flesus	..	..	..	..	..	..	..	..
Pleuronectes microcephalus	..	..	..	..	..	..	..	..
Solea vulgaris	..	..	..	..	..	..	..	..
Solea variegata	1	7	..	..	..	..	..	8
Solea lascaris	..	1	..	..	..	..	..	1
Solea lutea	1	..	..	..	..	..	..	1
Serranus cabrilla	..	..	..	..	..	..	..	..
Caranx trachurus	..	+	1	..	..	..	..	1
Mullus surmulletus	..	..	..	..	..	..	..	..
Morone labrax	..	..	..	..	..	..	..	..
Ammodytes sp.	..	1	1	..	..	..	..	2
Ammodytes lanceolatus	..	2	..	..	..	..	..	2
Cepola rubescens	..	..	+	..	..	..	..	+
Callionymus sp.	6	37	2	..	+	..	..	45
Labrus bergylta	1	1	..	..	..	..	..	2
Labrus mixtus	..	..	..	..	..	..	..	..
Ctenolabrus rupestris	1	24	2	..	..	..	..	27
Crenilabrus melops	1	+	..	..	..	..	..	1
Centrolabrus exoletus	..	..	..	..	..	..	..	..
Trachinus vipera	..	+	1	..	..	..	..	1
Scomber scombrus	..	2	..	..	..	..	..	2
Gobius spp.	..	2	1	..	..	..	..	3
Lebetus scorpioides	..	..	..	..	..	..	..	..
Blennius ocellaris	..	..	..	..	..	..	..	..
Blennius pholis	..	1	1	..	..	..	..	2
Blennius gattorugine	1	38	1	..	..	..	..	40
Chirolophis galerita	..	..	..	..	..	..	..	..
Agonus cataphractus	..	..	..	..	..	..	..	..
Trigla spp.	..	2	1	..	..	..	..	3
Cottus sp.	..	..	..	..	..	..	..	..
Liparis montagui	1	..	..	..	..	..	..	1
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	..	..	..	..	..
Pipe fish	..	..	..	..	..	..	..	..

THE ASCIDIANS *TRIDIDEMNUM ALLENI* AND *DISTAPLIA GARSTANGI*, NEW SPECIES FROM THE PLYMOUTH AREA

By N. J. Berrill

From the Plymouth Laboratory and McGill University, Montreal

(Text-figs. 1—3)

Two ascidians have been collected in the region of Plymouth that do not fit the descriptions of known species sufficiently well to be identified with them. They are species of *Trididemnum* and *Distaplia*.

These genera are represented in waters around the British Isles only by *Trididemnum tenerum* (Verrill) and *Distaplia rosea* Della Valle. If *Trididemnum niveum* should be a valid species and not a synonym for *T. tenerum* as considered by Hartmeyer (1924), it also is probably present. Accordingly, any species that cannot be identified with these forms must either be new, or must represent geographical extensions of species not previously recorded. In this last respect, the possibility of the Mediterranean *Distaplia magnilarva* reaching the western Channel must be considered. As the following discussions indicate, the conclusions are that the two forms described here cannot be properly identified with any of the above and are to be treated as new species.

Trididemnum alleni n.sp. is named after the late Dr E. J. Allen, so long the inspiring and humane director of the Plymouth Laboratory, while *Distaplia garstangi* n.sp. is so named as a small tribute to Professor Walter Garstang for his pioneering interest in the ascidians of Plymouth waters.

TRIDIDEMNUM ALLENI **sp.nov.**

Colonies are usually small, less than a centimetre in greatest length, and about 3 mm. thick. They are brilliantly white, an appearance retained even in preserved specimens of long standing. The surface is uneven. They are commonly attached to *Eunicella* and larger hydroids such as *Antennularia* at depths of from 10 to 30 m., and have been recorded with certainty only from the Plymouth area of the English Channel.

The dense white opacity of the colony is due to the presence of enormous numbers of calcareous spicules lying beneath a more superficial layer of bladder cells, together forming a light-reflecting layer. The density is such that the contained zooids are very hard to distinguish, and stained sections were found to be necessary for adequate examination.

The zooid is, in general, like those of most didemnids, but is distinctive in the proportions of its thorax, oesophagus and abdomen. The abdomen is

large, the oesophageal region long and slender, while the thorax is exceptionally small. There are three rows of stigmata as in all species of *Trididemnum*. There are seven to eight stigmata per row. The endostyle is as wide as the small branchial sac as a whole. The branchial siphon has eight lobes. The atrial siphon is relatively wide, while absolutely small, and is almost flush with the mid-dorsal surface of the thorax, although the six lobes are still discernible. The thoracic organ on each side is small, without noticeably raised margin.

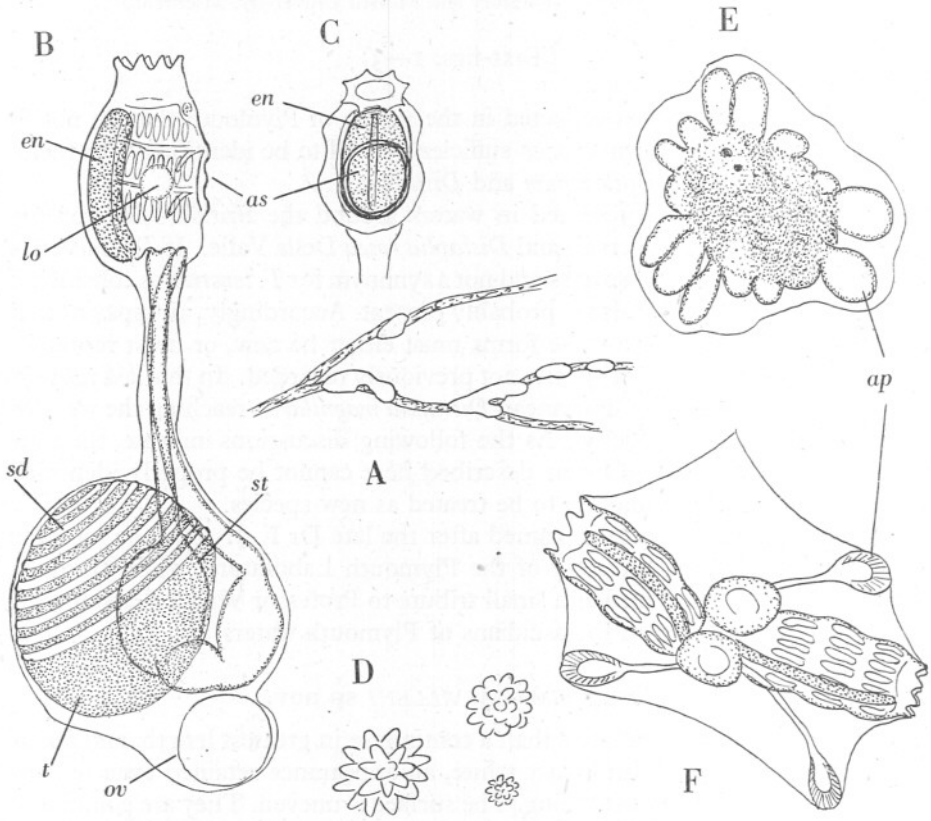

Fig. 1. *Trididemnum alleni*. A, colonies attached to *Gorgonia* branches, natural size. B, mature zooid showing relative proportions of thorax, oesophagus and abdomen, and general structure, from left side. C, thorax from dorsal side showing relative width of endostyle. D, spicules from common test. E, metamorphosing larva with numerous epidermal ampullae. F, completely metamorphosed individual when just active, with oozooid and first blastozooid equally developed. *ap*, ampulla; *as*, atrial siphon; *en*, endostyle; *lo*, lateral organ; *ov*, ovary; *sd*, sperm duct; *st*, stomach; *t*, testis.

The oesophageal region is very narrow and is as long as, or longer than, the thorax. The abdomen is relatively large, a great part consisting of the comparatively enormous testis. The sperm duct coils spirally around the single undivided testis about eight times. The epidermal ampullae, growing from the

mid-abdominal region, are small and hardly project beyond the silhouette of the whole zooid. They were seen only in sectioned material.

The above description is accordingly of a form that can hardly be identified with either *Tridemnum tenerum* or *T. niveum*. Hartmeyer assumes *T. niveum* to be a synonym of *T. tenerum*, though it is not at all certain that this is so. They are undoubtedly very similar. *T. tenerum* may contain spicules or may be entirely free of them. *T. niveum*, recorded with certainty only from the Mediterranean, and the French Atlantic coast, possesses the same striking external appearance of the form here described, which in fact is the only reason for suspecting that they may be identical.

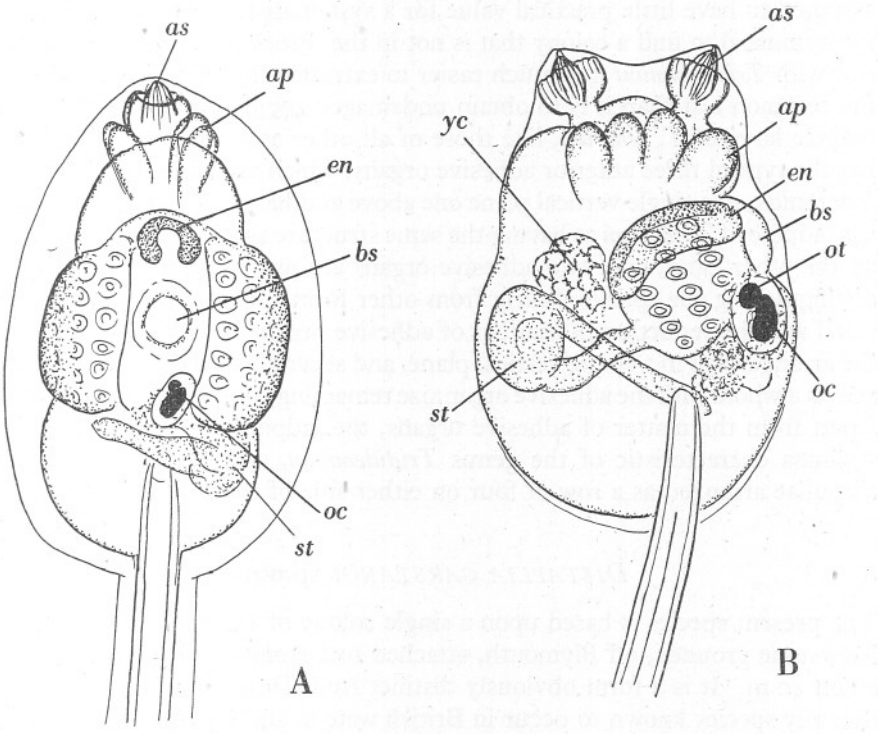

Fig. 2. Tadpole of *Tridemnum alleni*. A, from dorsal side. B, from left side. *ap*, ampulla; *as*, atrial siphon; *bs*, branchial siphon; *en*, endostyle; *oc*, ocellus; *ot*, otolith; *st*, stomach; *yc*, yolky cells associated with subsequent development of first blastozooid.

Lahille (1890), describing *T. niveum*, speaks of lateral thoracic organs being very clearly seen, and of five epidermal ampullae with voluminous terminals. In the Plymouth form both of these structures, though present, are extremely difficult to distinguish. In *T. tenerum* they are also strongly developed, so that *T. alleni* differs from both the other species in the same respect. According to Lahille, and to Harant & Vernières (1933), *T. tenerum* and *T. niveum* differ from one another not only in zooid proportions but in that the former has a

sperm duct with about a dozen spiral turns, the latter only eight. This has been confirmed for *T. tenerum* taken at Plymouth. So it only remains to discuss the question of identity between *T. alleni* and *T. niveum*. If Harant's illustration of *T. niveum* is accepted as typical, the body proportions are the reverse of *T. alleni*, the thorax being considerably larger than the abdomen and the oesophageal region being shorter than either. Moreover, the atrial siphon is situated in a decidedly more posterior position relative to the anus and rows of stigmata. Accordingly, on grounds of adult structure alone, identity of *T. alleni* with either *T. tenerum* or *T. niveum* is rejected.

The tadpole larvae are even more distinctive. As a rule, larval characters are assumed to have little practical value for a systematist, but in didemnids it is most unusual to find a colony that is not in the throes of sexual reproduction, and with *Trididemnum* it is much easier to extract fully-formed tadpoles from the common test than it is to obtain undamaged zooids for examination. The tadpole larva of *T. tenerum*, like those of all other ascidians so far described, has the typical three anterior adhesive organs, which are arranged, as in other didemnids, in a single vertical plane one above another. Salensky (1895) shows the tadpole of *T. niveum* as having the same structure as *T. tenerum*. In *T. alleni* on the other hand, only two adhesive organs are present, a unique condition distinguishing the species clearly from other forms. The tadpole is relatively small and the reduction in number of adhesive organs is due probably first to the arrangement in a single vertical plane, and secondly to reduction in tadpole size as a whole with the adhesive organ size remaining comparatively unaffected. Apart from the matter of adhesive organs, the tadpole has the three rows of stigmata characteristic of the genus *Trididemnum*, and has eight epidermal ampullae arranged as a row of four on either side of the adhesive organs.

DISTAPLIA GARSTANGI **sp.nov.**

The present species is based upon a single colony of *Distaplia* taken from the Mewstone grounds, off Plymouth, attached to a stone amidst shell gravel, in about 40 m. It is a form obviously distinct from *Distaplia rosea* Della Valle, the only species known to occur in British waters, and it cannot be identified either with *D. magnilarva* Della Valle, a Mediterranean species that might conceivably reach the western end of the Channel, though there are no records of it from the west or north-west coast of France, or with *D. clavata* (Sars), a northern species that apparently does not extend south even into Scottish waters.

Zooids of *Distaplia* species do not differ very markedly from one another, and while generically they are very easily recognized, specific distinctions are relatively difficult. Colonies, however, show specific characteristics. In the present instance it is in the form of the colony that the distinction mainly lies; and since differences in both zooid and tadpole can with care be distinguished, the new species seems to be justified.

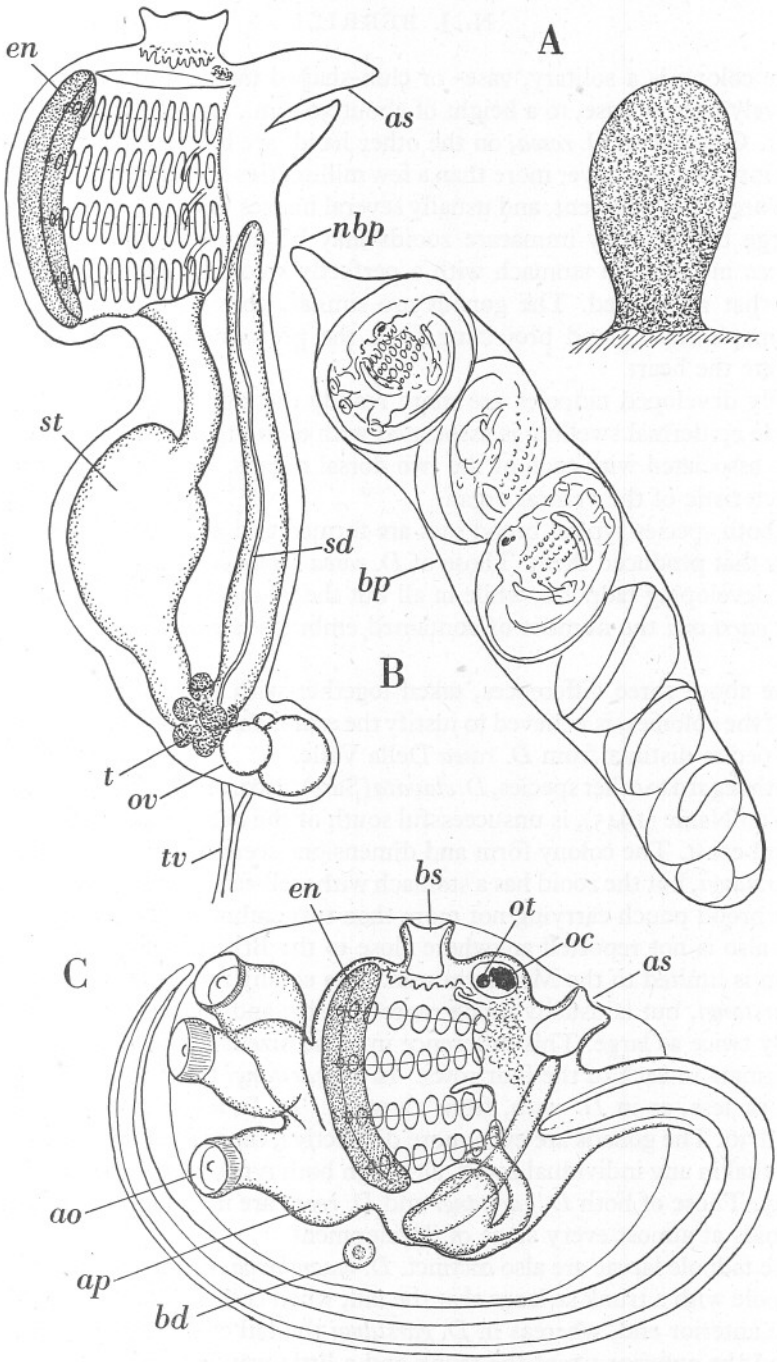

Fig. 3. *Distaplia garstangi*. A, whole colony, natural size. B, mature zooid with fully developed brood pouch just detached. C, tadpole from left side. *ao*, adhesive organ; *ap*, ampulla; *as*, atrial siphon; *bd*, bud; *bp*, brood pouch; *bs*, branchial siphon; *en*, endostyle; *nbp*, neck of brood pouch; *oc*, ocellus; *ot*, otolith; *ov*, ovary; *sd*, sperm duct; *st*, stomach; *t*, testis; *tv*, test vessels.

The colony is a solitary, vase- or club-shaped mass, growing erect from a relatively narrow base, to a height of about 30 mm., and of a yellowish-brown colour. Colonies of *D. rosea*, on the other hand, are low, consisting of pink or rose-tinted masses never more than a few millimetres in height, with a relatively broad area of attachment, and usually several masses united by narrow strands.

Large but sexually immature zooids may be distinguished from those of *D. rosea* in having a stomach with a perfectly smooth wall, instead of being somewhat reticulated. The gonads are similar, consisting in both forms of a hermaphrodite gland projecting from the posterior abdomen on the side opposite the heart.

Fully developed tadpoles are more readily distinguished. In *D. garstangi* a single epidermal swelling is associated with each organ. In *D. rosea* a single one is associated with each of the two dorsal organs, but a double ampulla is characteristic of the ventral organ.

In both species typical brood sacs are formed and may survive the parental zooids that produced them. Those of *D. rosea* rarely contain more than two or three developing tadpoles, while in all but the youngest pouch-bearing zooids of *D. garstangi* the number of contained embryos is rarely less than seven or eight.

The above three differences, taken together with the distinctive form and size of the colonies, is believed to justify the establishment of *Distaplia garstangi* as a species distinct from *D. rosea* Della Valle.

With regard to other species, *D. clavata* (Sars), according to Thompson (1934) and Van Name (1945), is unsuccessful south of the deeper water off the North Iceland coast. The colony form and dimensions seem to be similar to those of *D. garstangi*, but the zooid has a stomach with well-formed reticulate markings, and a brood pouch carrying not more than two embryos. *D. magnilarva* Della Valle also is not reported anywhere close to the British Isles, and as far as is known is limited to the Mediterranean. The colony form is not unlike that of *D. garstangi*, but is usually much more massive and contains zooids approximately twice as large. This difference in zooid size is reflected in the number of stigmata in each of the four rows. In *D. garstangi* the number is the same, more or less, as in *D. rosea*, from 12 to 15. In *D. magnilarva* it is between 25 and 30. The gonads are even more distinctive, those of *D. magnilarva* being unisexual in any individual zooid, although both types may coexist in the same colony. Those of both *D. garstangi* and *D. rosea* are invariably hermaphrodite in zooids at almost every stage of development.

The tadpole larvae are also distinct. *D. magnilarva*, as the name implies, has a tadpole with a trunk so large that the tail, when coiled, reaches only half way to the anterior end, whereas in *D. garstangi* the tail of the tadpole can extend around the anterior tip of the trunk and a little way beyond.

REFERENCES

DELLA VALLE, A., 1882. *Distaplia*, nouveau genre de Synascidies. *Arch. Ital. Biol.*, T. I, pp. 193–203.

HARANT, H. & VERNIÈRES, P., 1933. Tuniciers. In *Faune de France*, T. XXVII, pp. 1–99.

HARTMEYER, R., 1924. Ascidiacea, Pt. II. *Danish Ingolf. Exped.*, Bd. II, Pt. 7, pp. 1–275.

LAHILLE, F., 1890. *Recherches Tuniciers*. Toulouse.

SALENSKY, W., 1895. Ueber die Entwicklung von *Didemnum niveum*. *Mitt. zool. Stat. Neapel*, Bd. XI, pp. 488–630.

THOMPSON, H., 1934. Tunicata of the Scottish area. Pt. IV. *Fisheries, Scotland, Sci. Invest.*, 1934, No. I, pp. 1–44.

VAN NAME, W. G., 1945. The North and South American ascidians. *Bull. Amer. Mus. Nat. Hist.*, Vol. LXXXIV, pp. 1–476.

THE DEVELOPMENT AND GROWTH OF *CIONA*

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(Text-figs. 1—3)

Ciona intestinalis (L.) is probably the most cosmopolitan species of ascidians and has long been of general interest. The adult morphology has been well described in monographic form by Roule (1884), the physiology of the heart and circulation by Heine (1902), Enriques (1904) and Wolf (1932), of the nervous system by Magnus (1902), Hecht (1918, 1926), Cate (1928), Haffner (1933), and Bacq & Florkin (1935), and of the digestive system by Yonge (1925). Developmental studies include that of the early embryology by Conklin (1905), problems of fertilization by Morgan (1945) and Damas (1899, 1900). In no work, however, has there been a presentation of the entire *Ciona* organism from the tadpole stage through the critical post-larval stages to the young cionid ascidian. The present account portrays this period of development, together with a discussion of some significant but relatively obscure aspects of adult structure.

Eggs and the Rearing of *Ciona intestinalis*

While ascidians in general are difficult to rear to maturity under laboratory conditions, *Ciona* is relatively easy, and together with *Botryllus schlosseri* (Pallas) and *Diplosoma gelatinosum* (M.-Edw.) is liable to appear more or less spontaneously in large aquaria into which tadpoles may have been brought. Artificial fertilization is readily accomplished, and at almost any time of the year, since *Ciona* is sexually mature above a certain size and reproduction is seasonal only to the extent of the rhythm of the growth cycle. Normally eggs are set free spontaneously at dawn, although individuals kept in the laboratory may accumulate eggs and the oviduct become swollen. Eggs in good condition can usually be obtained from such forms at least for 2 or 3 days. In relatively young Cionas, with sexual maturity recently attained, eggs are greenish or yellow-green when viewed *en masse* in the oviduct. Later in the season a reddish tinge appears. The significance is not known.

Cionas usually are completely cross-fertile, the degree of self-fertility or sterility being more variable and the subject of extended investigations by Morgan (1945). Eggs sink in still water, but the buoyant 'floats' or outer follicle cells keep them in suspension with the slightest agitation. After fertilization the essential requirements for normal embryonic development are

the complete removal of excess sperm and oviductal fluid, by washing with fresh sea water, and above all, as Morgan (1945) has demonstrated, the use of glassware chemically and organically clean. Batches of abnormally developing *Ciona* embryo in apparently clean vessels are notoriously common. He has shown that abnormality is definitely due to a contaminating agent, traces of either cleaning fluid or organic and bacterial substances, and that washing in sea water and subsequent autoclaving is the best preventive procedure.

At usual room temperatures from 16 to 20° C., the eggs develop to the tadpole stage in about 24 hr. Hatching is effected by means of a proteolytic enzyme, the activity of which is inhibited below a *p*H of 7·0 (Berrill, 1929). Follicle cells and membranes may be artificially removed by crab-stomach juice diluted with sea water (about 1 part of 50) without significant damage to the fertilized egg or developing embryo (Berrill, 1932), and have been so removed by Morgan for experimental purposes.

The rearing of metamorphosed individuals to maturity is possible if a relatively large volume of water is employed. Cionas grow readily in an inverted bell jar with plunger, with the diatom *Nitschia* used as the basic food, and a dark paper shield used to control the amount of light and accordingly the density of the diatom culture. The usual nutrient salts are added from time to time to maintain the culture.

Tadpole Larvae and Metamorphosis

The small tadpole larvae (Fig. 1 A) are at first positively heliotropic and later negatively heliotropic and positively geotropic, the average free-swimming period being 12 hr. or more. The structure is comparatively simple, and the tadpoles have a relatively elongated trunk. The general structure of the tadpole and the process of metamorphosis have been well described by Willey (1893). His observations are mainly confirmed, including the frequent though not invariable secretion of a gas bubble at the anterior end of the attachment area, causing individuals to float towards the water surface, a phenomenon that accounts for the profusion of *Ciona* frequently found attached to the undersides of ships and floating warp, buoys, etc. Some additional detail is available, especially with regard to the sensory vesicle and tail. Willey's and the earlier accounts paid little attention to cellular constitution, and it is of some interest to bring information on *Ciona* into conformity with what is known concerning tadpoles of other species that have received more recent attention. The nature of the otolith as a single-celled organ has been recognized from the first, but the ocellus has been assigned an indefinite and excessive number of both retinal and lens cells. Actually, there are three lens cells with more or less spherical lenses, surrounded proximally by pigment cells in the form of a cup, into which extend the distal parts of eight or nine receptor cells as seen in optical section. What is significant is that this constitution of the sensory

vesicle, otolith and ocellus together, is the standard equipment of the great majority of ascidian tadpoles no matter how elaborate they may be in other ways. In the same manner the tail shows the generalized ascidian condition, namely, a central notochord consisting of yolk-containing vacuolated cells,

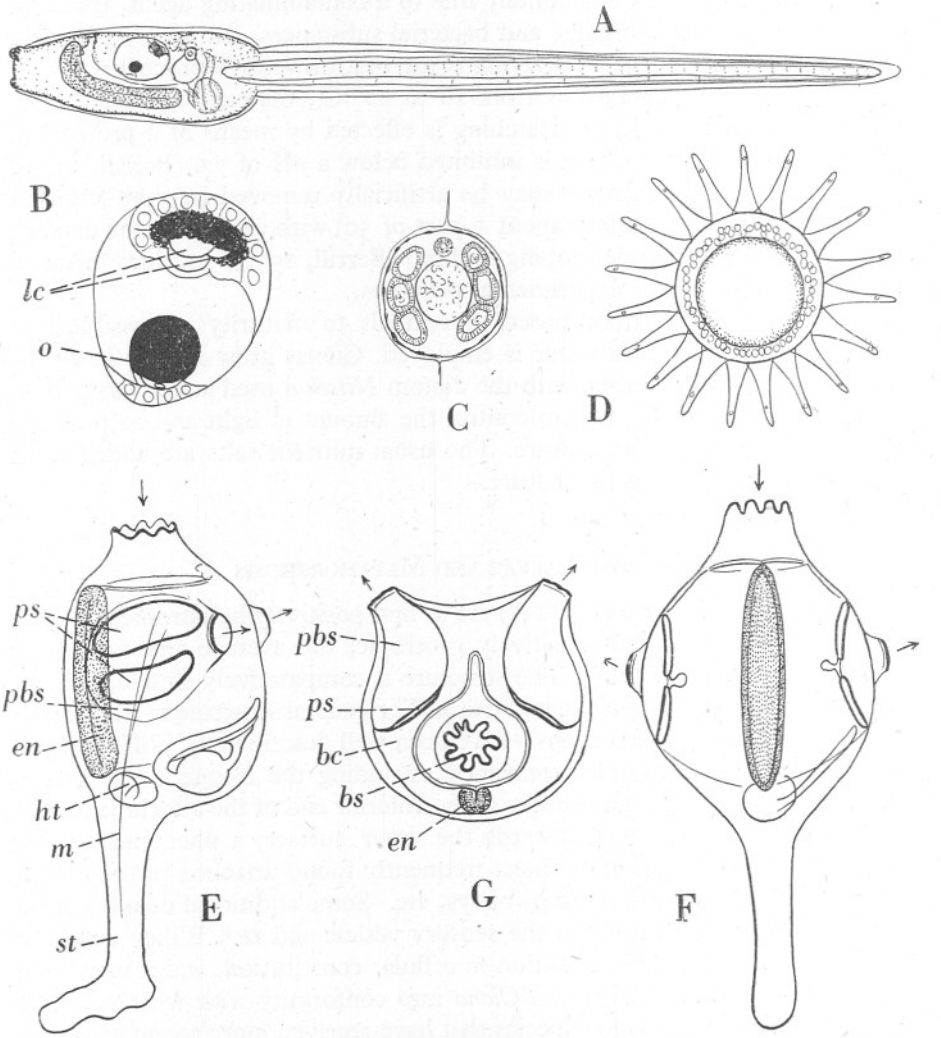

Fig. 1. *Ciona intestinalis*. A, tadpole larva. B, sensory vesicle of tadpole with unicellular otolith and ocellus with three lens cells. C, cross-section of tail showing central notochord, dorsal neural tube, and three muscle cells on each side. D, egg with characteristic 'floats' or outer follicle cells resting on membrane, and inner continuous layer of 'test' or inner follicle cells. E, first ascidian stage, with functional systems, from left side. F, the same from ventral or back side. G, the same from anterior or upper side. *bc*, branchial chamber; *bs*, branchial siphon; *en*, endostyle; *ht*, heart; *lc*, lens cells; *m*, longitudinal muscle; *o*, otolith; *pbs*, peribranchial sac; *ps*, protostigmata; *st*, stalk; ingoing arrow denotes the branchial siphon, outgoing arrows the two peribranchial siphons.

about forty in number, arranged in a single row, with a band of muscle tissue on each side, each consisting of three cells in cross-section, the cells having a central endoplasmic region containing the nucleus, and a cortical fibrillated contractile zone. The origin of the primary gill slits and the rotation of the main body axis during metamorphosis have been described in detail by Willey. The region between the endostyle and the anterior tip of the tadpole bearing the three adhesive papillae undergoes a marked extension, with a relative growth of the antero-dorsal epidermis. What Willey calls the pre-oral lobe becomes the stalk of attachment. It consists of epidermis, and the bilateral origin of the loose mesenchyme cells contained within it hardly justifies Willey's interpretation of them as homologues of pre-oral coelomic diverticula.

The Functional Ascidian

The completely metamorphosed individual has a beating heart, which shows the characteristic rhythmical reversal from the first, a pair of active protostigmata on each side, and a contractile longitudinal muscle extending from the trunk into the stalk. This stage has been previously illustrated, both by Willey (1893) and Berrill (1929), but its significance has been underestimated. It may well represent a primitive stage in ascidian evolution, no longer sexually mature, but retaining two features that later become greatly modified. One of these, the existence of protostigmata in place of the rows of definitive stigmata characteristic of the larger individuals, has long been the subject of description and speculation, the main emphasis having been upon the mode of origin of new protostigmata, and interpretation of tongue bars in an effort to establish homology with *Amphioxus* and *Balanoglossus*. The stage presents greater interest when the correlation of protostigmata with the persistence of the paired peribranchial siphons is recognized. The number of protostigmata on each side slowly increases with growth and extension of the branchial and peribranchial sacs until six are attained. This is a prolonged developmental phase that terminates more or less suddenly as a critical size is reached. During a relatively short developmental period, two changes occur together to give the typical ascidian condition. The six protostigmata each divide, first into two, then four, and finally eight definitive stigmata, while the pair of peribranchial siphons fuse to become the single mid-dorsal atrial siphon. On the one hand lateral peribranchial siphons and protostigmata are definitely correlated, and on the other rows of definitive stigmata and a single atrial siphon. A similar condition occurs in species of *Ascidia*, *Phallusia*, *Ascidiella*, *Corella* and *Diazona*.

Other changes take place during the growth period of what may be called the first ascidian form. While the number of protostigmata increases, the number of longitudinal muscle strands also increase from one to six or seven, the strands thereafter only increasing in individual thickness and not in number.

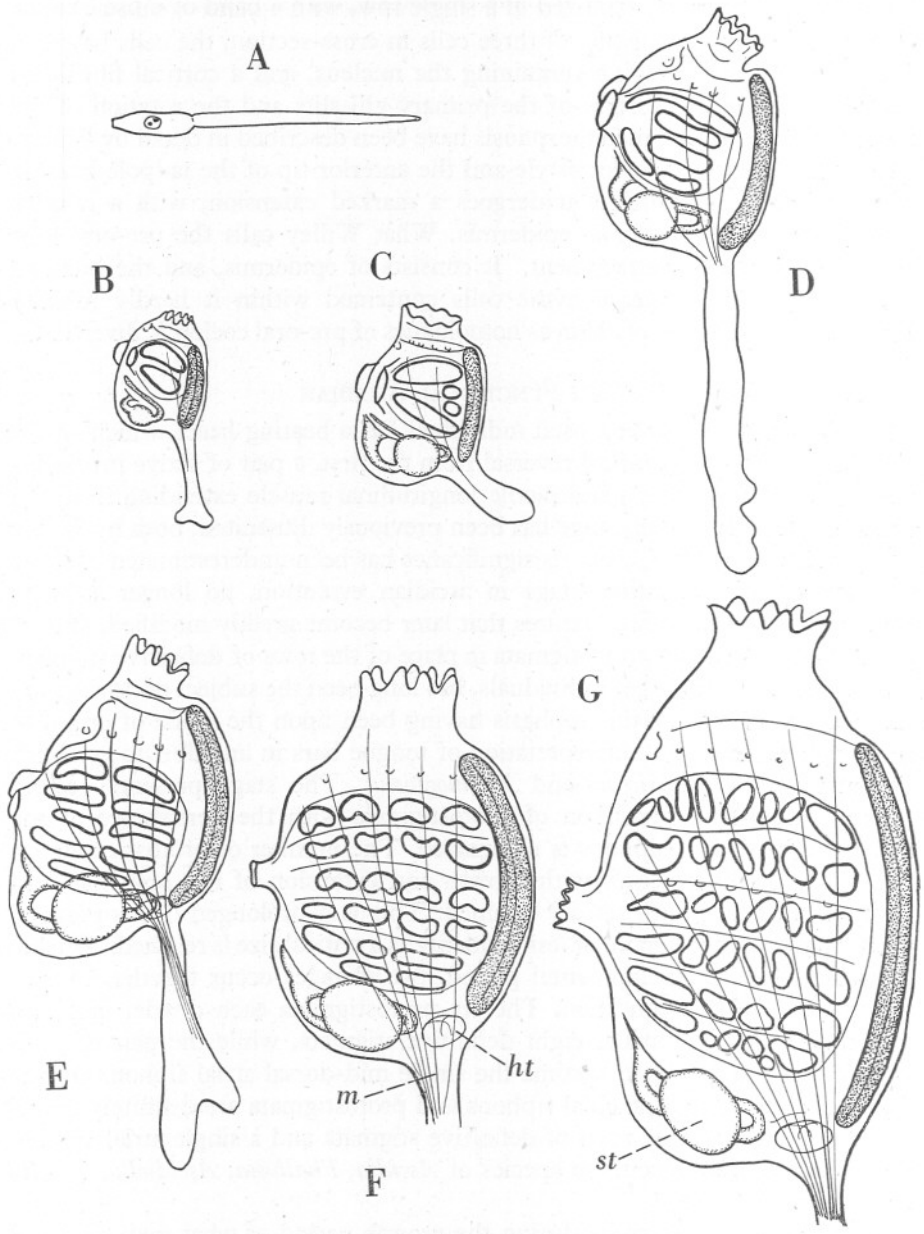

Fig. 2. *Ciona intestinalis*. A, tadpole drawn to same scale as remaining figures. B, C, D, three stages in growth of first ascidian stage with paired peribranchial siphons. E, F, G, three stages showing transition from first ascidian stage to second stage with single median atrial siphon, six rows of definitive stigmata, and final number of muscle bands. *ht*, heart; *m*, muscle bands; *st*, stomach.

Heart, Epicardium and Pyloric Gland

The heart develops, according to Damas (1899), as a mass of mesenchyme cells situated near the ventral endoderm and not derived from it, as thought by Willey. A pericardial vesicle is formed, one side of which invaginates to form the contractile tissue or heart proper. Willey concludes that the tunicate heart is not homologous with that of vertebrates since *Amphioxus* lacks a heart and pericardium, an assumption of a phyletic sequence not necessarily valid. Whatever the relationship may be, it is significant that the heart opens anteriorly into the subendostylar blood vessel, possibly homologous with and at least equivalent in position to the ventral aorta of other chordates, and that posteriorly it connects with vessels distributed over the alimentary canal. When first active it occupies the space between the bend of the intestine and the base of the endostyle. The heart itself, as in all tunicates, is structurally peculiar, apart from the characteristic rhythmical reversal. The blood flows, not through a true cardiac tube, but along a deep longitudinal invagination of the pericardial wall, a functional canal being formed by approximation of the lateral lips to form the 'raphe' of the heart.

With growth of the individual, and noticeable during the first ascidian stage, the heart and pericardium grow not only in absolute size but relatively to the distance between the intestine and endostyle base. The nature of this growth is complex and in it may lie the answer to the question, whether the cionid visceral topography is primitive or derived from the diazonid. Growth occurs from the middle region with the relative position of the two ends of the heart remaining unaffected. The posterior side of the pericardium grows ventrolaterally in such a way that the invaginated cardiac canal is drawn out as a V-shaped tube. It may be more correct to say that the cardiac tube extends between two fixed points and accordingly inevitably develops a V-shaped flexure, and that the pericardial wall necessarily keeps pace with its growth. On the other hand, the anterior wall of the pericardium grows no more than the distance between the intestine and endostyle, so that actually only the cardiac invagination becomes V-shaped.

The epicardia or perivisceral sacs have been variously interpreted. Their development is best described by Damas (1899). They appear during the first ascidian stage as broad posterior extensions of the pharynx, one on each side, enveloping the digestive canal and heart. As growth proceeds they extend posterior to the viscera to form large perivisceral cavities, one enveloping the heart, intestine, right side of the stomach, and the developing gonad, and the other mainly the left side of the stomach. They effectively form a pair of visceral body cavities, with the visceral organs suspended from one another or from the body wall by mesenteries consisting of two epicardial epithelia with enclosed mesenchymal tissue. The openings to the pharynx become narrower but remain as relatively large communications, and there can be no doubt of

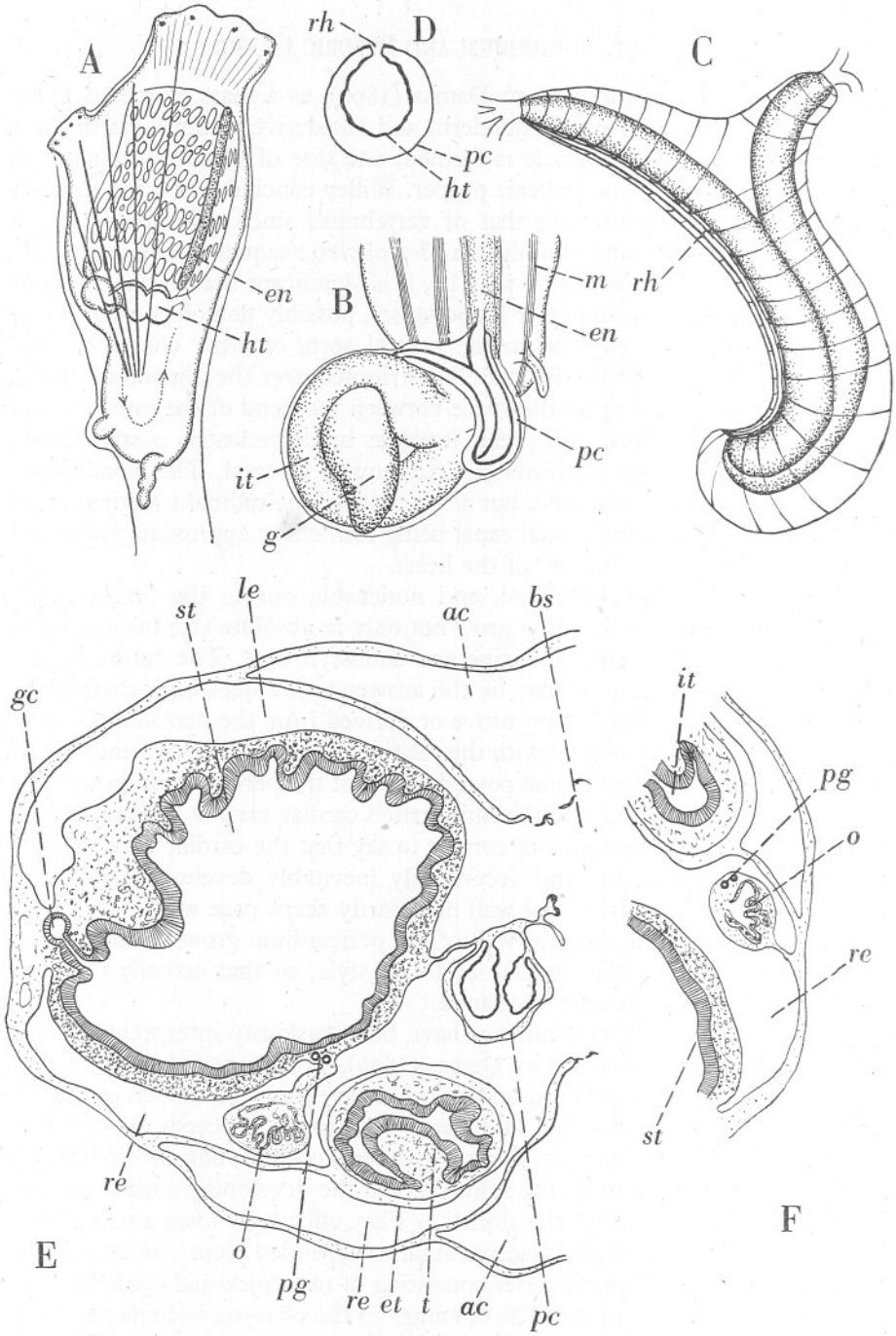

Fig. 3.

an exchange of fluid. Roule (1884) looked upon the perivisceral cavities as primitive but corresponding to the primary blastocoelic cavity of the larva. Newstead (1893) and Garstang (1928) recognize the homology with the epicardium of the other forms as suggested by Van Beneden & Julin (1886) but regard the latter condition the more primitive and the epicardium primarily a budding organ. Kupffer's original interpretation (1870) of the epicardial sacs as homologues of the vertebrate coelom, even though based on a faulty conception of their connexions, has never received adequate consideration and a strong case can be made out for this point of view.

Two other visceral structures are of some interest, the pyloric gland and the gastric caecum. Ascidians in general, together with the Thaliaceans, have a so-called pyloric gland of completely obscure function, arising as a single or bifurcating duct from the wall of the stomach near its junction with the intestine, which extends to and ramifies over the wall of the adjacent loop of the intestine as a system of fine canals. If the intestinal distribution is functional and not merely of topographic convenience, it suggests some sort of recovery process from the wall of the intestine into the cavity of the stomach. In any event, in view of its virtual universal occurrence among Tunicates, the absence of any description or illustration in Roule's minutely detailed and accurate monograph raised the question whether it did exist in *Ciona*, a point of some importance if *Ciona* should appear to be an ascidian prototype. Willey illustrates a young *Ciona* just after metamorphosis in which a typical pyloric gland appears, but no gland is discernible in a dissected adult. Sections of a 10 mm. individual, however, demonstrate its presence and the reason for its obscurity in the adult condition. The ducts leading from the stomach to the intestine are caught between two opposing sheets of the epicardium and are confined within the epicardial mesentery joining the stomach and the ovary, and the ovary and the intestine. The ducts are forced down into the tissue surrounding the ovarian epithelium and in certain sections appear to be structures isolated as part of the gonad itself. Willey calls the pyloric gland the caecum and concludes that the pyloric gland of ascidians and the hepatic caecum of *Amphioxus* are homologous. This may or may not be, but there is another diverticulum of the stomach wall usually and more accurately called

Fig. 3. *Ciona intestinalis*. A, later stage showing subdivision of six primary rows of definitive stigmata into double rows, relative growth of heart, and course of circulation in stalk. B, posterior part of mature *Ciona* removed from tunic, showing typical V-shaped heart and its relationship with the endostyle and intestine. C, enlarged view of heart and pericardium, showing V-shaped heart within nondivided pericardium. D, cross-section through heart near one end showing involution of heart within pericardium, and 'raphe' of heart. E, entire longitudinal section through posterior region of 10 mm. individual. F, partial section of same, several sections from E, showing passage of ducts of pyloric gland from stomach wall through gonad mesentery toward intestine. *ac*, atrial chamber; *bs*, branchial sac; *en*, endostyle; *et*, epicardial lining enveloping intestine; *g*, gonad; *gc*, gastric caecum; *ht*, heart; *it*, intestine; *le*, left epicardial cavity; *m*, muscle band; *o*, ovarian epithelium; *pc*, pericardium enveloped by epicardia; *pg*, ducts of pyloric gland; *re*, right epicardial cavity; *rh*, raphe of heart; *st*, stomach; *t*, typhlosole.

the gastric caecum that has an equal claim. It is shown in the post-larval stages of *Corella parallelogramma* (O. F. Müll.) figured by Hŭus (1924), and can be seen in sectioned material of *Ciona* in young individuals as a tubular outgrowth from the posterior wall of the stomach, ending blindly as a small round sac. Its function is unknown and its homologies equally obscure.

During the course of later development of *Ciona intestinalis* f. *typica*, the post-abdominal stalk dwindles and individuals are attached by the base of the abdominal region. In the other two varieties, *longissima* and *gelatinosa*, the stalk survives, merely becoming relatively wide and, according to Arnbach & Brien (1932), is essentially equivalent to the post-abdomen of polyclinids, with the longitudinal body muscles extending to its tip and the epicardium of the left side extending into it between the afferent and efferent blood sinuses.

REFERENCES

ARNBACH-CHRISTIE-LINDE, A. & BRIEN, P., 1932. Remarques au sujet du postabdomen des Cionidae. *Ann. Soc. Zool. Belg.*, T. LXIII, pp. 41–53.

BACQ, Z. M. & FLORKIN, M., 1935. Mise en évidence, dans le complexe 'ganglion nerveux glande neurale' d'une ascidie (*Ciona intestinalis*), des principes pharmacologiquement analogues à ceux du lobe postérieur de l'hypophyse des vertébrés. *Arch. Internat. Physiol.*, T. XL, pp. 422–8.

VAN BENEDEN, E. & JULIN, C., 1886. Recherches sur la Morphologie des Tuniciers. *Arch. Biol.*, T. VI, p. 237–476.

BERRILL, N. J., 1929. Studies in tunicate development. Pt. I. General physiology of development of simple ascidians. *Phil. Trans. Roy. Soc. Lond.*, B, Vol. CCXVIII, pp. 37–78.

—— 1932. Mosaic development in the Ascidian egg. *Biol. Bull.*, Vol. LXIII, pp. 381–6.

CATE, J. T., 1928. Contribution à la question de la fonction du système nerveux de *Ciona intestinalis*. *Arch. Néerland Sci. La Haye*, T. XIII, pp. 391–401.

CONKLIN, E. G., 1905. The organization and cell lineage of the ascidian egg. *Journ. Acad. Nat. Sci. Philadelphia* (2), Vol. XIII, pp. 1–119.

DAMAS, D., 1899. Les formations épicardiques chez *Ciona intestinalis* (L.). *Arch. Biol.*, T. XVII (1901), pp. 1–25.

—— 1900. Étude du sac branchial chez *Ciona intestinalis* (L.). *Arch. Biol.*, T. XXXVI (1901), pp. 1–32.

ENRIQUES, P., 1904. Della Circolazione sanguigna nei Tunicati (*Ciona intestinalis*). *Arch. Zool. Ital.*, Vol. II, pp. 11–17.

GARSTANG, W., 1928. The morphology of the Tunicata, and its bearings on the phylogeny of the Chordata. *Quart. Journ. Micr. Sci.*, Vol. LXXII, pp. 51–187.

HAFFNER, K. VON, 1933. Die überzähligen Siphonen und Ozellen von *Ciona intestinalis* (L). *Zeitschr. wiss. Zool.*, A, Bd. CXLIII, pp. 15–52.

HECHT, S., 1918. The physiology of *Ascidia atra* Leseur. *Journ. Exp. Zool. Philadelphia*, Vol. XXV, pp. 229–99.

—— 1926. The effect of exposure period and temperature on the photosensory period of *Ciona*. *Journ. Gen. Physiol.*, Vol. VIII, pp. 291–301.

HEINE, P., 1902. Untersuchungen über den Bau und die Entwicklung des Herzens der Salpen und der *Ciona intestinalis*. *Zeitschr. wiss. Zool.*, Bd. LXXIII, pp. 429–95.

HŬUS, J., 1924. Genital Organe und 'ganglio-genital Strang' bei *Corella parallelogramma* Mull. *Nord. Skr. Selsk. Kristianna*, No. 19, pp. 1–50.

JUST, E. E., 1934. On the rearing of *Ciona intestinalis* under laboratory conditions to sexual maturity. *Yearb. Carnegie Inst. Washington*, 1933, 270 pp.

KUPFFER, C. W., 1870. Die Stammverwandtschaft zwischen Ascidien und Wirbelthieren. Nach Untersuchungen über die Entwicklung der *Ascidia canina* (Zool. dan.) = *Ciona*. *Arch. mikr. Anat.*, Vol. VI, pp. 115-72.

MAGNUS, R., 1902. Die Bedeutung des Ganglions bei *Ciona intestinalis*. *Mitt. Zool. Stat. Neapel.*, Bd. XV, pp. 483–6.

MORGAN, T. H., 1938–42. The genetic and the physiological problems of self-sterility in *Ciona*. I–IV. *Journ. Exp. Zool.*, Vol. LXXVIII, pp. 271–334; Vol. LXXX, pp. 19–80; Vol. XC, pp. 199–228.

—— 1945. The conditions that lead to normal or abnormal development of *Ciona*. *Biol. Bull.*, Vol. LXXXIII, pp. 50–62.

NEWSTEAD, A. H. L., 1893. On the perivisceral cavity of *Ciona*. *Quart. Journ. Micr. Sci.*, Vol. XXXV, pp. 119-28.

ROULE, L., 1884. Recherches sur les Ascidies simples. *Ann. Mus. Hist. Nat. Marseilles*, Zool., Vol. II, pp. 7–270.

WILLEY, A., 1893. Studies on the Protochordata. I. On the origin of the branchial stigmata, preoral lobe, endostyle, atrial cavities, etc., in *Ciona intestinalis*, L., with remarks on *Clavelina lepadeformis*. *Quart. Journ. Micr. Sci.*, Vol. XXXIV, pp. 317–60.

WOLF, E., 1932. Pulsation frequency of the advisceral and abvisceral heartbeat of *Ciona intestinalis* in relation to temperature. *Journ. Gen. Physiol.*, Vol. XVI, pp. 89–98.

YONGE, C. M., 1925. Studies on the comparative physiology of digestion. III. Secretion, digestion and assimilation in the gut of *Ciona intestinalis*. *Brit. Journ. Exp. Biol.*, Vol. II, pp. 373–88.

THE BIOLOGY OF *CRANGON VULGARIS* L. IN THE BRISTOL CHANNEL AND SEVERN ESTUARY[1]

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(Text-figs. 1–20)

CONTENTS

Introduction

This paper records observations on the biology of the common shrimp, *Crangon vulgaris* L. The bulk of the work consisted of field observations and measurements, but supplementary evidence on such matters as food, habits, moulting, growth, mating, etc., was obtained in the laboratory and in aquarium tanks. All field work and measurements were carried out by one of us (A.J.L.) and the general direction of the research, analysis of some of the results and the preparation of this paper by the other (C.M.Y.). Acknowledgements for important assistance are due to Mr M. Haines of Berkeley, Mr R. Knapp of Oldbury, Mr Pullen of Severn Beach, Messrs Selwick and Brewer of Stolford, Mr Stone of Burnham-on-Sea and Messrs Watts of Weston, all of whom collected specimens. Mr McGurk, Bailiff to the Severn Fishery Board, kindly permitted one of us (A.J.L.) to accompany him on visits to the fisheries.

[1] Studies on the Biology of the Bristol Channel, No. 17.

Various members of the Staff of the Department of Zoology, University of Bristol, assisted in measuring the shrimps, more than 28,000 of which were dealt with. The essential financial assistance was provided by the Leverhulme Trustees and by the Colston Research Society of the University of Bristol.

Collection and Measurement

Initially, in August 1937, the upper part of the southern shores of the Estuary of the Severn was surveyed; later, in December, Weston was included and in the following spring work was extended to Bridgwater Bay. The shrimps caught in one putt (see next section for a description of this) during one tide were placed in formalin, twice a week during 1938 and 1939 and once a week in 1940, by Mr R. Knapp of Oldbury on Severn (see Fig. 1, station 2). The samples obtained from Bridgwater Bay (Stolford, station 6) were of 'unriddled' shrimps. These were taken monthly at spring tides and consisted of 500–1000 shrimps. Periodic visits were paid to the collecting areas so that catches could be examined. Temperatures and salinities were recorded. Maximum and minimum thermometers were maintained in the estuary at Berkeley (station 1) and Oldbury (station 2) during 1938 and 1939. Temperature records from Weston were kindly supplied by the Medical Officer of Health.

All shrimps were measured and where possible (i.e. above 20 mm. long) the sex determined. Measurement was from the tip of the rostrum to the end of the telson and carried out on a graduated glass plate illuminated from below. The exclusion of direct daylight by a board fixed along one side made accurate measurement easier.

General Description of the Fisheries

The Estuary of the Severn. This region possesses one of the largest recorded range of tides in the world. Extensive mud flats extend along the south bank of the Channel from Watchet to Berkeley (see Fig. 1). Invertebrates living in this mud provide food for fish and shrimps. The higher reaches of the estuary are more sandy and rocky as the river is here confined by high banks and the strong current prevents the finer silt from settling. Since prehistoric times the local inhabitants have engaged in fishing. There are references in the Domesday Book to 72 places where 'fixed engines' were fished. The majority of these have long since disappeared and some of the few remaining are now falling into disuse. Those still fished usually fail to support the fishermen throughout the year.

Fish and shrimps are taken by means of nets and basket filters ('fixed engines') which are secured to stakes driven into the substratum of the foreshore. They are situated so that a strong tidal current flows through them and they are usually visited at each low tide by the fishermen although when the catches are poor the night tides are missed. An excellent general account of these fisheries is given by Matthews (1933).

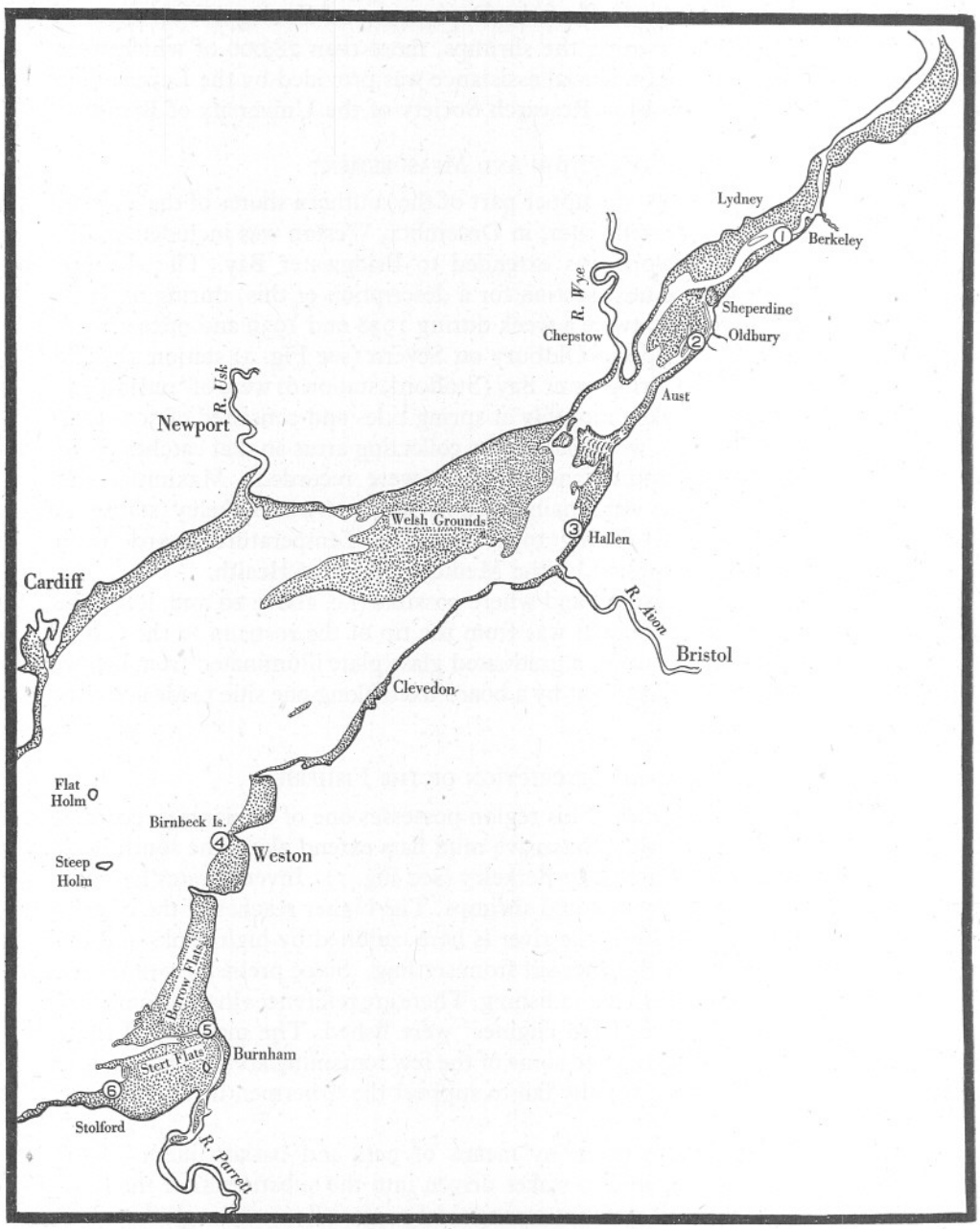

Fig. 1. Map of the Severn Estuary and upper reaches of the Bristol Channel showing the positions of stations 1–6.

At the three collecting stations in the Severn (1–3) only baskets are in use. These are either putchers or putts, the former being used during the summer for trapping salmon while the putts are maintained throughout the year for catching shrimps and small fish. The putt is conical and up to 15 ft. long with a diameter at the mouth of 5–7 ft. It consists of three parts. The front part is called the kype. The central part, or butt, contains a valve of split withies which retains the larger fish. The hindermost part is known as the forewheel, it also possesses a valve and is closed by a wooden bung. The kype is held in position between six stakes while the butt and forewheel are fixed in the cleft of two Y-shaped stakes. The shrimps are removed by loosening the forewheel and removing the bung.

At Hayward Rock near Berkeley (station 1) there is one of the best natural configurations in the estuary for basket fishing. The natural curve of the river bank opposite directs a very strong current inside Table Rock and over Hayward Rock. The Black Rock, about one mile higher up, tends to pull the water in towards the south bank and at the same time the sand banks on the north side push the current over. Both factors act as the tip of a funnel forcing the current to flow between Table Rock and the south bank. Hayward Rock tends to divert this back again to the main stream and an artificial hedge of withy and hazel helps to complete the funnel formation. Twenty putts are fished here.

An important fishery has existed since the fifteenth century at Oldbury (station 2), a plan of that date showing ranks of baskets in similar positions to those occupied now. The salmon pool is over two miles long. The baskets are placed where a strong subsidiary current drains the pool. Forty putts are staked in two ranks.

At Hallen (station 3) there was until recently a fishery consisting of 120 putts. Owing to the exposed situation, these were of stronger construction and of more open mesh work while the mouths were of smaller diameter.

The Bristol Channel. In this paper a necessarily arbitrary distinction is made between the Severn Estuary above Avonmouth and the Bristol Channel to the west of this port. At the three stations (4–6) in the Channel the hose type of shrimp net is used. The net is cone-shaped with a rectangular mouth of $5\frac{1}{2}$ ft. long by 4 ft. high. Two circular hoops of cane hold the cod end open and there is a non-return valve of netting inside; a reeving rope draws together the meshes round the rear opening and passes to a stake behind. The belly of the net is of 1 in. mesh netting with $\frac{1}{2}$ in. mesh at the cod end. The mouth of the net is tied at the four corners to two stakes, one at each side.

There still exist three fisheries in the Bristol Channel. About 40 shrimp nets fish the ebb tide at Anchor Head, Weston-super-Mare (station 4). This fishery is not worked throughout the whole year. At Burnham-on-Sea (station 5) a rank of 12 nets was maintained by an elderly fisherman; he has since died and the fishery has probably lapsed. Samples of shrimps were frequently

taken from this fishery when they were unobtainable elsewhere. The largest shrimp fishery is at Stolford (station 6). Here about 400 nets are staked, but within living memory over 1000 were in use. A plan prepared in 1770 and in the possession of Lord Clifford shows over fifteen divisions of the Ooze with further subdivisions of fishing rights. The nets are more than a mile from the shore on the widely extended mud flats and the mud is so deep that peculiar sledges called 'mud horses' are pushed by the fishermen. These serve the double purpose of preventing the men from sinking far into the mud and of carrying the catch back to the shore. Many hundredweight of shrimps are taken daily in the summer.

Conditions of Life

Crangon vulgaris is specialized for life on a soft substratum of sand or mud. Havinga (1929) states that it rests quietly buried in the substratum during the day and feeds by night. This is certainly what happens in the aquarium but in the Bristol Channel and Estuary of the Severn there is no difference between the catches of the day and the night tides. Probably the exceptionally high turbidity of the water nullifies the effect of light. But the animals probably always rely on burrowing to escape from their enemies.

When placed in aquaria with sand on the bottom, shrimps remain buried during the daytime although the long flagellae of the second antennae may lie flat along the surface. These are used as tactile organs when seeking food. When burrowing the animal makes shuffling movements with the pereiopods, extending these slightly outward and backward, the pleopods at the same time beating rapidly. When a small hollow has been excavated, the animal alternately expands and contracts the branchiostegites thus forcing water out of the gill chambers and pushing the sand out and up around its sides. As a result the body sinks slowly down. Finally the flagellae of the antennae, with a breast stroke action, move sand around and over the back. The flagellae may also be withdrawn but the two small olfactory rami of the first pair of antennae always remain projecting vertically out of the sand and by their means food is detected. When walking along the surface the first three pairs of pereiopods are tucked away along each side of the mouth, the third pair, which project in front of it, being used as tactile organs. While swimming or walking, solid objects such as the walls of the aquarium, food and the like are tapped by the dactylopodites of these appendages. The last two pairs of pereiopods only are used for locomotion.

Although generally omnivorous, like most Decapoda, *Crangon* appears to prefer animal food. The mud flats it inhabits form a feeding ground for many small worms, molluscs and crustaceans. At Stolford a principal food appears to be *Nereis diversicolor* and shrimps have often been caught while eating worms longer than themselves. In the spring the thorax sometimes appears bright green due to ingested algae. This condition occurs locally and

shrimps taken two miles away may contain no algae. Ehrenbaum (1890) states that shrimps feed mainly on polychaetes, especially *N. pelagica*, and Havinga (1929) agrees with this. He also includes in their food, *Ulva lactuca* and *Enteromorpha intestinalis* and, in brackish water, *Corophium* sp., *Gammarus locusta* and *Mysis vulgaris*. These animals occur in the Channel and estuary and, together with small gastropods, bivalves, fish eggs and fry, form the food of *Crangon*.

The animal can withstand a wide range of temperature. The winter migration down channel, especially from the estuary, is, as shown below, due to inability to withstand low salinity combined with low temperature. Under aquarium conditions shrimps have survived after ice has formed over the surface of the undiluted sea water. Havinga (1930) states that *Crangon* can survive shore temperatures as high as 30°C. In the estuary at Oldbury, maximum numbers appeared after the temperature exceeded 10°C., reduction in numbers during June and July being a result of migration of berried females seaward before hatching of the larvae. At Stolford, in the Channel, the largest numbers were caught during July and August when temperatures rose as high as 20°C.

Crangon is euryhaline; Mathias (1938) found that death occurs after exposure to freshwater for 7–8 hr. but that animals (sex unstated) survive exposure for more than a day to sea water diluted by 255 times its volume of freshwater. The capacity to withstand low salinities is influenced by temperature, especially in connexion with development, as noted by Balss (1930) for a wide variety of decapod Crustacea, by Otto (1934, 1937) for *Heteropanope* and *Eriocheir*, by Broekhuysen (1936) who made a special study of the shore crab, *Carcinides maenas*, and later by Panikkar (1940, 1941) for *Leander serratus* and *Palaemonetes varians*. Caudri (1937) extended Broekhuysen's observations to *Crangon* and found that at a temperature of about 4°C. the optimum salinity for survival of young shrimps was 34‰ whereas at 18·9°C. lowest mortality was between 20 and 30‰. Broekema (1941), in a paper not seen until after the first draft of this paper was completed, has extended these findings greatly as a result of work prompted by the observations of Havinga (1930) on the seasonal migrations of *Crangon* in the Zuiderzee (prior to the closure of this by the dyke). She has confirmed Caudri's statement that the salinity optimum shifts downward with increasing temperature. For animals two years old it lies at 35‰ for a temperature of 3·5°C. and at 28–29 ‰ for temperatures between 20 and 22°C. For animals about one year old it lies at 18–19‰ for a temperature of 22°C., the optimum salinity apparently moving higher with increasing age. The salinity range for normal development was also influenced by temperature as Broekhuysen (1936) had already found for *Carcinides*.

Broekema also found that *Crangon* is to some extent homoiosmotic although changes in the osmotic pressure of the medium were reflected by smaller

changes in that of the body fluids, i.e. resembling *Leander serratus* and *L. squilla* (Panikkar, 1941). Like *Leander* spp., in normal sea water *Crangon* is hypotonic in respect to the medium, being isotonic with it at a salinity of about 21·5‰ at 20° C. and at a salinity of about 23‰ at 4° C. Experimental evidence indicated, moreover, that osmo-regulation proceeds more efficiently at high temperatures and indeed may be largely inhibited at low temperatures. This may provide the explanation of the inability of *Crangon* (and similar Decapoda) to withstand exposure to low salinities during the winter.

Although Broekema made certain observations on ovigerous females, no mention of the sex of the animals used in other experiments is made and they were presumably mixed. But as noted by Havinga (1930) and abundantly confirmed in this work (see Table IV), there is a marked difference between the sexes in their toleration of low salinities. The males are largely or completely absent fom the upper reaches of the Severn Estuary during the winter. This difference led to the carrying out of initial experiments on the effect of salinity on respiration in the two sexes. It was hoped in this way to get some indication of possible differences in the capacity for osmo-regulation in the two sexes.

Pure sea water, salinity *c.* 34‰, was diluted with glass distilled water and complete aeration ensured. Experiments were conducted in conical flasks containing 500 c.c. of water containing 0·5 % urethane. The animals were kept in water of the same salinity overnight to allow time for physiological adjustment and were anaesthetized with urethane 30 min. before the experiment began. Each experiment lasted 4 hr., the temperature being maintained always at 15° C. The oxygen content of the water was estimated before and after each experiment and the results converted into oxygen consumed per gram wet weight per hr.

The results are shown in Fig. 2. The females showed a higher respiratory rate down to 35 % normal salinity, below that it was higher in the males. These died at salinities below 10 % but females actually survived exposure to fresh pond water for several days. The lowest respiratory rate for the males was in water of 50-60 % normal salinity and for females 25 %. Oxygen consumption increased only moderately in higher salinities but rapidly in lower salinities, that for the males rising to 2·09 c.c. oxygen per hr. at 10 % salinity. While too much weight cannot be placed on these preliminary experiments (circumstances prevented their continuation), they do at least confirm the conclusions derived from field observations, namely that males cannot withstand such low salinities as females and that optimal salinity, at a temperature of 15° C., is higher for males than females. The powers of osmo-regulation in the male are not as great as in the female.

There is evidence from various sources of the effect of light on *Crangon*. Thus Havinga (1930) records that the animals remain swimming within a beam from an artificial source of light and so are easily caught. Plankemann (1935) found that light of short wave-length speeds up moulting, while Nouvel-

Van Rysselberge (1937) states that exposure during successive nights to artificial light has the opposite effect of delaying moulting. In the exceptionally turbid waters of the estuary and Channel it is very doubtful whether the small amount of light that can penetrate has any significant effect on the behaviour or metabolism of the shrimps.

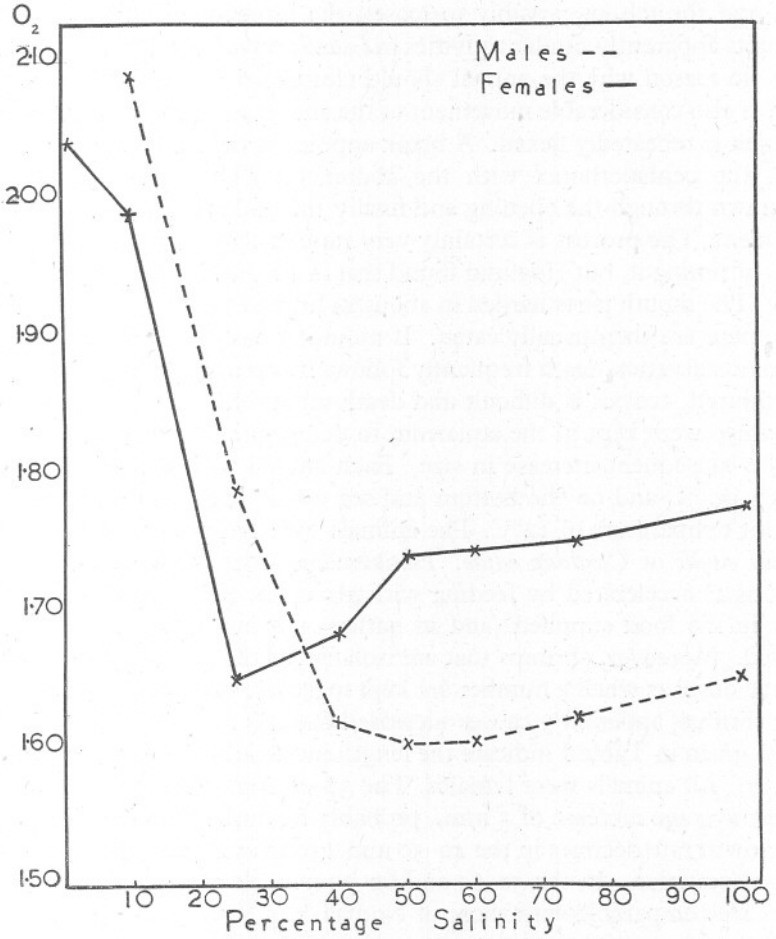

Fig. 2. Graph showing the effect on respiration of exposure of male and female *Crangon vulgaris* to varying salinities at 15°C. Figures for oxygen given in c.c. utilized per hr. per gram wet weight of animal; salinity in percentages of normal sea water.

Moulting and Growth

Crangon becomes more opalescent immediately before moulting; Vitzou (1882) noted a similar change in *Leander*. This is probably due to the formation of the new integument beneath the old one. Food is not eaten during two or three days prior to ecdysis which usually occurs at night. Höglund (1943) has

observed a similar period of starvation in *L. squilla* but finds that moulting may occur at any time throughout day or night. This difference may well be correlated with the different habits of the two animals, *Crangon* normally leaving the protection of the substratum only in darkness. During this preliminary period the chelipeds stroke the peduncules of the eyes, the antennal scales and the telson, possibly to loosen the integument although Höglund interprets apparently similar activities in *Leander squilla* as cleansing. But there seems no reason why the animal should cleanse what is about to be cast off. There is also considerable movement of the antennae and antennules while the abdomen is repeatedly flexed. A break appears at the intercalary piece which unites the cephalothorax with the abdomen. The head and thorax are withdrawn through the opening and finally the abdomen is freed by a quick movement. The process is certainly very rapid although there was no opportunity of timing it, but Höglund found that in *L. squilla* it takes only from 9 to 22 sec. The mouth parts harden in about 24 hr. and the softer parts of the cast integument are then usually eaten. If moulting has been preceded by a long period of starvation death frequently follows its occurrence. If the animal has been injured, ecdysis is difficult and death often follows.

Shrimps were kept in the aquarium to determine the frequency of ecdysis and the consequent increase in size. Each animal was placed in a tank with about $\frac{1}{2}$ in. of sand on the bottom and sea water was kept in circulation at a constant temperature of 12° C. The animals were fed daily with the tissues of *Mytilus edulis* or *Cardium edule*. Plankemann (1935) found that the rate of moulting is accelerated by feeding with glycogen, but as the content of this varies in the food supplied (and in nature) the influence of this cannot be assessed. Moreover, shrimps that are isolated, as these had to be, do not feed as voraciously as when a number are kept together; the constant movement of many shrimps apparently causes increased feeding in all.

Data given in Table I indicate the length increase after moulting during the summer. All animals were females. The 30–40 mm. length group shows the greatest average increase of 3 mm., probably because they are still immature. The growth rate declines in the 40–50 mm. group as more material is deflected to egg production. In the 50–60 and 60–70 mm. groups it is still less. These figures are comparable with those of Nouvel-Van Rysselberge (1937), namely 2·0–2·5 mm. increase at 30–40 mm., 2·5–2·0 mm. at 40–50 mm. and 1·5–1·0 mm. at 50–60 mm. lengths. This work was done during the summer at Monaco and the shrimps moulted every 10–12 days. Personal observations showed that at 12° C. shrimps moult at much longer intervals, 13–30 days or even more. There is much variation in both length increase and the duration of the intermoult period due, probably, to fluctuations in environmental factors. Nouvel-Van Rysselberge has shown that the rate of growth is less under aquarium conditions than in nature.

Females above 50 mm. long normally carry eggs during the spring and

summer. There is no increase in length at the moult into the egg-laying condition. Possibly the demands of the ovary are largely responsible for this but there are also greater demands for chitin for the egg-carrying setae which now appear. Plankemann (1935) has shown that there is a steep rise in the curve of chitin formation during June and this may well be associated with the additional needs for chitin during the period of egg-carriage.

After hatching of the larvae the females normally pass into a resting, 'neuter' condition with the usual increase in length. But occasionally they may pass

TABLE I. INCREASE IN LENGTH OF FEMALE *CRANGON VULGARIS* AFTER INITIAL MOULT IN AQUARIUM

Initial length (mm.)	New length (mm.)	Increase (mm.)	Initial length (mm.)	New length (mm.)	Increase (mm.)
36	39	4	45	48	3
32	36	4	41	45	3
37	40	3	44	47	3
37	39	2	42	44	2
39	42	3	44	47	3
37	40	3	42	44	2
31	34	3	48	51	3
30	33	3	44	46	2
32	35	3	47	50	3
33	35	2	44	46	2
	Average increase: 3 mm.				2·6 mm.
56	58	2	60	62	2
50	52	2	63	65	2
54	56	2	61	62	1
52	55	3	63	64	1
53	56	3	64	65	1
55	57	2	65	66	2
58	60	2	67	68	1
53	55	2	68	69	1
52	54	2	63	65	2
51	53	2	—	—	—
	Average increase: 2·2 mm.				1·3 mm.

directly into a second period of egg-carriage and do not increase in size. The duration of the egg-carrying intermoult is longer than normal, approximately 35 days at 12°C.

H. & L. Nouvel (1937) found that, out of a number of Caridea studied, failure to copulate does not prevent subsequent spawning except in *Athanas nitescens*, but that the unfertilized eggs are lost. This is also true for *Leander squilla* (Höglund, 1943) and for *Crangon*. But whereas these workers state that the length of the intermoult is *not* reduced when eggs are lost, in *Crangon* it did appear that the intermoult periods were the same length as for 'neuter' females, namely between 13 and 30 instead of 35 days. But there was such a wide variation in the length of intermoult periods in *Crangon* that too much weight cannot be put on these findings.

During the winter, observations similar to those recorded above were carried out at atmospheric temperatures. The intermoult period was 60–70 days with

little or no length increase. Plankemann (1935) states that there is no moulting between November and March, while Höglund (1943) found moulting at long intervals during the winter in *Leander squilla* but no growth. As shown in Fig. 15, there is little difference in the size distribution of shrimps taken from the Bristol Channel throughout the winter months.

Under natural conditions there is little doubt that, as already suggested by Nouvel-Van Rysselberge, growth is greater than that recorded in the aquarium (Table I). Reference to Fig. 15 shows an increase in length of young females from around 35 mm. to around 45 mm. between June and July, probably as a result of two moults (see p. 652). This possible length increase of 5 mm. (at this size) in successive moults is, at first sight, borne out by a more or less regular appearance of peaks at 5 mm. intervals in many of the graphs. But it has been pointed out by Mr. G. M. Spooner that, in certain sets of data, an artificial bias must exist which gives peaks at the major scale divisions, i.e. at whole 5 mm. intervals (at the expense of adjacent points). The effect, he explains, clearly shows for the total 1939 catches in Fig. 18; and it is questioned whether the pronounced peaks in Fig. 10 (March-June), Fig. 16, and Fig 20 have any real significance: for any natural periodicity which these graphs could have brought out will have been largely obscured or exaggerated. Owing to the separation of the two authors and their preoccupation with other work, it has been impossible to correct this bias, which does not affect general conclusions drawn from these graphs.

Reproduction

Secondary sexual characters. There are marked external differences between the sexes. In the male the external (olfactory) branch of the first antenna is larger, possessing, in an animal 72 mm. long, 20 more segments than in a female of the same length. The basal joint of the second antenna bears a long flagellum which is the same length as the body in the female but longer than this in the male. Although, as in all Decapoda, the genital openings are in different positions in the two sexes, these can only be easily seen in animals about to spawn.

In animals 20 mm. long and under, the endopodite of the first pleopod is of similar size in both sexes, but in the males it is bent in a hooked position over the joint between the basipodite and the exopodite. It is so small as to be barely visible to the naked eye. In females over 25 mm. this endopodite is relatively long and lies parallel to the exopodite whereas in the male it is too small to be seen by the naked eye. The endopodite of the second pleopod is biramous in the males. The inner branch or appendix masculina is spinous on one side while the outer branch resembles the unbranched endopodite of the female and is similarly clothed with long, plumose setae (Fig. 8).

The females live longer and grow larger than the males. Females have been

obtained up to 85 mm. long from tip of antennal scale to the end of the telson; the largest male was 72 mm. long, but few exceed 60 mm.

Female reproductive organs. The female usually becomes mature during the second year. There is a gradual preparation for the carriage of eggs. The endopodite of the first pleopod grows rapidly in comparison with the rest of the limb and there is a slow increase in the ovary with a sudden development during the spring of the second year.

The paired ovaries are united anteriorly and again in the region in front of the junction of the abdomen and thorax. They extend from the dorsal surface of the gizzard ('cardiac' stomach) to the third abdominal segment. The details of internal structure are essentially as described by Herrick (1911) for *Homarus americanus*.

Growth in each ovary is slow up to a body length of about 40 mm. (Fig. 3A), but increases greatly with the approach of egg laying in the summer of the second year (Fig. 3B). Immediately preceding spawning the eggs can be seen through the integument as a whitish translucent mass in the greatly distended ovaries. After spawning the ovary is reduced to about one-tenth of its former mass (Fig. 3C), but during the summer new eggs are rapidly formed and by the end of the period of egg-carriage the ovary may have regained half its former size. After the last spawning of the season, however, there is little ovarian activity and the animal passes into the winter resting condition with the ovaries only slightly exceeding their minimum size (Fig. 3D). Spawning may next take place as early as January or February, but there is a quiescent period during October and November when no egg-carrying females are found.

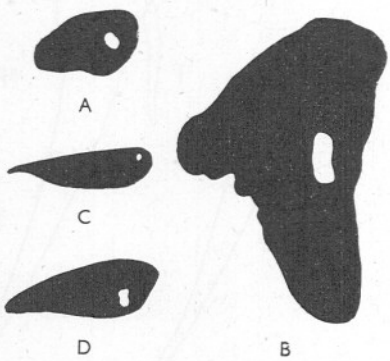

Fig. 3. *Crangon vulgaris*, comparative cross-sectional areas of left ovaries from: A, immature virgin shrimp, 37 mm. long (May); B, ripe virgin shrimp, 55 mm. long (June); C, egg-carrying shrimp, 60 mm. long (July); D, resting shrimp, 60 mm. long (October). Region occupied by primordial ova shown white, by ripening ova shown black.

The oviducts leave the ovaries about one-quarter of their length from the anterior end. In immature females the epithelium is only 1·3μ thick, but before spawning this increases to 3μ and the cells become glandular. There is a slow return to the original condition after spawning. Yonge (1937) has shown that in *Homarus vulgaris* the oviduct secretes the inner, chitinous membrane around the egg. Conditions in *Crangon* are similar.

Development of the female pleopods. The pleopods undergo considerable changes during development. At a body length of 16 mm. the endopodite of the first pleopod is very small (Fig. 4A), but then begins to increase relatively to the

rest of the appendage and to move away from the exopodite. In animals 46 mm. long five spur-like projections appear on its inner side and two series of spurs arise on the basipodite (Fig. 4B, *sp*). As the maturity is approached, at a length of about 50 mm., a number of curved 'raking' setae appear at the end of the endopodite (Fig. 4C, *rs*). The function of these is a little uncertain; although non-plumose they are *not* concerned with egg-carriage. At the same time the spurs increase in size and others appear on the basipodites of the second and third pairs of pleopods, but only the basal series on the fourth pair. Sollaud (1922) termed such structures 'caractères sexuels secondaires tardifs' and they are characteristic of the 'neuter' condition. No spurs appear on the fifth pair of pleopods which never carry eggs.

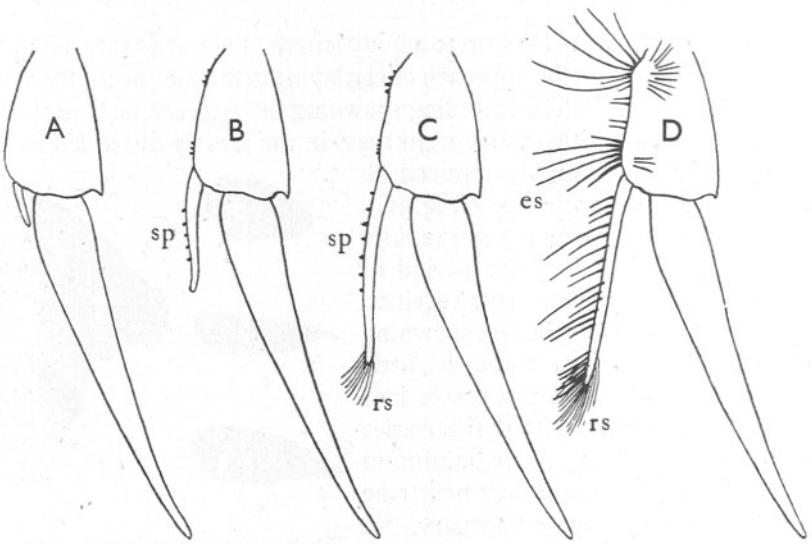

Fig. 4. *Crangon vulgaris*, outline sketches of first pleopod of female in animals of length: A, 16 mm.; B, 46 mm.; C, 50 mm.; D, 50 mm. All drawn the same size to emphasize the relative increase in size of the endopodite. *es*, egg-carrying setae; *sp*, spurs representing precursors of egg-carrying setae; *rs*, 'raking' setae. Plumose setae not shown.

When sexually mature the female moults into the egg-carrying condition. There is an increase of about one-tenth in the width of the abdomen and the pleura become somewhat larger. Since these observations were made, Höglund (1943) has described in detail similar changes in *Leander squilla*. Long non-plumose egg-carrying setae (Fig. 4D, *es*) replace the spur-like projections previously present while additional shorter egg-carrying setae appear close to these. Similar setae also appear on the coxopodites of the last two pairs of thoracic legs. The appearance of the first two thoracic appendages and the pleopods in the 'neuter' intermoult is contrasted in Fig. 5 with their condition in the spawning intermoult when the eggs become attached. There

is also an increase in the size and number of the plumose setae on all the pleopods, on the margin of the pleura, around the genital openings and especially along two sides of the long endopodite of the first pleopod. These setae protect the egg mass, laterally and ventrally, and, by their movements, create respiratory currents. A detailed account of the modifications associated with egg-carriage in *Crangon* will be included in a general paper dealing with such modifications throughout the Caridea which is being prepared by one of us (C.M.Y.).

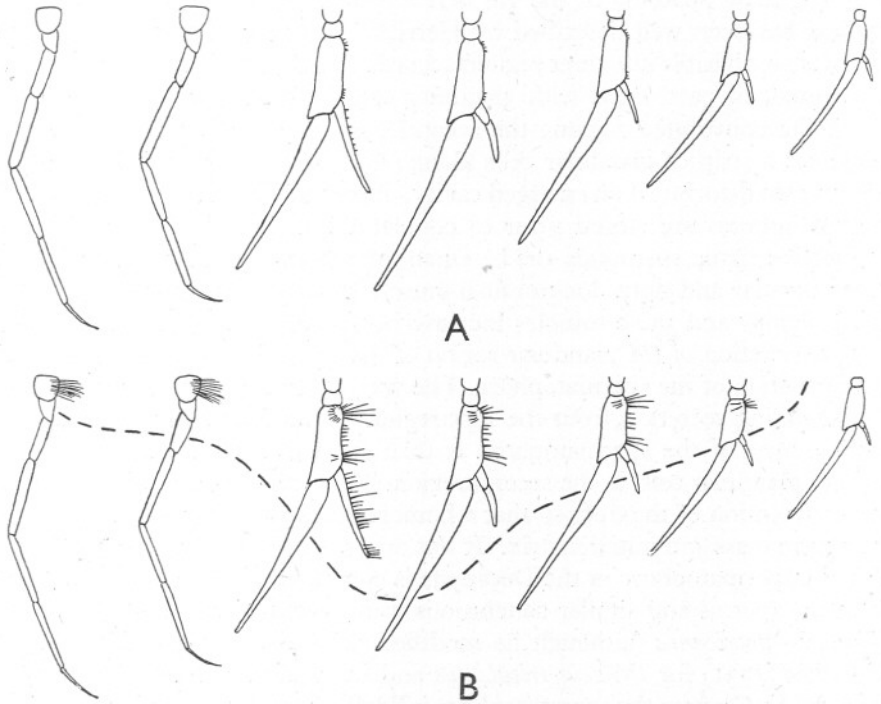

Fig. 5. *Crangon vulgaris*, semi-diagrammatic representation of the last two pereiopods and all pleopods of one side in: A, female in the intermoult preceding egg-carriage; B, in the egg-carrying intermoult. The egg-carrying setae and their spur-like precursors are shown but not the 'raking' setae nor any of the plumose setae. The area occupied by the egg mass is indicated by the broken line.

In the decapod Crustacea the eggs are secured to the appendages by cement secreted by contained tegumental glands as described by Yonge (1937) in *Homarus vulgaris*. In *Crangon* the intimate association of the glands with the egg-carrying setae is clearly demonstrated by the reduction of both during the 'neuter' periods between successive sexual intermoults. The glands are greatly reduced and the setae revert to the spurs already described. This alternation continues throughout the remainder of the life of the female as briefly recorded elsewhere (Lloyd & Yonge, 1940).

Male reproductive organs. The testes are situated in the same region as the ovaries and are also united anteriorly and centrally. They become very active when the males attain lengths of about 40 mm. when all stages in the maturation of spermatozoa are present and ripe spermatozoa occur in the vasa deferentia. These leave the centre of the testes laterally. The proximal portion is convoluted but the distal part passes direct to the opening on the base of the last pereiopod. Striated muscle is abundant near the opening and the contraction of this assists in the expulsion of the spermatophores.

The general anatomy of the vas deferens and the function of the various regions has been well described by Herrick (1911) for *Homarus americanus*. The duct is divisible into three regions according to the nature of the epithelium. The proximal part, lined with glandular cells, extends for a short distance down the convoluted region; the second part, which is much the longest, possesses a strip of glandular cells along one side only; the third region, or ductus ejaculatorius, is an enlarged cavity, devoid of glandular cells, where the spermatophores are stored prior to copulation. Only a thin layer of elastic connective tissue surrounds the basement membrane in the first region, but inner circular and outer longitudinal muscle layers surround the second and third regions and these muscles increase in thickness towards the opening.

The secretion of the glandular region of the vas deferens is concerned with the formation of the spermatophore. The sperms are apparently embedded in a coagulating secretion from the first region of the duct and the outer protective layer of the spermatophore is then formed around the mass by the strip of glandular cells in the second region. This strip forms a spiral owing to the convolution of the duct so that a homogeneous layer is laid down around the sperm mass and initial matrix. It was originally shown by Grobben (1878) that the spermatophore in the Decapoda is composed of two substances apart from the sperms and similar conclusions were reached by Herrick (1894) for *Homarus americanus* (although he modified this somewhat later (1911)), by Mouchet (1931) for *Penaeus trisulcatus* and by Spalding (1942) for *Carcinus maenas*. In *Crangon* the spermatophore is finally extruded as a thin strand-like vermicelli containing masses of sperms at irregular intervals.

Development of the male pleopods. As noted above, the endopodite of the first pleopod is minute and bent in small males (Fig. 6A). At a body length of 35 mm. it has lengthened and possesses three hooked and two straight spines (Fig. 6B). Finally, at sexual maturity, it is bent more acutely (Fig. 6C) and bears twelve hooks and eighteen spines along the outer side (Fig. 7). At this stage the appendix masculina has fully developed on the endopodite of the second pleopod (Fig. 8); it possesses eighteen strong spines along the side and end of the ramus. As noted by Nouvel (1939), it is late in developing and at a length of 35 mm. the ramus has only three or four spines.

Copulation. The process of copulation in *Crangon* has been described by Nouvel (1939) and is essentially similar to that in other Caridea such as *Athanas*

nitescens, *Leander squilla* and *Alphaeus dentipes* (H. & L. Nouvel, 1935, 1937). The process was observed by placing a male in an aquarium tank containing a female which had just moulted from the 'neuter' to the egg-carrying condition. After certain preliminary behaviour, described by Nouvel, the male turned the now passive female on to her back and then bent his body in a U-shape transversely across that of the female about the junction of the thorax and abdomen, so that the ventral regions of the two animals were in contact.

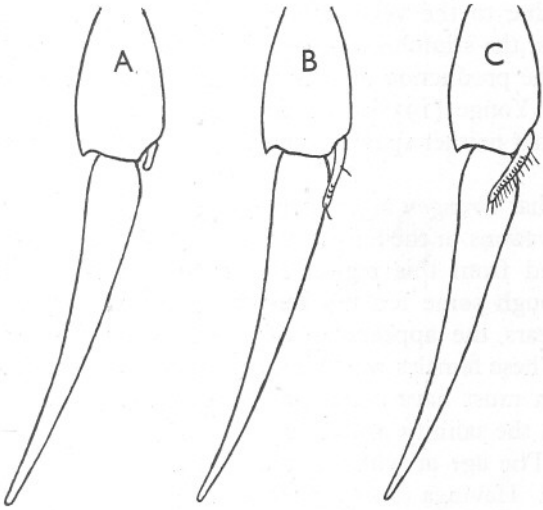

Fig. 6.

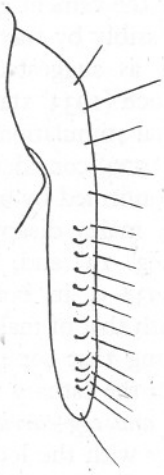

Fig. 7.

Fig. 8.

Fig. 6. *Crangon vulgaris*, outline sketches of first pleopod of male in animals of length: A, 10 mm.; B, 35 mm.; C, 57 mm. All drawn the same size to show relative increase in size and change in form of the endopodite.

Fig. 7. *Crangon vulgaris*, endopodite of first pleopod of male 57 mm. long enlarged to show hooks and spines.

Fig. 8. *Crangon vulgaris*, endopodite of second pleopod of male 72 mm. long showing appendix masculina (inner ramus).

Nouvel describes the male as sliding his body under that of the female. The male does not apparently grasp the female by any of his appendages and, despite the contrary statements of Havinga (1929), there are no copulatory organs, the spermatophores being applied to the ventral side of the female usually more or less adjacent to the genital opening. Contact was maintained for about five seconds after which the animals fell apart, motionless. The female recovered first and after a few minutes buried herself in the sand. Throughout, the still soft-shelled female is apathetic, as noted by Nouvel, and does not seek copulation. The male alone shows activity and is ready to copulate again within a few minutes. Nouvel states that the females sometimes permit

a second copulation, but this was not personally observed. Nouvel also records the copulation of large females, up to a length of 58 mm., with males of from 30 to 36 mm.

Eggs are laid within two days of moulting into the egg-carrying condition, irrespective of copulation as already stated. If copulation has occurred, spawning normally follows within 24 hr. Nouvel states that small females spawn immediately after copulation, larger ones after 24 hr, but very large ones after 48 hr. Where copulation has not occurred the eggs fail to develop and drop off. This is apparently due to the very limited amount of secretion produced by the cement glands, the stimulus of copulation being apparently necessary possibly by way of the production of some hormone which affects these glands as suggested by Yonge (1937). In the anomuran, *Diogenes pugilator*, Bloch (1933) states that neither spawning nor moulting takes place without sexual stimulation.

Havinga (1929) considered that *Crangon* might copulate in brackish water and this is confirmed by observations in the Severn Estuary. In both 1937–8 and 1938–9, males disappeared from this region about the beginning of February (Fig. 14) and, although some females remained throughout the winter in 1938–9, in both years the appearance of egg-carrying females coincided with that of males. These females were all carrying newly-spawned eggs indicating that copulation must have occurred recently and therefore necessarily in the estuary when the salinity would lie between 10 and 15 °/₀₀.

Spawning and egg-carriage. The age at which sexual maturity is attained varies greatly with the locality. Havinga (1929) gives a minimum length of 43 mm. in the Zuiderzee; Wollebaek (1908) of 36 mm. in the colder waters off Norway; Meyer (1935*a*) found that some 50 % of females between 35 and 40 mm. long were carrying eggs during May in the Bay of Jade in Oldenburg. In the Bristol Channel the smallest egg-carrying females measured 45 mm. and were taken in March and June (Fig. 9). But in the lower salinity of the estuary the minimum length was 47 mm. and very few were less than 50 mm. (Fig. 10).

As the time for spawning approaches, the animal refuses to eat and retires into a sheltered position. The pressure of the ovary on the stomach may prevent normal intake of food. Following moulting and copulation, the female cleans the egg-carrying setae by stroking movements with the tips of the second pair of pereiopods. During spawning the animal lies on one side with the abdomen bent under the thorax and the eggs then pass back in chains from the genital openings assisted by movements of the spoon-like endopodites of the first pair of pleopods. The 'raking' setae around the tips of these possibly assist by combing the eggs back. The second pair of pereiopods also help. H. & L. Nouvel (1937) state that in other Caridea the pereiopods assist in the same way, but Höglund (1943), in his beautifully detailed account of spawning in *Leander squilla*, denies this. Here the female spawns while resting upright

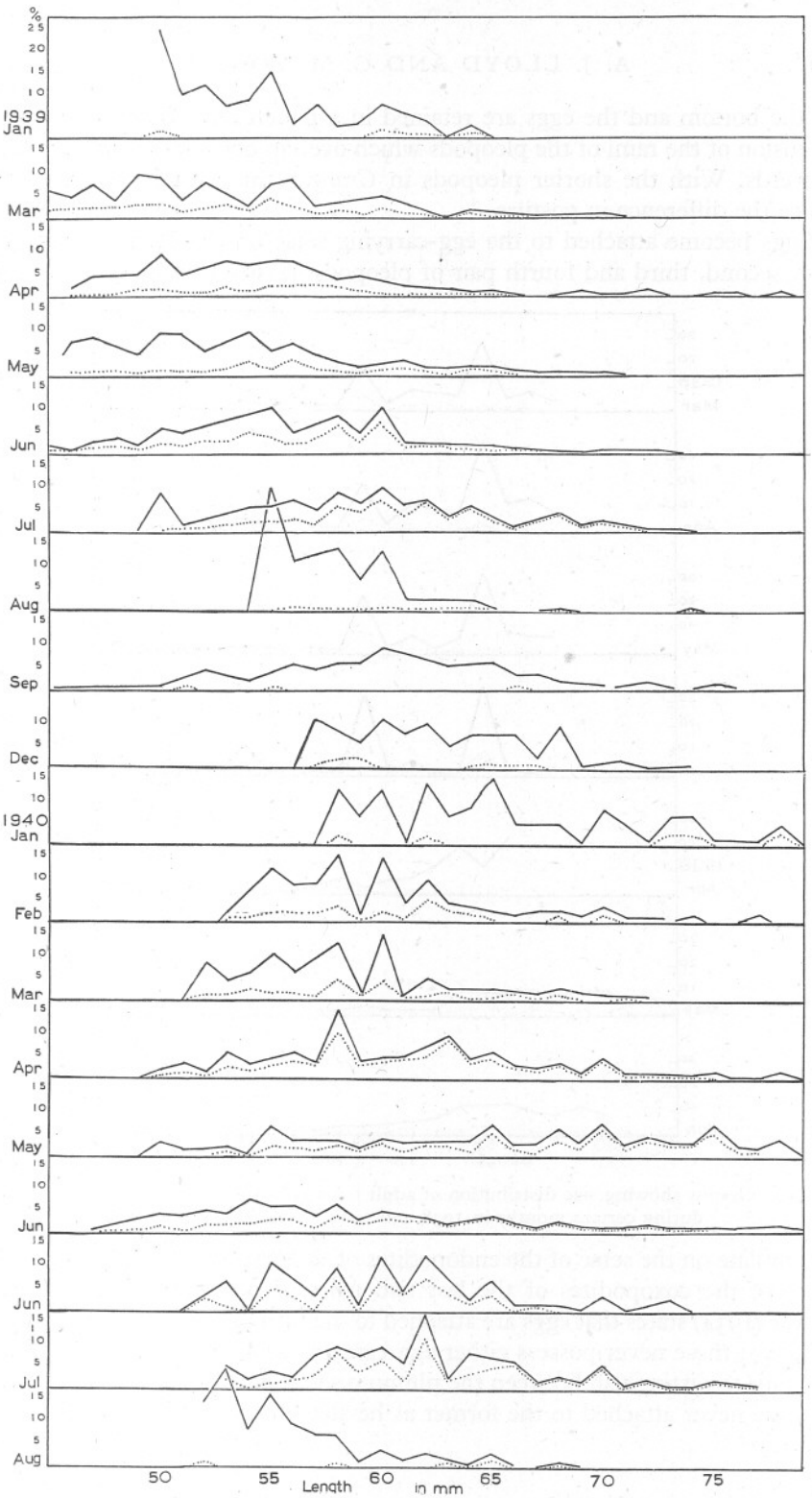

Fig. 9. Graphs showing size distribution in successive months of adult females in the Bristol Channel during 1939 and 1940. The continuous lines represent total female population above the minimum length for egg-carriage (i.e. adults), the dotted lines the percentage of egg-carrying individuals.

on the bottom and the eggs are retained in a pouch formed by the forward extension of the rami of the pleopods which overlap one another from behind forwards. With the shorter pleopods in *Crangon* this would be impossible, hence the difference in posture.

Eggs become attached to the egg-carrying setae on the basipodites of the first, second, third and fourth pair of pleopods in the order given, then they

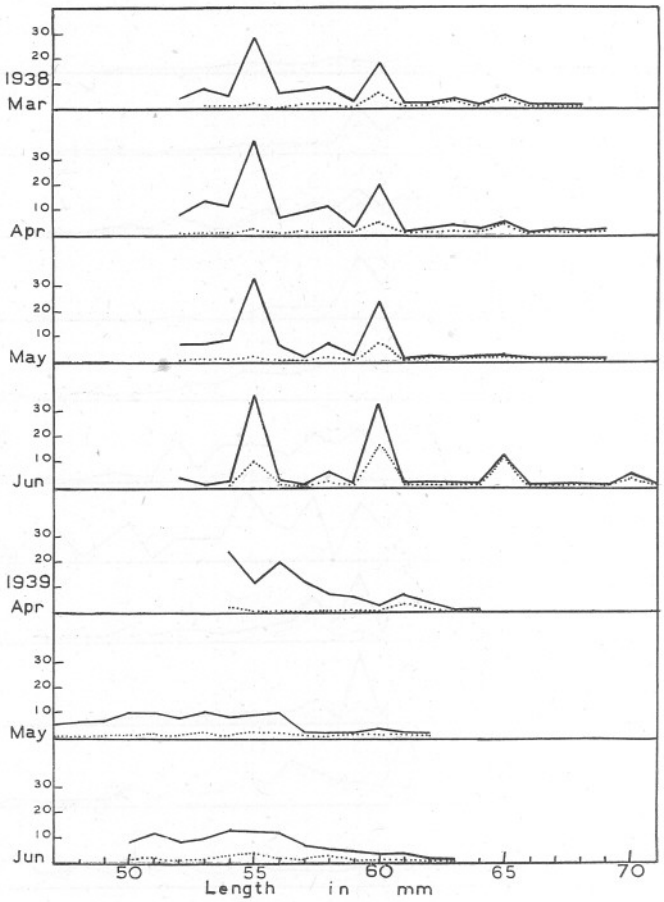

Fig. 10. Graphs showing size distribution of adult females in the Severn Estuary (Oldbury) during certain months in 1938 and 1939. Details as for Fig. 9.

accumulate on the setae of the endopodites of the first pair of pleopods and on those of the coxopodites of the last two pairs of pereiopods (see Fig. 5). Meyer (1934) states that eggs are attached to the fifth pair of pleopods, but this is not so; these never possess either egg-carrying setae or cement glands. He also fails to distinguish between the plumose setae and the egg-carrying setae; eggs are never attached to the former as he states.

The egg mass is so attached that the exopodites with their fringing plumose setae are free to move and set up respiratory currents around the egg mass. There is a space between the ventral body wall and the eggs through which water can circulate. The eggs become firmly cemented to the setae in about 30 min. This is in close agreement with Höglund's statement that in *Leander squilla* this process takes from a $\frac{1}{2}$ to 1 hr. He estimated that the actual process of egg extrusion only takes from 4 to 8 min.

After the egg mass is securely attached, the animal swims vigorously but it does not feed so voraciously as during the preceding intermoult period when the demands of the ovary were so great. The pleopods frequently beat very actively and the female shows a marked preference for well aerated water.

The newly attached egg is spherical and from 0·35 to 0·4 mm. in diameter. Later it enlarges, due to stretching of the outer, cuticular membrane (see Yonge, 1946), but almost exclusively in one diameter so that it becomes elliptical before hatching. At this time it becomes greenish-grey in colour and

TABLE II. ONE-DAY SAMPLES OF ADULT FEMALE SHRIMPS FROM DIFFERENT STATIONS IN THE BRISTOL CHANNEL SHOWING CONDITION OF THESE AND RESTRICTION OF 'CEMENTED' INDIVIDUALS TO THE MONTHS OF APRIL AND MAY

	1939			1940		
	'Neuter'	Cemented	Egg-carrying	'Neuter'	Cemented	Egg-carrying
January	—	—	—	100	0	5
February	—	—	—	352	0	33
March	386	0	48	319	0	56
April	259	15	178	105	72	68
May	632	32	184	121	35	158
June	739	0	523	204	0	210
July	1220	0	380	146	0	84
August	614	0	16	475	0	0
September	306	0	4	560	0	0
October	249	0	0	—	—	—
November	293	0	1	—	—	—
December	317	0	8	—	—	—

the eyes of the larvae are visible. Towards the end of the egg-carriage, Meyer (1935*a*) states that the egg mass is frequently probed and loosened by the second pereiopods which also assist in the final liberation of the larvae. This has been confirmed.

After hatching the egg membranes and strands of cement remain attached to the pleopods until the next moult. The period between hatching and moulting is longer in the spring than in the summer and for that reason 'cemented' shrimps were taken exclusively during April and May in the Bristol Channel (Table II). Analysis of collections made in April at Stolford and at Plymouth both show significant proportions of 'cemented' animals (Fig. 11).

Spawning seasons. Ehrenbaum (1890), Havinga (1930) and Meyer (1935*a*) have all observed spawning *Crangon* in both summer and winter months along

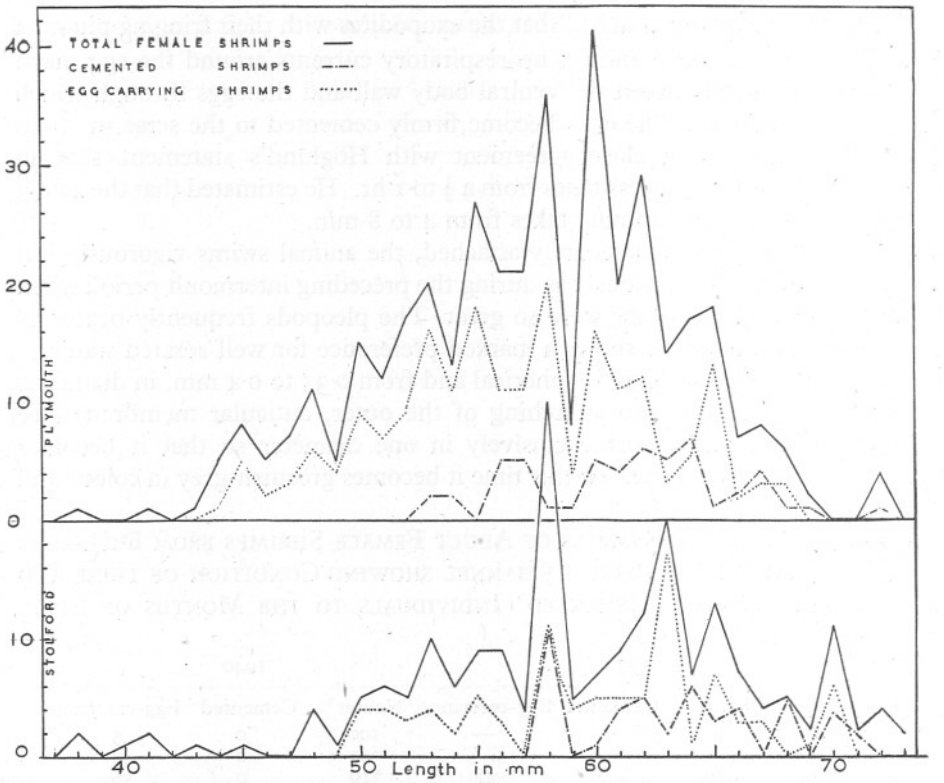

Fig. 11. Graphs showing size distribution of total female population with proportion carrying eggs and proportion not moulted since the larvae were hatched (i.e. cemented). Graphs based on counts of samples obtained from Stolford and from Plymouth in April 1940.

TABLE III. PERCENTAGE EGG-CARRYING *CRANGON VULGARIS* IN RELATION TO TEMPERATURE AND SALINITY THROUGHOUT THE YEAR IN THE CHANNEL AND ESTUARY

	Bristol Channel				Severn Estuary			
	Weston		Stolford		Oldbury			
	Salinity 1940 (‰)	Temperature 1940 (°C.)	Percentage egg-carrying		Salinity 1938 (‰)	Temperature 1938 (°C.)	Percentage egg-carrying	
			1939	1940			1938	1939
January	22·1	5·5	5	9	7·1	5·5	—	—
February	21·8	5·5	20	15	9·0	5·0	—	—
March	22·6	7·2	33	15	11·8	8·1	19	—
April	23·2	10·5	27	59	15·0	9·9	16	5·5
May	24·2	11·6	33	61	16·3	11·1	16	15
June	25·4	14·6	48-55	51-70	17·8	14·0	42	23
July	26·0	17·8	72-44	48	19·9	16·4	—	—
August	27·1	20·6	10	3	20·6	19·0	—	—
September	27·9	16·7	1	—	24·7	17·2	—	—
October	28·5	13·3	0	—	17·2	11·6	—	—
November	25·0	12·2	0	—	16·8	10·5	—	—
December	22·0	7·7	5	—	3·6	7·5	—	—

the continental shores of the North Sea. Ehrenbaum and Meyer, working at Caroliensiel and Jade Bay respectively, found two spawning periods, one extending from spring to the end of July and the other from November until February. Havinga, working in the Zuiderzee, found three spawning periods, in October, April and June.

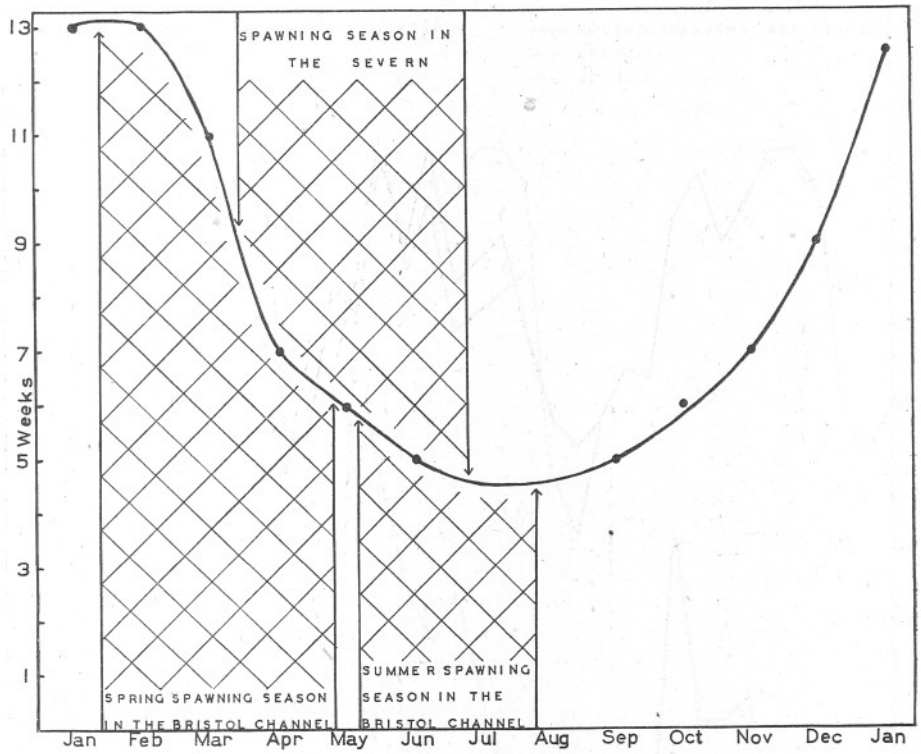

Fig. 12. *Crangon vulgaris*, diagram showing the spawning seasons in the Severn Estuary and the Bristol Channel and the probable duration in weeks of egg-carriage (based on data from Havinga, 1930) at temperatures prevailing throughout the year.

In the Bristol Channel there are probably spring and summer spawning periods, although as shown in Table III and Fig. 13, the two overlap. The former starts at the end of January or in early February and lasts until mid-April or the beginning of May (Fig. 12). The peak of this spawning was in March in 1939 (33% of all females) and in April in 1940 (59%), spawning being delayed in the latter year owing to the severe winter of 1939–40. Figures are given in Table III and displayed graphically in Fig. 13 (Stolford). Meyer (1935*a*) records greater numbers (65–80%) of egg-carrying females during spring in Jade Bay. At the end of this spring spawning, in April or early May, large numbers of 'cemented' females were taken (Table II and Fig. 11). At the

temperatures prevailing in the Channel during the spring (Table III), the eggs were probably carried for some 7–10 weeks as indicated in Fig. 12. This figure was prepared using Havinga's data for the duration of egg development at various temperatures combined with personal observations on egg-carrying shrimps in the aquarium.

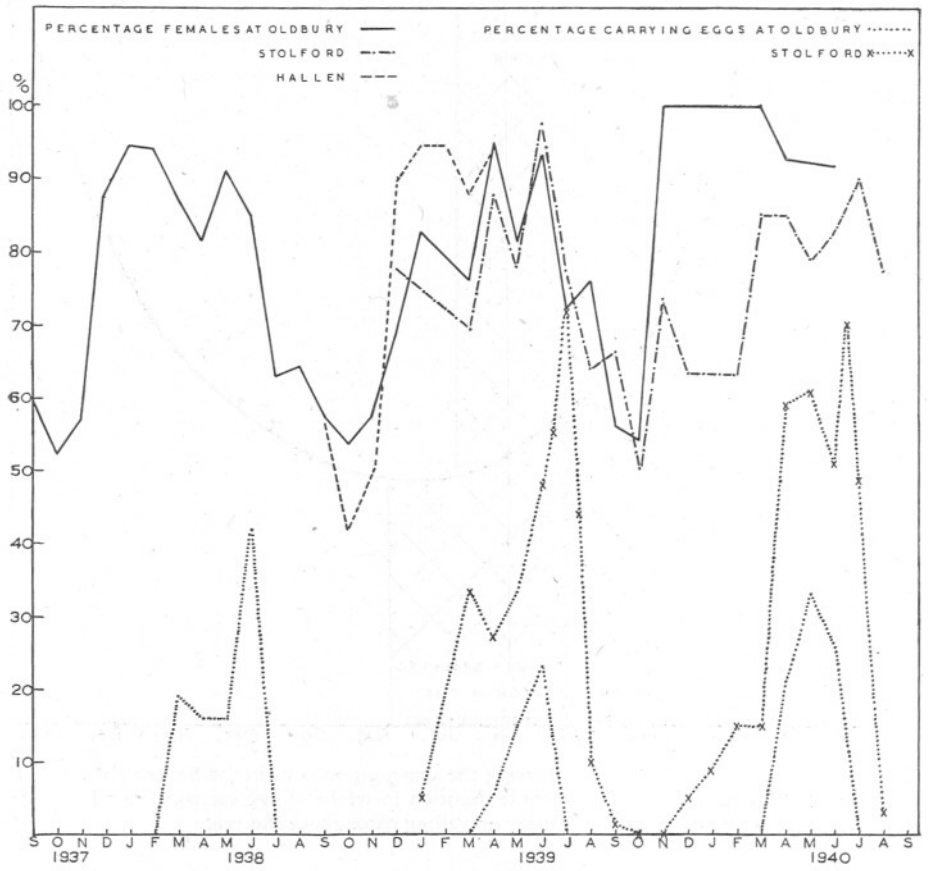

Fig. 13. Graphs showing percentages of total female and of egg-carrying individuals in the Severn Estuary (Oldbury, Hallen) and the Bristol Channel (Stolford) from 1937 to 1940.

Summer spawning in 1939 began in May and in 1940 during early June. Egg-carrying shrimps reached a maximum of 72 % in July 1939 and at the end of June 1940 (Table III; Fig. 13). Havinga records 95 % females carrying eggs during these months. This second period of egg-carriage is largely over by the end of July although a few egg-carrying females were obtained in August and 1 % in September 1939. But apart from these few there is a resting period from September to November. About 5 % of the females taken at Stolford in December were carrying eggs but there was no general winter spawning like

that recorded from the North Sea by Meyer (1935*a*) who found 69% of females carrying eggs from mid-October to mid-December and 40% up to mid-January. Thus at Stolford, as representative of conditions in the Bristol Channel, berried shrimps represent 5% and more of the total female population for nine months in the year, they are negligible in numbers during September and absent during October and November. In the zones of highest salinity in the Zuiderzee and Westerschelde, Havinga (1930) found that 50-60% of females were carrying eggs during eleven months of the year with a resting period either in January or February.

Unlike the Channel, egg-carrying shrimps occur in the Severn (at Hallen and Oldbury) only during the spring from March or April to June (Table III; Fig. 13). As already noted, there is good evidence that these animals copulate and spawn in these waters. The percentage of females carrying eggs reached a maximum of 42 and 23 in June 1938 and 1939 respectively. After June no spawning females were found until the following spring. Havinga (1930) obtained approximately 40% of berried shrimps from March–April until September–October in regions of low salinity comparable to those in the Severn Estuary.

The absence of winter spawning in the estuary is due to the lower salinities (minimum of 3·6‰ in December at Oldbury compared with 21·8 at Weston in February) which cause seaward migration of the males and, in some years, of the females also (see Fig. 14). Berried females do not appear until the return of the males when a salinity of approximately 12‰ prevails. The liberated larvae need a still higher salinity, hence the general tendency for seaward migration of berried animals prior to hatching.

Life History

The larvae of *Crangon* have been described by Ehrenbaum (1890), Havinga (1929) and Lebour (1931). The length at hatching is 2 mm. which increases to from 4·6 to 4·7 mm. at the end of the fifth (last) larval stage when the animal leaves the plankton. Ehrenbaum thought that the planktonic period extends over some five weeks in the spring in the North Sea, but it is influenced by temperature. The variations in this (5–21° C.) during the ten months of the breeding season in the Bristol Channel must have a great effect on the length of time passed in the plankton. The length of the sixth (first post-larval) stage decreases to about 4·3 mm., that of the seventh, eighth and ninth stages being 6, 7·5 and 10·5 mm. respectively.

In the Bristol Channel quantities of *Crangon* around 6 mm. long (i.e. second post-larval stage) were taken at Kilve, near Stolford, during May. They were presumably products of the spring spawning, while collections of shrimps ranging in the main between 15 and 25 mm. in length taken at Stolford in June must have arisen from eggs carried in December and January (Table III).

Meyer (1935*b*) found that larvae liberated in February attained a length of 22 mm. by the end of July and of 31 mm. by the end of September in Jade Bay.

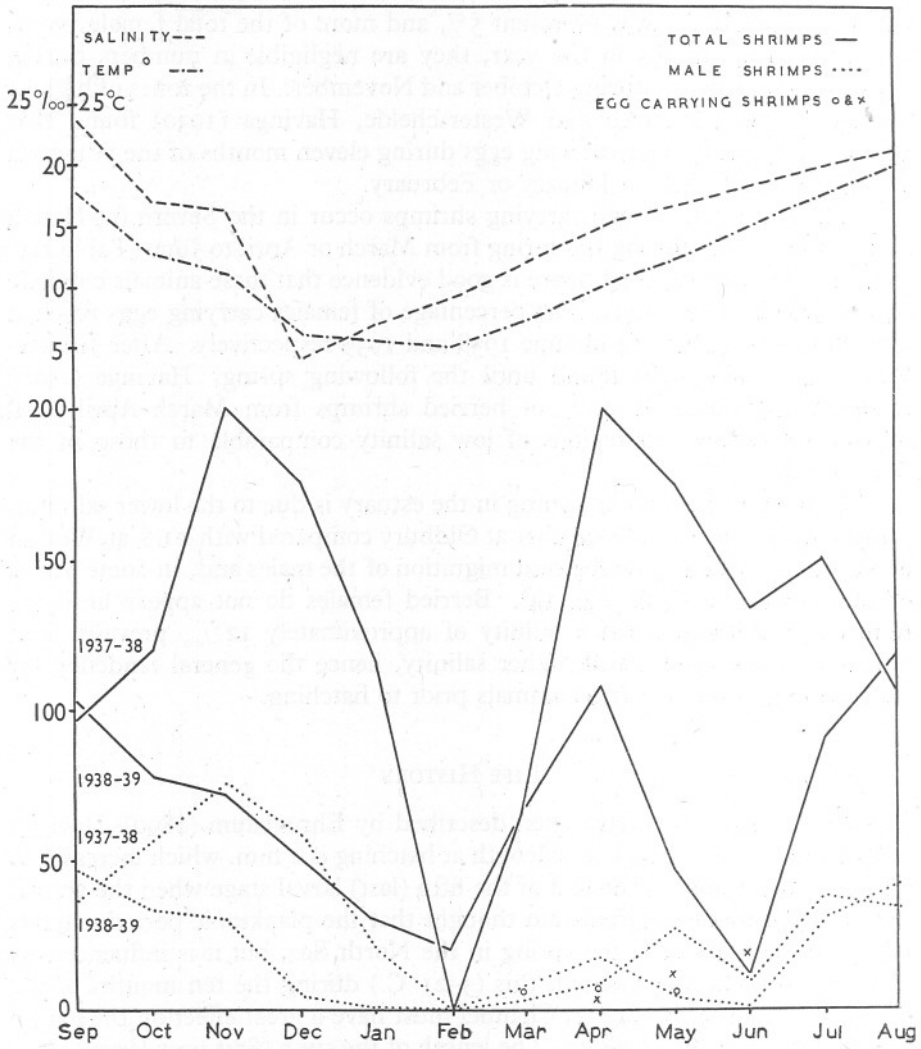

Fig. 14. Graphs based on bi-weekly counts of animals caught at Oldbury, showing fluctuations in numbers during 1937 to 1938 and 1938 to 1939 both in the total population and in the male population in the Severn Estuary. Graphs for salinity and temperature are based on figures for 1938 to 1939. Presence, and percentage, of egg-carrying females denoted by circles (1937–38) and crosses (1938–39).

This was followed by a further length increase of 7 mm. over the following winter. But in the Bristol Channel these winter spawned animals are few

compared with those produced during the spring and summer which constitute the main size groups during each month although random migrations frequently make it impossible to distinguish the different classes. In the estuary, shrimps 10–15 mm. long were taken at Shepardine in July. They may have been the products of animals spawning in March.

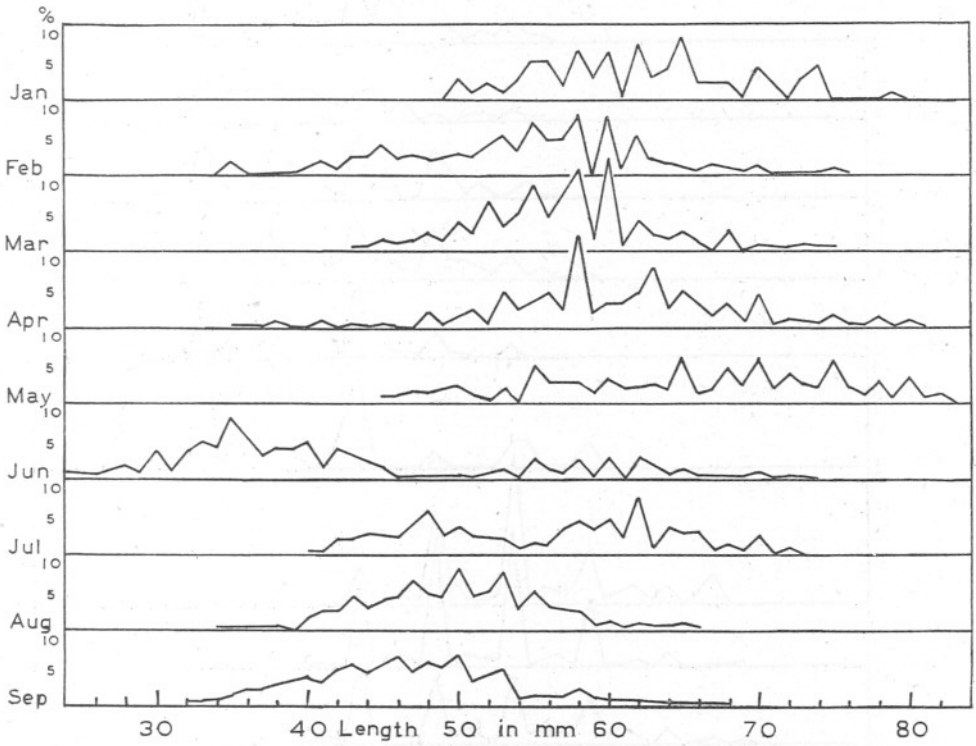

Fig. 15. Graphs showing size distribution in successive months of females collected from the Bristol Channel from Jan. to Sept. 1940.

The young shrimps move offshore in the autumn and do not reappear until the following summer when in June 1939 and June 1940 (Fig. 15), animals spawned the previous spring and summer appeared in the Channel at lengths of between 25 and 45 mm. Havinga (1930) gives the length at the end of one year as 35 mm.; Meyer (1935*b*) estimates it as about 37–38 mm. But it is difficult to be precise when the spawning period is so long.

During the first year of life the growth rate of the two sexes appears to be very similar. Subsequently the females grow more rapidly although, owing to the frequent periods of egg-carriage when growth is arrested and the cessation of growth during the winter, all workers agree on the difficulty of interpreting growth data. In the North Pacific species, *Crago* (*Crangon*)

franciscorum and *C. nigricauda*, Israel (1936) found that a differential growth rate sets in at an early age, the females growing more rapidly and becoming 25% larger than the males.

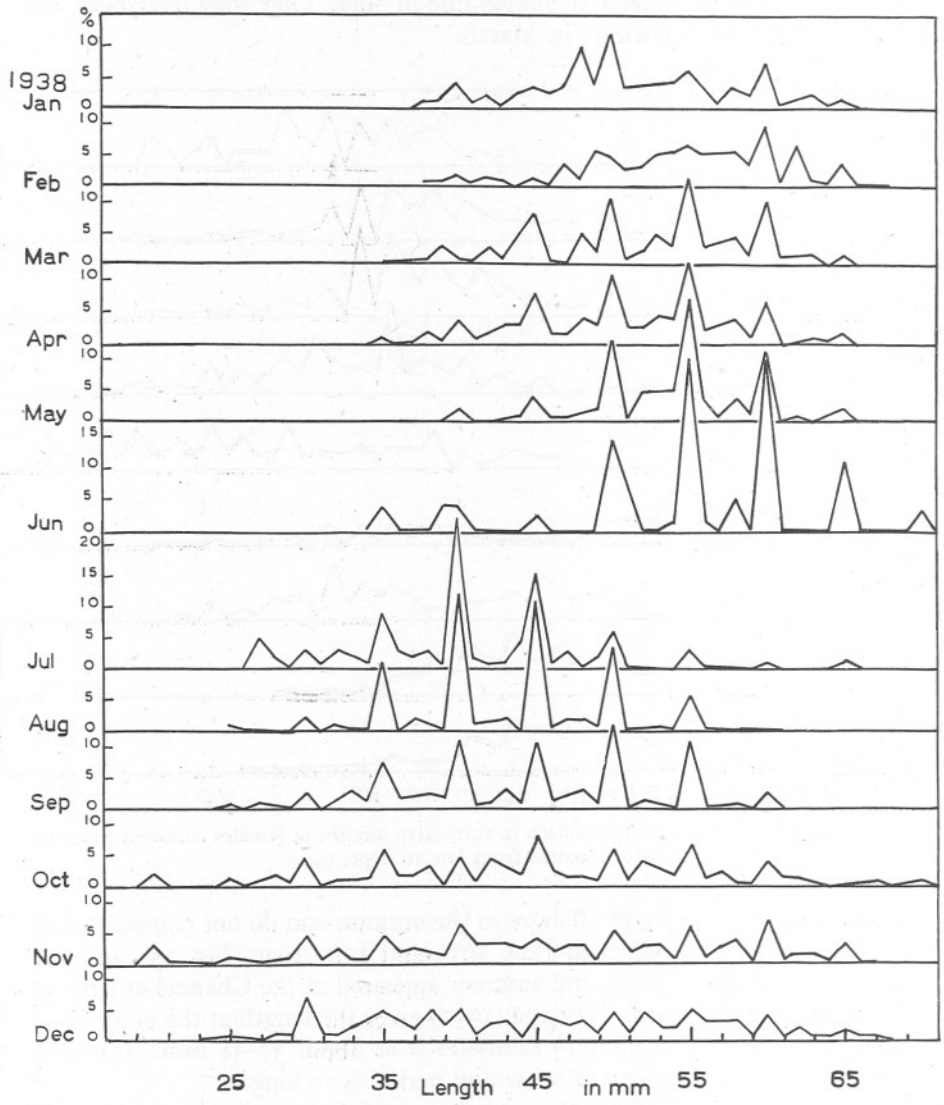

Fig. 16. Graphs showing size distribution in successive months of females collected from the Severn Estuary from Jan. to Dec. 1938.

As shown in Fig. 15, young females which enter the population in the Channel in June add some 10 mm. to their length in the following month, presumably as a result of two 'neuter' moults. They are then largely between 45–55 mm. long

and so capable of moulting into the egg-carrying condition and spawning. The arrest of growth due to this is indicated by the general similarity of the graphs for length during July, August and September. In the Severn (Fig. 16), a similar female population, up to 45 mm. long, appears in July after the older females present throughout the first part of the year have spawned and then migrated seaward. As shown in Fig. 13 and Table III, breeding is completed in June in the Severn (Oldbury) and indeed only a small section of this first year population reaches the minimum size for spawning (50 mm., see p. 642) in these estuarine waters.

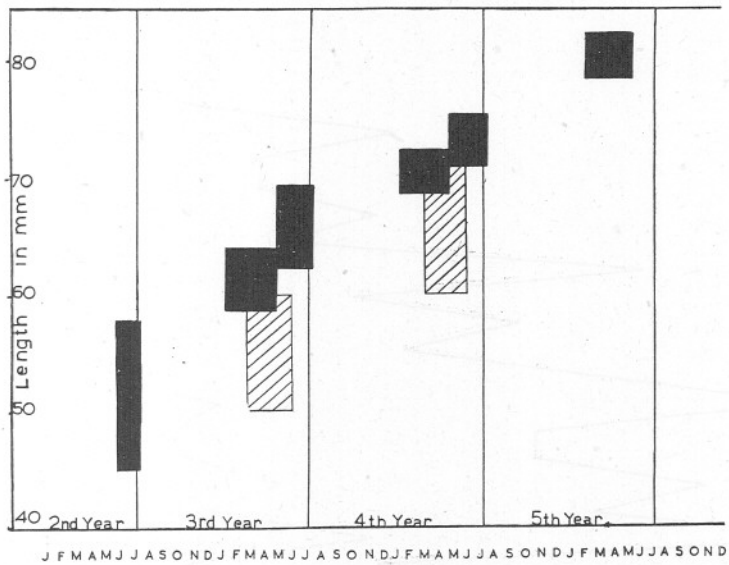

Fig. 17. Diagrams showing length of spawning females and the spawning periods in the Bristol Channel (shown black) and in the Severn Estuary (shown shaded).

The evidence would thus seem to indicate that spawning begins in the Channel about the beginning of the second year of life when the females are mainly between 45–55 mm. long but that in the Severn not until a year later. As shown in Fig. 17, there is probably only one breeding period in the Channel in the second year but there are two such periods in both the third and fourth years at lengths of about 60–70 mm. and of up to 75 mm. respectively. A few females survive the fourth winter to reappear at lengths of about 80 mm. in the fifth year, as in May, 1940 (Fig. 15). In the Severn there is only one spawning period annually (Fig. 17), the great bulk of the breeding animals being in their third year, at lengths of between 50 and 60 mm., and a few in their fourth year when over 60 mm. as shown in Figs. 10 and 16.

After sexual maturity has been attained, at a length of about 50 mm., mortality must be high, as indicated in Fig. 18. Only 25 out of some

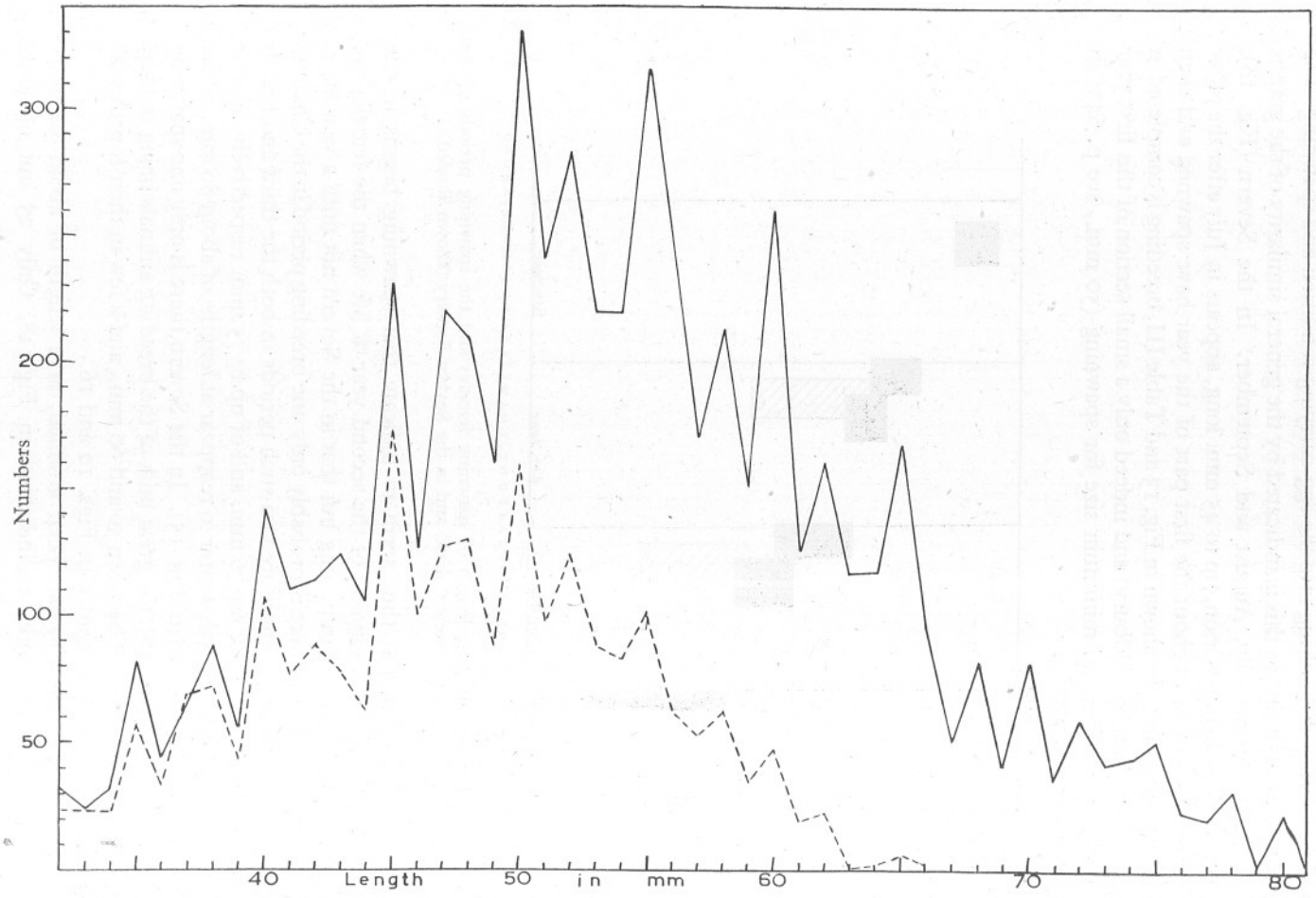

Fig. 18. Graph showing size distribution of all females (continuous line) and males (broken line) collected from the Bristol Channel during 1939.

22,000 females measured exceeded 80 mm. in length although Havinga obtained occasional specimens as long as 91 mm.

It is difficult to be certain about the growth rate of the males because of the smaller numbers taken; the reasons for this are discussed later. Young males appeared in the Channel at lengths of under 40 mm. in July and December 1939 (Fig. 19) and under 35 mm. during June and July 1938 in the Severn (Fig. 20).

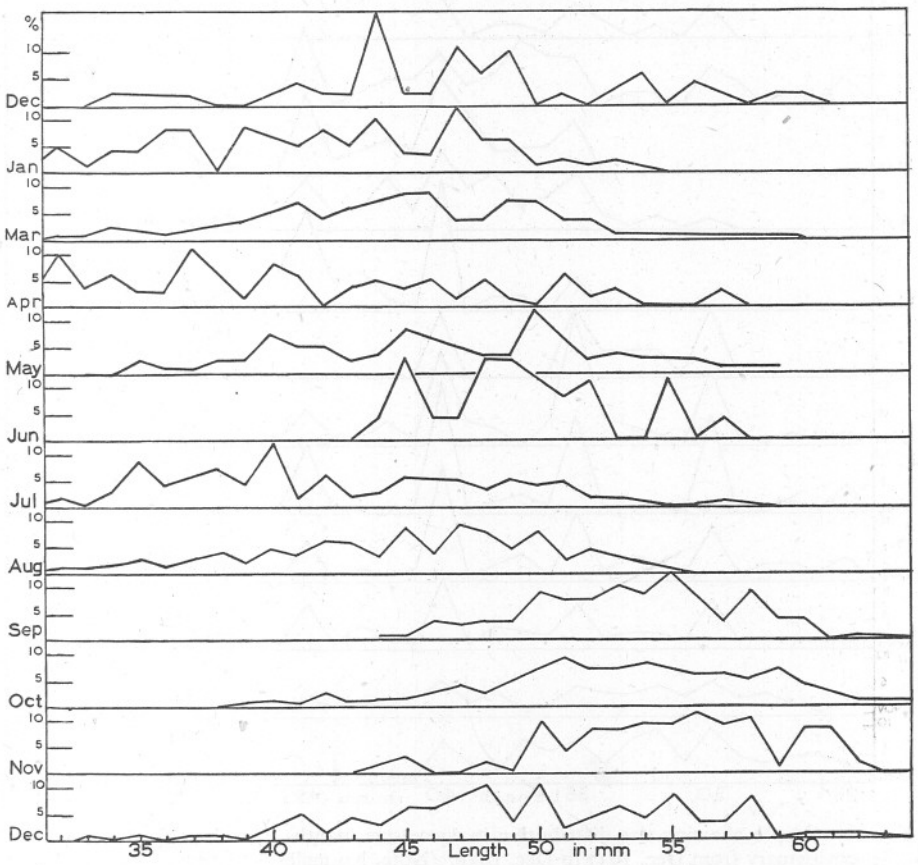

Fig. 19. Graphs showing size distribution in successive months of males collected from the Bristol Channel from Dec. 1938 to Dec. 1939.

Probably males do not enter these estuarine waters until the end of the first year of life and then quickly become mature. Comparison of the size groups of the two sexes in the Severn from July to September (Figs. 16 and 20) reveals that the males are smaller. The spring population in the estuary appears to consist of second-year males with maximum numbers between 40 and 45 mm. long (Fig. 20) together with third-year females largely between 50 and 60 mm.

long (Fig. 16). During the summer an extreme length of 55 mm. is attained by some males but animals of this size are rare, the death-rate being high after lengths of 50 mm. are reached as shown in Fig. 18. Two males 70 mm. long were taken in the summer and these may have been four years old.

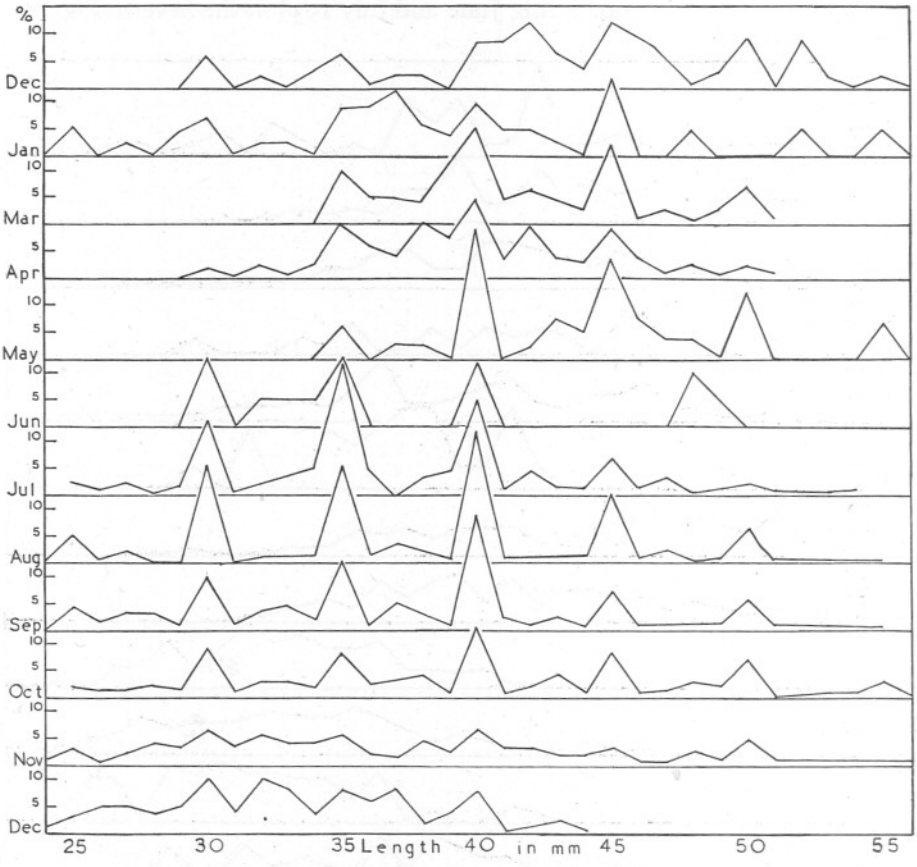

Fig. 20. Graphs showing size distribution in successive months of males collected from the Severn Estuary from Dec. 1937 to Dec. 1938. (Note. No males were found in February.)

Migrations

Ehrenbaum (1890), Havinga (1930) and Meyer (1935*b*) all recorded an offshore migration of *Crangon* to deeper waters in the North Sea during the winter and an inshore migration in the spring. Israel (1936) reports similar movements of *C. franciscorum* and *C. nigricauda* in the Pacific. Similar migrations, as already stated, occur in the Bristol Channel and Severn Estuary. These migrations are clearly related to salinity and temperature.

Data for the Severn were obtained primarily at Oldbury (Fig. 1, station 2), for the Channel at Weston (station 4). Low water salinities were lowest at Oldbury in December (Table III; Fig. 14) and though salinity rose from 3·6‰ in that month to 9·0‰ in February in the salmon pool where the shrimps were caught, observations in mid-channel indicated that the salinity there was lowest in February. This is certainly true at Weston (Table III), although figures are much higher, namely 21·8‰. During the spring and summer, salinities rise, reaching a maximum of 24·7‰ in September at Oldbury and of 28·5‰ in October at Weston. There is little difference between the temperatures in the two regions; in both the lowest figures are in February (5·0 and 5·5° C.) and highest in August (19 and 20·6° C.).

During February few (1939), or no (1938), *Crangon* were taken at Oldbury (Fig. 14) but, beginning in March, there was an extensive migration into the estuary. The females, in the main 50–55 mm. long, were much more numerous than the males (Fig. 14). Only a few females carried eggs. The migration reached its maximum in April after which numbers declined because many females left the Severn to liberate the larvae in more saline waters. This movement was reflected in an increase of approximately 70% in the numbers taken at Stolford (station 6) during early July.

During June and July the estuary was restocked by the appearance of females up to 45 mm. long (Fig. 16) and males up to 35 mm. long (Fig. 20). This migration reached maximum dimensions early in November in 1937 but sooner in 1938 (Fig. 14). A seaward migration followed and this continued during the winter. Males were completely absent in February in both 1938 and 1939 and females also in 1938. This winter migration is closely associated with the declining temperature and salinity as shown in Fig. 14. On the other hand shrimps are never completely absent from the Channel where similar temperatures but higher salinities prevail (see above). It is thus apparently the low salinity of the estuary which is the prime factor causing seaward migration. Similar migrations occur, although to a smaller extent, in the Channel but are most marked near the mouths of rivers flowing into the Channel, for instance at Burnham (station 5).

There was little difference between the percentages of females at each station during any month (Fig. 13) and any fluctuations were shown simultaneously at Oldbury, Hallen and Stolford. Thus the movements of *Crangon* take place in a regular manner throughout the area being apparently influenced by alterations in environmental factors equally at each station.

The percentage of males taken at these three stations was 36 at Oldbury, 30 for Hallen and 27 for Stolford. The higher figure at Oldbury is probably due to the use there of a stramin net round the end of the putt which caught smaller animals than was possible at the other stations. But even this figure represents a low ratio of males. A number of factors are probably responsible for this. First, the males live for a shorter time than the females. Second, they

are unable to withstand the low salinity, combined with low temperature, in the winter. The greatest influx of males at each station occurred during September to October when they may constitute 40–50% of the population as shown in Table IV.

This Table also includes Havinga's data for the Zuiderzee and Westerschelde, where high salinities are about 26‰ and low salinities from 5 to 10‰, i.e. comparable in many respects with those in the Channel and Severn respectively. The percentages of males obtained in the Channel are in the main not unlike those obtained in the most saline zones of the Westerschelde, but the brackish waters of the Severn appear to have a larger population of males than those of similar waters in the North Sea where the males only appear between July and October. Possibly higher temperatures in the Severn may explain the presence of males over the greater part of the year.

TABLE IV. PERCENTAGE OF MALE *CRANGON VULGARIS* THROUGHOUT THE YEAR IN ZONES OF HIGHEST (H.S.Z.) AND LOWEST SALINITY (L.S.Z.) IN DUTCH WATERS (FROM HAVINGA, 1930) AND IN THE BRISTOL CHANNEL AND SEVERN ESTUARY DURING 1939

	Percentage male shrimps					
	Zuiderzee		Westerschelde		Bristol Channel and Severn Estuary	
	H.S.Z.	L.S.Z.	H.S.Z.	L.S.Z.	Stolford H.S.Z.	Oldbury L.S.Z.
January	51	—	—	—	25	18
February	—	—	45	—	—	0
March	47	—	31	0	31	14
April	50	0	29	0	12·5	5
May	19	0	23	0	22	19·5
June	14	0	27	0	2·5	7
July	66	49	24	—	23	38
August	78	—	39	43	36	34
September	68	27	29	61	34·5	44
October	53	13	25	—	50	46
November	73	—	48	—	26	0
December	56	—	53	—	36	0

(Note. The graph in Fig. 14 does not cover the last four months of 1939.)

Although both sexes are unable to withstand low salinity when combined with low temperature, the field observations here recorded, confirming those of earlier workers, combined with the results of the experiments on the effect of varying salinity on respiration in the two sexes, reveal clearly the greater susceptibility of the males. There is apparently a well-marked physiological distinction between the sexes in respect of osmo-regulation which may be the result of fundamental metabolic differences. As already recorded, females can withstand exposure to freshwater for considerable periods and it may be that an annual invasion of freshwaters is prevented by the inability of the males to withstand such conditions. That dependence of the larvae on saline conditions is no such bar to freshwater life by the adults is shown in *Eriocheir*.

Summary

Collections of some 22,000 female and 6000 male *Crangon vulgaris* were made throughout the year from the shrimp fisheries of the Severn Estuary and Bristol Channel. All animals were measured.

The habits of the species are described; it can withstand a wide range of temperature but, though euryhaline, resembles other Decapoda in the inability to withstand low salinity combined with low temperature.

Osmo-regulation is apparently largely inhibited at low temperatures and to a greater extent in the males than the females.

Growth rate decreases with increasing age; in the female there is no increase in length when moulting from the 'neuter' to the egg-carrying intermoult.

The duration of this intermoult, if spawning is successful, is about double that of the normal intermoult under the same temperature conditions.

Growth almost ceases in the winter.

Secondary sexual characters are described, especially the differences between the endopodites of the pleopods in the two sexes.

Females become mature at a minimum length of 45 mm. in the Channel and seldom less than 50 mm. in the Estuary. The effect of the female sexual cycle on the size of the ovary and the form of the pleopods is described.

The process of copulation is described; it can occur in the brackish waters of the estuary. Egg-laying always follows within two days of moulting into the egg-carrying condition but eggs are not retained if copulation has not occurred.

The females lie on their sides during the act of spawning and the eggs are firmly attached within thirty minutes to the egg-carrying setae on the basipodites of the first to fourth pair of pleopods, then to those on the endopodite of the first pleopod, finally to those on the coxopodites of the last two pairs of pereiopods.

The period of egg-carriage varies from about four weeks in mid-summer to thirteen weeks in the winter.

There are probably two overlapping periods of spawning in the Channel, in spring and summer, and only one, starting somewhat later in the spring, in the estuary.

The adult life history is deduced from measurements taken throughout the year. During the first year the growth rate is similar in the two sexes but subsequently the females grow more rapidly. Females live longer and attain a maximum size of over 80 mm., the two largest males taken being 70 mm. In the Channel the females probably spawn once in the second year of life, twice in the third and fourth years, while a few may survive to spawn in the fifth year. In the estuary spawning is apparently confined to the third and fourth years.

There is a pronounced migration in winter from all stations but especially from the less saline estuarine areas where males were absent in the coldest months and, in one year, females also. In the spring the females return to the

estuary before the males but migrate seaward again after spawning, the estuary being restocked during July by animals spawned the previous year. Except during September and October the males are always much less numerous than the females at all stations.

Complete penetration of fresh waters by *Crangon vulgaris* is possibly prevented by the great susceptibility of the males to low salinity.

REFERENCES

BALSS, H., 1930. Wanderungen bei Decapoden (Crustaceen). *Erg. de Biol.*, Bd. 6, pp. 305–26.

BLOCH, F., 1933. Fécondation et maturation de l'œuf chez un Pagure, *Diogenes pugilator* Roux. *C.R. Acad. Sci., Paris*, T. 196, pp. 429–31.

BROEKEMA, M. M. M., 1941. Seasonal movements and the osmotic behaviour of the shrimp *Crangon crangon*. Acad. Thesis, Groningen, 100 pp.

BROEKHUYSEN, G. J., 1936. On development, growth and distribution of *Carcinides maenas* (L.). *Arch. néerl. Zool.*, T. 2, 257–399.

CAUDRI, L. W. D., 1937. Einfluss der Temperatur und des Salzehalts auf die Sterblichkeit von Garnelen (*Crangon crangon* L.). *Arch. néerl. Zool.*, T. 3, 179–96.

EHRENBAUM, E., 1890. Zur Naturgeschichte von *Crangon vulgaris* Fabr. *Mitt. sekt. Küsten- u. Hochseefisch.*, Jahrg. 1890, 124 pp.

GROBBEN, C., 1878. Beiträge zur Kenntniss der männlichen Geschlechtsorgane der Dekapoden, nebst vergleichenden Bemerkungen uber die der übrigen Thoracostaken. *Arb. zool. Inst. Wien*, Bd. 1, pp. 57–150.

HAVINGA, B., 1929. Krebse und Weichtiere. *Handb. Seefisch. Nordeuropas*, Bd. 3, pp. 53–87.

—— 1930. Der Granat (*Crangon vulgaris* Fabr.) in den Holländischen Gewässern. *J. Con. Inter. Exp. Mer*, Vol. 5, pp. 57–87.

HERRICK, F. H., 1894. The reproduction of the lobster. *Zoologist*, Vol. 18, pp. 413–17.

—— 1911. Natural history of the American lobster. *Bull. U.S. Bur. Fish.*, Vol. 29, pp. 149–408.

HÖGLUND, H., 1943. On the biology and larval development of *Leander squilla* (L.) forma *typica* de Man. *Sven. Hydro.-Biol. Komm. Skr.*, Ny Ser., Biol., Vol. II, Nr. 6.

ISRAEL, H. R., 1936. A contribution toward the life histories of the Californian shrimps, *Crago franciscorum* (Stimpson) and *Crago nigricauda* (Stimpson). *Div. Fish Game California, Bur. Com. Fish., Fish Bull.*, No. 46.

LEBOUR, M. V., 1931. The larvae of Plymouth Caridea. I. The larvae of Crangonidae. *Proc. Zool. Soc. Lond.*, 1931, (1), pp. 1–9.

LLOYD, A. J. & YONGE, C. M., 1940. Correlation between egg-carrying setae and cement glands in Decapod Crustacea. *Nature*, Vol. 146, p. 334.

MATHIAS, P., 1938. Sur la résistance de *Palaemon squilla* L. et de *Crangon vulgare* F. à la diminution de salure de l'eau. *Bull. Soc. zool. France*, T. 63, 337–43.

MATTHEWS, L. H., 1933. The sea fish and fisheries of the Bristol Channel. *Proc. Bristol Nat. Soc.*, (4), Vol. VII, pp. 442–62.

MEYER, P. F., 1934. Ein Beiträge zur Eiablage der Nordseekrabbe (Granat) *Crangon vulgaris* Fabr. *Zool. Anz.*, Bd. 106, pp. 145–57.

—— 1935*a*. Ein Beiträge zur Frage der Laichperiodizität bei der Nordseekrabbe (Granat) *Crangon vulgaris* Fabr. *Zool. Anz.*, Bd. 109, pp. 23–32.

MEYER, P. F., 1935*b*. Wachstums- und Altersuntersuchungen an der Nordseekrabbe (Granat) *Crangon vulgaris* Fabr. *Zool. Anz.*, Bd. 111, pp. 145–52.

MOUCHET, S., 1931. Sur l'appareil génital mâle de *Peneus trisulcatus* Leach. *Bull. Soc. zool. France*, T. 61, pp. 458–67.

NOUVEL, H. & NOUVEL, L., 1935. Observations sur la biologie d'une crevette: *Athanas nitescens* Leach. *Bull. Inst. Ocean. Monaco*, No. 685.

—— 1937. Recherches sur l'accouplement et la ponte chez les Crustacés Décapodes Natantia. *Bull. Soc. zool. France*, T. 62, pp. 208–21.

NOUVEL, L., 1939. Observation de l'accouplement chez une espèce de crevette *Crangon crangon*. *C.R. Acad. Sci., Paris*, T. 209, pp. 639–41.

NOUVEL-VAN RYSSELBERGE, L., 1937. Contribution à l'étude de la mue, de la croissance et de la régénération chez les Crustacés Natantia. *Rec. Inst. zool. Torley-Rousseau*, T. 6, pp. 9–161.

OTTO, J. P., 1934. Über den osmotischen Druck der Blutflüssigkeit von *Heteropanope tridentata* (Mainland). *Zool. Anz.*, Bd. 108, pp. 130–5.

—— 1937. Über den Einfluss der Temperatur auf den osmotischen Wert der Blutflüssigkeit bei der Wollhandkrabbe. *Zool. Anz.*, Bd. 119, pp. 98–105.

PANIKKAR, N. K., 1940. Influence of temperature on osmotic behaviour of some Crustacea and its bearing on problems of animal distribution. *Nature*, Vol. 146, p. 366.

—— 1941. Osmo-regulation in some palaemonid prawns. *Journ. Mar. Biol. Assoc.*, Vol. 25, pp. 317–59.

PLANKEMANN, H., 1935. Beiträge zur Physiologie der Garneelenhäutung. *Schr. naturw. ver. Sch.-Holst.*, Bd. 21, pp. 195–216.

SOLLAUD, E., 1922. Recherches sur l'embryogénie des Crustacés Décapodes de la sous-famille des 'Palemoninae'. *Bull. Biol. France Belg.*, Suppl. 5, pp. 1–234.

SPALDING, J. F., 1942. The nature and formation of the spermatophore and sperm plug in *Carcinus maenas*. *Quart. J. Micr. Sci.*, Vol. 83, pp. 399–422.

VITZOU, A. N., 1882. Recherches sur la structure et la formation des téguments chez les Crustacés Décapodes. *Arch. Zool. exp. gen.*, Bd. 10, pp. 451–577.

WOLLEBAEK, A., 1908. Remarks on Decapod Crustaceans of the North Atlantic and the Norwegian Fjords (I and II). *Bergens Mus. Aarb.*, 1908, Nr. 12.

YONGE, C. M., 1937. The nature and significance of the membranes surrounding the developing eggs of *Homarus vulgaris* and other Decapoda. *Proc. Zool. Soc. Lond.*, A., Vol. 107, pp. 449–517.

—— 1946. Permeability and properties of the membranes surrounding the developing egg of *Homarus vulgaris*. *Journ. Mar. Biol. Assoc.*, Vol. 26, pp. 432–8.

NOTICES OF BOOKS

Biological Field Stations

By Homer A. Jack

Waltham, Mass.: The Chronica Botanica Co.;
London, W.1: Wm. Dawson and Sons, Ltd. Price $2.50.

Dr Homer Jack has done a good service to biology by providing an up-to-date summary of the biological stations of the world. It includes a list of all stations identified as being in existence in 1940, and since the war must have altered the position it therefore forms a valuable record. Descriptive details are given of each laboratory stating briefly the facilities available together with reference to their previous mention in the literature.

The history of the development and growth in number of such laboratories is outlined and references to previous accounts, among which those of Kofoid in 1910 and T. Wayland Vaughan in 1937 stand out. The number of institutions stated to be in existence in 1940 is 270 of which about 120 are marine, and it is noticeable how the numbers vary from country to country. A mere numerical comparison is, as the author points out however, misleading, the true criterion being the size of the laboratories and the results they produce. There are no major additions to the list of marine laboratories given in 1937 by Wayland Vaughan, though mention might be made of a new station at Belle Isle (Miami Beach) established by the University of Miami, with Dr F. C. Walton Smith as Director.

This publication should be available to students in all biological libraries.

F.S.R.

Fishes and Shells of the Pacific World

By John T. Nichols and Paul Bartsch

The Pacific World Series
New York: The Macmillan Company, 1945. Price 12*s.* 6*d.*

This most useful little book is designed specially for those with a taste for natural history who find themselves for the first time on the shores of the Pacific, particularly service men who are interested in fishes and fishing and in marine animal life generally. The larger part of the work is devoted to fishes.

There are good simple drawings of many of these with notes on their habits. Identification of the fishes most commonly met with should be easy. The first part contains a general review of the fishes with three chapters on the Origin and Distribution of Pacific Fishes, Different Kinds of Fishes, and Collecting Specimens. The second part deals with Fishes of Particular Interest with four chapters on Sharks and Rays, Important Fish Groups, Peculiar Fishes, and Game Fishes. A newcomer to any part of the large area involved is bound to be interested, will learn much, and will be incited to learn more by observation.

Part III on shells is less detailed but more personal and contains delightful accounts of the molluscs to be found and their habits, obviously by one who knows them thoroughly in their native haunts. The notes on the Sulu squids and their cleverness are specially noteworthy.

This book is thoroughly recommended to both trained and untrained naturalists. M.V.L.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1945–46

The Council have to report with very great regret the death on 16 May 1945, of Dr Stanley Kemp, F.R.S., Secretary of the Marine Biological Association and Director of the Plymouth laboratory. During his term of office Dr Kemp rendered distinguished service to the Association, and the loss of one so widely experienced within the ranks of biologists is greatly to be deplored.

During the year the staff of the Plymouth laboratory has suffered a further loss in the death in July of Dr Alexander Sand, F.R.S., a physiologist of brilliant promise.

The Council also regret to report the deaths of the following, who have rendered services to the Association: Prof. E. S. Goodrich, F.R.S., who for ten years represented Oxford University and was lately a Vice-President; Prof. J. Stanley Gardiner, F.R.S., a Vice-President and one of the first elected Honorary Members; and Sir Peter Chalmers Mitchell, F.R.S., who for many years served as a representative of the British Association for the Advancement of Science.

The Council and Officers

Prof. James Gray, C.B.E., M.C., F.R.S., was elected President of the Association in July in place of Dr G. P. Bidder, who had served for the preceding six years.

On the occasion of the retirement of Dr G. P. Bidder from the Presidency, Prof. J. Gray spoke at the Annual General Meeting on 4 July 1945 of the great services rendered to Marine Biology by Dr Bidder, who in his reply recalled the early days of the Association. In view of the very interesting reminiscences related at this meeting it is hoped to print the speeches in a forthcoming number of the *Journal*.

During the year the following Annual Governors have been appointed: A. L. Wagg, Prime Warden of the Fishmongers' Company; Dr C. F. A. Pantin, F.R.S., for Cambridge University; Prof. A. C. Hardy, F.R.S., for Oxford University; and Prof. H. G. Jackson, for the British Association.

Four ordinary meetings of Council were held during the year, three in the rooms of the Royal Society and one at Plymouth. At these the average attendance was sixteen. A special meeting of Council was held on 4 July 1945 in the rooms of the Royal Society to consider the appointment of a new Director. The Association is indebted to the Council of the Royal Society for the use of their rooms for these meetings.

Articles of Association

At the Annual General Meeting of the Association held on 4 July in the rooms of the Royal Society a special resolution was passed which effected certain changes in the Articles of Association. The main alteration affected Article 6. Its purpose is to give flexibility by enabling the President to be himself Chairman of Council, or by allowing, if the Council so desire, a Chairman to be appointed in addition to the President. The President's appointment is to be for terms of five years, but is not to exceed ten years.

It was also necessary to incorporate in the Articles the Council's decision to elect Honorary Members of the Association.

The Plymouth Laboratory

The work of repairing buildings has proceeded slowly but steadily throughout the year. Apart from the Director's house, all the major repairs to the laboratory buildings have now been completed, so that the pre-war working accommodation is again available. Minor interior repairs to the main building are being delayed until better materials are available. The Easter Class building has been reinstated, and a new circulation bench and tanks have been built in the north building.

The aquarium windows have been restored, and it is hoped that the aquarium itself may be repaired before long.

The restoration of the laboratory to full working order has entailed a great amount of devoted work by the technical staff of the laboratory. Especially is this so as regards the many valuable instruments and apparatus owned by the Association, from which all traces of the ravages of war have now been removed.

The Ship and Motor Boat

The *Salpa* has remained under requisition by the Admiralty, and it has been decided that she is now too old for continued use by the Association. A 90 ft. Motor Fishing Vessel (M.F.V.) is being chartered from the Admiralty for a year or so. This is a wooden vessel of 22 ft. 3 in. beam with a Crossley Diesel engine of 240 h.p. at 340 r.p.m. and a speed of $9\frac{3}{4}$ knots. In general lay-out it compares well with the *Salpa* and has somewhat more deck space. The vessel is nearing completion at the Wivenhoe Shipyard near Colchester.

The motor boat *Gammarus* has worked continuously through the year. A new 7 h.p. Kelvin-Ricardo engine has been purchased to replace the $3\frac{1}{2}$ h.p. Kelvin-Poppet motor. The *Gammarus* is thus now provided with two 7 h.p. engines.

Collection of marine animals from one of the trawlers working from Plymouth has been continued, but we are prevented from obtaining certain animals through the lack of a research ship.

The Staff

Since April 1945, Mr F. S. Russell has returned from the R.A.F.V.R. and took up his duties as Director at Plymouth on 27 August; Mr E. Ford returned from the R.A.F.V.R. on 8 May and took charge of the laboratory in the interim after Dr Kemp's death; Dr W. R. G. Atkins returned from the Instruments Section of the Meteorological Office on 1 May; Mr G. A. Steven completed his service with the Colonial Office on 15 October, and Mr G. M. Spooner returned from the Foreign Office on 19 July.

The whole scientific staff are thus once more at work at the laboratory. These long absences have to a certain extent been beneficial to those concerned, in spite of much loss of ground. All have gained in general experience, and some, especially Dr Atkins, Mr Steven, and Dr Cooper, who returned from the Ministry of Supply in December 1944, have made many useful fresh contacts and have had experience of new methods. They will naturally, however, have to spend much of their time at first in reading and getting generally up to date.

Of the technical staff, Mr A. E. Stoate returned to the laboratory from the R.A.F.V.R. (Balloon Barrage) in September; Mr W. H. Gladwell from the Royal Marine Police in October; and Mr T. R. Tozer from the R.A.S.C. in March 1946.

The Council wish to record their grateful appreciation of the valuable services rendered to the Association by Mr E. Ford as Assistant Director of the Plymouth Laboratory since 1935. During this period he has also had the difficult duty of taking charge during the interregna following on the retirement of Dr E. J. Allen and again on the death of Dr Stanley Kemp. The large amount of administration involved has necessarily curtailed the time available for Mr Ford's scientific work, and the Council wish to place on record their gratitude for his unfailing devotion to the affairs of the Association.

Dr J. F. Danielli, Research Fellow of St John's College, Cambridge, has been appointed Physiologist at the laboratory in place of the late Dr Sand, as from 1 January 1946.

The Council have to report that Dr Marie V. Lebour retired from the staff of the laboratory on 31 March 1946. During her thirty years of service at Plymouth Dr Lebour has gained a world-wide reputation by her distinguished researches, to the lasting benefit of the Association. All will wish her many happy years of retirement.

The Council record with grateful pleasure that Mr William H. Searle has now given fifty years of loyal and valuable service as Fisherman Collector at the laboratory.

During the year Dr H. W. Harvey was elected a Fellow of the Royal Society.

Mr G. M. Spooner has been awarded the M.B.E. in recognition of his distinguished war services at the Foreign Office.

The Director has accepted an invitation to serve as a member of the Colonial Fisheries Advisory Committee in place of the late Dr Kemp.

Dr W. R. G. Atkins and Dr H. W. Harvey have continued their work on the Marine Corrosion Committee of the Iron and Steel Institute.

Occupation of Tables

The following have occupied tables at the Plymouth laboratory during the year:

Dr ANNA BIDDER, Cambridge (Library).
C. BOCQUET, Paris (General).
J. R. G. BRADFIELD, Cambridge (General Biology).
Dr S. P. CHU (Nutritional requirements of Phytoplankton).
Lt./Cdr. A. COBHAM, London (Sponges).
J. E. CRADDOCK-WATSON (General Biology).
P. J. CURTIS (General Biology).
Dr J. F. DANIELLI, Cambridge (Cytochemistry of fertilization in *Pomatoceros*).
Miss B. M. M. DAVIS, Manchester (General Biology).
Dr VERA FRETTER, London (Prosobranchs).
Prof. L. GALLIEN, University of Caen (French Scientific Mission).
N. G. L. GUPPY, Cambridge (General Biology).
Dr T. J. HART, Discovery Committee (Falkland Islands' fisheries).
P. H. T. HARTLEY (Library).
Dr R. S. HAWES, Exeter (Gregarines of Polychaetes).
Dr G. E. C. HERKLOTS, Hong Kong (Library).
Lt. G. L. HOFFMAN, Iowa State Fisheries (Parasites of fishes).
N. A. HOLME, Cambridge (Mollusca).
Dr G. R. HOWAT, Gold Coast (Marine Plankton).
Dr M. W. JEPPS, Glasgow (Sponges).
G. A. JONES, Manchester (General Biology).
R. H. LAWS, Cambridge (General Biology).
F/Lt. F. L. LITCHFIELD (General Zoology).
Miss J. LORCH, London (Bone formation in fish larvae).
A. G. LOWNDES (Density and fats of aquatic organisms).
R. E. MACKIE (General Zoology).
A. W. MANSFIELD, Cambridge (General Zoology).
Dr M. W. PARKE (Algae).
Prof. HANS PETTERSSON, Göteborg (General).
A. RIFAAT, Fouad I University, Cairo (Plankton).
Hon. M. ROTHSCHILD (Colour responses under reduced temperatures).
J. SHAW, Cambridge (General Zoology).
Dr J. E. SMITH, Cambridge (General Zoology).
Dr S. SMITH, Cambridge (General Zoology).
Miss N. G. SPROSTON (Parasites of marine animals).
R. SUBRAHMANYAN, Madras University (Algae).
D. H. TAYLOR (General Zoology).
Y. R. TRIPATHI, Allahabad University (Parasites of fishes).
Miss V. VATI, Lucknow University (Embryology of fishes).

No Vacation Courses in marine biology were held during 1945 owing to lack of living accommodation in Plymouth, but the Easter Courses under Mr D. P. Wilson and Mr G. A. Steven were resumed in March 1946.

Mr A. Gillespie has on two occasions brought a number of students from Blundell's School to see the laboratory and do shore and boat collecting.

The Danish Research Vessel *Atlantide* visited Plymouth *en route* for the west coast of Africa for three days at the end of October 1945. Dr Anton Bruun was scientist in charge, and he had with him two Danish assistants, Jorgen Knudsen and Torbin Wolff, and Dr F. C. Fraser of the Natural History Museum. It was a pleasure to welcome members of the expedition at the laboratory.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

During the latter part of the war the Army Photographic Research Unit devised a method of determining the depths and extinction coefficients of shallow water by air photography using colour filters. The War Office has just released a comprehensive report on this 'Transparency Method' by Major J. Grange Moore, M.A. This work, intended for use in connexion with combined operations, has obvious ecological applications, and has already been used in a coastal survey in Scotland to determine the position of large underwater beds of brown algae.

The author records in his report the help given by Dr W. R. G. Atkins throughout this work, in connexion with oceanographical literature and methods. Dr Atkins visited Larkhill and made many contacts with the A.P.R.U. The physics of light penetration and scattering was discussed with the staff of the A.P.R.U. and Prof. T. Le Grand, who visited Plymouth for the purpose. Dr L. H. N. Cooper also joined in the work later on and paid several visits to Portreath to measure extinction coefficients of samples taken at the same time as were air photographs. These determinations were made using the Pulfrich photometer; the function measured is not the same as with the submarine photometer method, and Dr Cooper discussed these and other theoretical considerations with the A.P.R.U. staff. This collaboration occupied both Dr Atkins and Dr Cooper for a considerable portion of last summer.

Dr Atkins is at present engaged largely in preparing for publication the results of work done up to 1941 on the recording of daylight.

Dr Cooper made phosphate examinations of offshore water during the winter of 1944–5. These observations, supplemented by similar records kept by Dr Harvey for each winter of the war, show that the winter phosphate maximum has remained at practically the same low level that has persisted since 1931.

Plankton

Dr H. W. Harvey has studied the growth of a green flagellate in sea water taken from different localities and enriched with nutrient salts and iron. During late summer and early autumn this plant would cease growth after only two or three divisions in water taken from the entrance to Plymouth

Sound, whereas it would grow readily, producing a considerable crop, in water taken from offshore. In late autumn equally rapid growth and crop production took place in water from both inshore and offshore. It proved possible to track down the probable cause of this infertility of late summer and early autumn inshore water towards this flagellate to lack of manganese. The addition of as little as one part per billion of this element considerably increased the crop, while the addition of half a milligram per cubic metre resulted in very heavy production with increased size of the plant.

The addition of small quantities of manganese, within the range in which it has been found by analyses in sea water, showed a marked effect on the growth rate and crop production of three other autotrophic flagellates—two Crysomonads and one Cryptomonad—and of a marine species of *Chlorella*. These experiments, using *Chlamydomonas* as analyst to assess manganese at great dilutions, are indicating that during late summer and autumn the relatively large quantity of organic detritus in the sea adsorbs manganese, reducing the quantity in solution.

The growth of a diatom—*Coscinodiscus excentricus*—has been followed in inshore and offshore water taken in August and in November. The observations bear out previous results on the growth of diatoms in waters of the English Channel and off the coast of Japan, that waters taken from different positions and depths and at different seasons support the growth of several species of diatoms to different degrees after similar enrichment with nitrate, phosphate and iron. The cause or causes of these marked differences are unknown; they were not due, or wholly due, to lack of manganese in the English Channel waters.

Some observations have also been made of the numbers of flagellates of all kinds in the water at the entrance to Plymouth Sound. By using dark-ground illumination and a cell 0·1 mm. deep, between 1000 and 2000 motile cells per cubic centimetre were seen. This is some ten times more than found by Allen and Nelson, in water from the same position at the same seasons, using the 'dilution method' of culture.

Mr D. P. Wilson has completed for the *Journal* his paper on the triradiate and other forms of *Nitzschia closterium* (Ehr.) Wm. Smith, forma *minutissima*. In a discussion on the nomenclature of the species it is shown that it may possibly be distinct from *Nitzschia closterium* (Ehr.) Wm. Smith and not merely a form of it. For the time being, however, it is proposed to retain the name Allen and Nelson originally gave to it. Many features unusual for a diatom are shown, including the ability to grow in length without auxospore formation, which may not occur in the species at all. Silicification is extremely weak; this it appears is normal and not due to cultural conditions, for cells obtained from natural sources are almost as lightly silicified as are cultured ones. Triradiate cells have been seen in natural samples and there is now no doubt that they are a normal feature and not due to poor cultural conditions. Indeed, new evidence points entirely the other way, and it is suggested that triradiate and cruciform cells are products of especially favourable conditions

rather than the reverse. A comparison is made with triradiate *Fragilaria construens* which have been reported from deposits in the Crystal Lake, Wisconsin, where they were at times very abundant. It is suggested that this abundance of aberrant *Fragilaria* also indicates that conditions were specially favourable to the species, rather than unfavourable as has been proposed.

Mr Wilson has interested himself in the unusual abundance of *Physalia* in the south-western area during the summer and autumn of 1945. A fine living specimen of *Physalia*, kindly sent to the laboratory early in August by Major A. A. Dorrien Smith of Tresco, Isles of Scilly, gave an opportunity to obtain a set of photographs of the living animal, including what are probably a unique series of it catching and eating a fish. Some of these photographs were published in *The Illustrated London News* on 1 September, with an appeal for information of strandings of other specimens. This has brought in many records which serve to show that the majority of the strandings took place along the shores of the Bristol Channel and that few were stranded on the English Channel coast. Mr Wilson is collaborating with Prof. J. H. Orton, who has collected additional records, in the production of a paper on the occurrences, to which will be added some records of strandings of loggerhead turtles and some other organisms of oceanic origin.

During the year Dr M. V. Lebour has been chiefly working on the inshore plankton, the catches still being very poor, probably because of the large amount of oil in the Sound. She is now finishing a paper which contains a good deal of new work on records chiefly relating to larval forms in relation to the breeding seasons of certain animals. The larvae of the Decapods, Molluscs and Annelids are named as far as possible and references given to the literature of each species identified for the benefit of future workers.

She has published in the *Proceedings of the Zoological Society* a paper entitled 'The eggs and larvae of some Prosobranchs of Bermuda', embodying work carried on at the Bermuda Biological Station. Forty-three larval forms are described, many of which were reared from the egg in the laboratory or followed from planktonic stages until metamorphosis.

Fauna of the Sea Floor

Mr G. M. Spooner has resumed the studies which had been interrupted by the war. He is writing accounts of the work reported in previous Reports of the Council (*Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 444 and 691). This work began as a study of that part of the fauna of estuaries which takes cover amongst weeds and other objects covering the ground. Gammarids form by far the most important element of this fauna. Study of the succession, along the length of an estuary, of *Gammarus* forms (species and subspecies) has led to a promising method of ecological grading, using the composition of *Gammarus* samples as a 'biological indicator'. Additional morphological work proved necessary for the sake of being able to identify reliably immature and the

earlier mature stages, and to obtain a clearer view of variation between local populations.

Mrs E. W. Sexton has, during the past year, continued the study of the diversity of form in the amphipod *Jassa falcata* (Montagu), especially in the male. She is tracing the history of the species from its establishment in 1808, to decide whether the polymorphism has been unchanged all the time, and whether the variation in form is not by any means all due to development. It is a great opportunity to be able to deal with a cosmopolitan species like this, with its wide range of variants in every collection taken, for, although instances of such occurrences among the Amphipoda have been recorded before, the cases have been few, and the number of specimens affected small.

A short paper has been prepared by Mr Wilson on the way in which *Sepia officinalis* catches its prey. Some photographs he has taken show points not previously recorded, and it was thought well to publish these pictures and to add some notes on the subject which have accumulated over a number of years.

Dr Lebour has published a paper in Vol. XXVI, No. 2, of the Association's *Journal* entitled 'Notes on the Pycnogonida of Plymouth'. In it a new species *Phoxichilidium tubulariae* is described. *Anoplodactylus angulatus* Dohrn is added to the British fauna, and the species of the Phoxichilidiidae, which were in much confusion, generally revised.

A paper on *Teredo* in Plymouth waters has now been finished by Dr Lebour and is in course of publication in the next number of the *Journal*.

Fishes and Fisheries

Mr E. Ford, who was engaged in administrative duties until the Director's return, has taken the opportunity in the absence of a research vessel to resume the study of vertebral variation in teleostean fishes, which had been interrupted by the war. A report on the condition in the order Isospondyli is ready for publication during the current year, and includes data obtained during a brief visit to the British Museum (Natural History) in November of this year. Mr Ford has been in consultation with representatives of the Ministry of Agriculture and Fisheries, and of the Devon Sea Fisheries Committee, regarding the experimental use of small-mesh trawls for catching sprats in the Brixham area during the coming winter. Contact with fishing interests in Cornwall has been restored in connexion with a complaint by mackerel fishermen at Pentewan of damage to the fishery alleged to be due to the discharge of china-clay waste products into neighbouring streams. Problems of the inshore fisheries in general in the two counties were discussed at a meeting of a Sub-Committee set up in connexion with an economic and social survey organized by University College of the South-West, Exeter.

Mr G. A. Steven, when he left the laboratory in 1941, was carrying out researches on the life history and biology of the mackerel at the western end

of the English Channel. The results of this investigation are now being written up. Part of Mr Steven's time has also been devoted to preparing for the full resumption of sea-going activities when a suitable vessel becomes available.

Research on Parasites

The work being undertaken at the laboratory by Miss N. G. Sproston on the parasitic fungoid organism in mackerel has continued.

The examination of mackerel for *Ichthyosporidium Hoferi* (vide *Journ. Mar. Biol. Ass.*, Vol. XXVI, pp. 72–98) has lately been extended, and samples have been obtained from time to time throughout the year from north-east Scotland and south-west Ireland, for comparison with samples caught in the Plymouth area. These additional samples are due to the kind co-operation of Dr James M. Shewan of the Torry Research Station, Aberdeen, and Mr C. F. Hickling, then Port Fishery Captain at Milford Haven. The general conclusions reached indicate that this organism is endemic in mackerel, but that at some (as yet unpredictable) periods, it shows a remission. Such a reduction in numbers of infected fish occurred during the middle of 1945 in samples from both Aberdeen and Plymouth.

In the same sample, however, the disease may be active in some fish and passive—in cystic form—in others; or it may show a secondary activity, when the thick fibrous cysts, of host origin, are broken down by the out-growing hyphae. So far it has not been possible to correlate such transitory immunity with either the condition of the fish or its sexual phase. Investigations are now being concentrated upon any possible effect the fungus may have on the fish as a stock; but understandable difficulties are encountered in obtaining sufficient fish for statistical treatment of the findings.

Visits have been made to Aberdeen, Milford Haven and Mevagissey, Cornwall, so that fish caught along with mackerel could be examined in a fresh state for the presence of a similar infestation to that of mackerel. So far no indication of the parasite has been found in herring; but it is now known that pilchard are equally liable to attack, and that in them the fungus grows with a similar luxuriance to that in mackerel. In these two fishes the cysts do not occur in the muscles, so that infected organs are removed on gutting. There is no reason to believe that it is in any way injurious to man or other animals; but in fresh pilchard a slight deterioration in flavour was detected in heavily infested fish: this, however, is not serious from the canner's point of view. Moreover, cysts of a similar nature were found on occasions in tinned pilchard from California.

Work is being continued on the ecology of parasites of marine fishes from the Plymouth area; and this year these have included some unusual visitors to these waters: two sturgeon, an electric- and an eagle-ray, and also the rare moon-fish. Their parasitic fauna is of considerable interest owing to this extension of their normal geographic distribution; and it may be noted that the moon-fish roves over the warmer oceans of the whole world, and, like the

sun-fish, some of its parasites are constant and are found on individuals caught as far apart as England and Japan. Copepods belonging to a genus new to science were found on this moon-fish; these and other parasites are now being studied and will be described elsewhere.

Algal Investigations

The practical work on the Laminariaceae and Fucaceae, which has been carried out over a period of four years by Dr Mary Parke with the assistance of Miss E. Clay, has been completed and the results of this work are now being analysed. In September 1945 Miss Clay was appointed to the staff of the Scottish Seaweed Research Association Ltd.

The life histories of three species of the Laminariaceae, *Laminaria Cloustoni*, *L. digitata* and *L. saccharina*, and three species of the Fucaceae, *Ascophyllum nodosum*, *Fucus serratus* and *F. vesiculosus*, have been followed in two localities, one on the south coast of Devon and the other on the west coast of Scotland.

Detailed information on the range of growth, longevity and reproduction of these species has been obtained by following the behaviour of individual marked plants of known age which had developed on concrete blocks or on areas cleared of their original populations. In five of the species monthly observations were started on individual plants a few months old and were continued until the plants either became detached or reached their third year of growth. In the sixth species, *Ascophyllum nodosum*, observations on individual plants over a period of three years were not possible, due to the slow rate of repopulation and to the rapid depopulation of the sporelings on the cleared areas.

The more economic side of the investigation has included observations on the seasonal variation of the species, the speed and flora with which cleared areas become repopulated, and the effects of various degrees of cutting on the regenerative powers of all aged plants at different times of the year.

Analysis of the wealth of data obtained is now being undertaken, but it is too early to give the main conclusions.

The Library

European and other countries have been quick to take the opportunity of renewing contacts on the cessation of hostilities. All copies of the *Journal* which have been held back from distribution to other libraries and institutions owing to the war have now been sent out, and exchange publications have been received. Gaps in periodicals purchased have been filled and, apart from German, Italian and Japanese publications, the library is once more practically up to date and complete.

The thanks of the Association are due to those institutions and authors who have presented books or papers, and have otherwise helped in re-establishing the library so quickly.

Published Memoirs

Vol. XXVI, No. 2 of the *Journal* of the Association was published in August 1945; and Vol. XXVI, No. 3, is in the press, but its publication is delayed by paper shortage.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the *Journal* of the Association:

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

ATKINS, W. R. G., 1945. Conditions for the vernal increase in the phytoplankton and a supposed lag in the process. *Nature*, Vol. 156, p. 599.

HARVEY, H. W., 1945. *Recent Advances in the Chemistry and Biology of Sea Water*. 164 pp. Cambridge University Press.

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

HÖRSTADIUS, G. (geb. Kjellström) & HÖRSTADIUS, SVEN, 1940. Untersuchungen über die Eiweissverdauung in vivo und in vitro bei einigen Gastropoden. *Pubb. Staz. Zool. Napoli*, Vol. XVIII, pp. 151–249.

LEBOUR, MARIE V., 1945. The eggs and larvae of some prosobranchs from Bermuda. *Proc. Zool. Soc.*, Vol. CXIV, pp. 462–89.

LOWNDES, A. G., 1945. The displacement method of weighing living aquatic organisms. *Nature*, Vol. 155, pp. 520–1.

LOWNDES, A. G., 1945. Swimming of *Monas stigmatica*. *Nature*, Vol. 155, p. 579.

LOWNDES, A. G., 1945. The swimming of *Euglena* and flagellar movement in general. *School Science Review*, June 1945, pp. 319–30.

ROSS, D. M., 1945. Facilitation in sea anemones. I. The action of drugs. *Journ. Exper. Biol.*, Vol. XXII, pp. 21–31.

ROSS. D. M., 1945. Facilitation in sea anemones. II. Tests on extracts. *Journ. Exper. Biol.*, Vol. XXII. pp. 32–5.

SPROSTON, NORA G., 1945. The genus *Kuhnia* n.g. (Trematoda: Monogenea). An examination of the value of some specific characters, including factors of relative growth. *Parasitology*, Vol. 36, pp. 176–90.

SPROSTON, NORA G., 1945. A note on the comparative anatomy of the clamps in the superfamily Diclidophoroidea (Trematoda: Monogenea). *Parasitology*, Vol. 36, pp. 191–4.

YOUNG, J. Z., 1944. Giant nerve-fibres. *Endeavour*, Vol. III, pp. 108–13.

Membership of the Association

Honorary Members. During the year it was decided to elect Honorary Members to the Association from those who have rendered distinguished services to marine biology, their number to be limited to 20. The first honorary members to be elected are: G. P. Bidder, Sc.D., Dr H. B. Bigelow, Dr R. Dohrn, Prof. J. Stanley Gardiner, F.R.S., Prof. W. Garstang, D.Sc., Prof. J. Hjort, F.R.S., Prof. S. A. S. Krogh, F.R.S., and Dr Th. Mortensen.

Founders. The name of Mr Arthur W. W. Brown has been added to the list of Founders.

Annual and Life Members. The total number of annual members on 31 March 1946 was 324, being 10 more than on 31 March 1945. The number of life members was 53.

Associate Members. There are now 5 associate members, Dr H. Muir Evans and Mr G. H. Wailes having been elected during the year.

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 for the year:

From the Fishmongers' Company (£500); The Royal Society (£50); Magdalen College, Oxford (£25); and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the laboratory: The Universities of Cambridge (£105), London (£105), Oxford (£52. 10*s*.), Bristol (£25), Birmingham (£31. 10*s*.), Manchester (£10. 10*s*.), Leeds (£10. 10*s*.), Sheffield (£5); the British Association (£50), the Physiological Society (£30), the Ray Lankester Fund (£20), University College, Leicester (£10. 10*s*.), and the Imperial College of Science and Technology (£10).

The Council also wish to thank Mr Arthur W. W. Brown for the very generous gift of £100 towards the Special Apparatus Fund; and Mr H. Dollner for the gift of three microscope objectives.

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1946–47:

President

Prof. JAMES GRAY, C.B.E., M.C., Sc.D., F.R.S.

Vice-Presidents

The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS WATERHOUSE, K.B.E.
Sir SIDNEY HARMER, K.B.E., Sc.D., F.R.S.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
Lord MILDMAY OF FLETE, P.C.
The Rt. Hon. Sir REGINALD DORMAN-SMITH
Sir JOSEPH BARCROFT, Kt., C.B.E., F.R.S.
Prof. WALTER GARSTANG, D.Sc.

COUNCIL

To retire in 1947
Prof. F. W. ROGERS BRAMBELL, D.Sc.
Prof. H. MUNRO FOX, F.R.S.
O. D. HUNT
L. HARRISON MATTHEWS, Sc.D.
Prof. JAMES RITCHIE, D.Sc.

To retire in 1948
Prof. C. M. YONGE, D.Sc., F.R.S.
Admiral Sir JOHN EDGELL, K.B.E., C.B., F.R.S.
Prof. J. H. ORTON, D.Sc.
E. BALDWIN, Ph.D.
G. P. WELLS

To retire in 1949
G. E. R. DEACON, D.Sc., F.R.S.
Prof. J. E. HARRIS, Ph.D.
N. A. MACKINTOSH, D.Sc.
Prof. E. HINDLE, Sc.D., F.R.S.
R. S. WIMPENNY

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
A. T. A. DOBSON, C.B., C.V.O., C.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
Major E. G. CHRISTIE-MILLER
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
Prof. H. GORDON JACKSON, D.Sc. (British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

BALANCE SHEET 1945–46

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1946

	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:						
Accrued Expenses	284	1	0			
Subscriptions received in advance	30	9	0			
Grant received in advance	125	0	0			
				439	10	0
BANK OVERDRAFT—COUTTS AND COMPANY				3046	7	9
AQUARIUM GUIDE PRINTING FUND:						
As at 31st March 1945	22	1	6			
Add: Sale of Aquarium Guides		7	0			
				22	8	6
SPECIAL APPARATUS FUND:						
As at 31st March 1945	110	4	11			
Less: Expenditure	100	0	0			
				10	4	11
E. T. BROWNE—BEQUESTS FUNDS:	£	s.	d.			
Building Fund, as at 31st March 1945	1191	12	4			
Interest on Investment	36	4	1			
	1227	16	5			
Library Fund, as at 31st March 1945	1052	18	2			
Interest on Investment	32	2	6			
	1085	0	8			
Special Apparatus Fund, as at 31st March 1945	2393	8	3			
Interest on Investment	72	13	2			
	2466	1	5			
Scientific Publications Fund, as at 31st March 1945	1795	0	11			
Interest on Investment	54	9	11			
	1849	10	10			
				6628	9	4
'SALPA" DEPRECIATION FUND:						
As at 31st March 1945	5338	17	4			
Add: Amount receivable from Ministry of War Transport on account of Hire	402	0	0			
Interest on Investments	158	18	4			
				5899	15	8

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director at 31st March 1941 plus Additions at Cost:						
S/S "Salpa"	2000	0	0			
Motor Boat "Gammarus":	£	s.	d.			
As at 31st March 1945	100	0	0			
Additions during the year ...	50	0	0			
	150	0	0			
Nets, Gear and General Equipment:						
As at 31st March 1945	30	0	0			
Additions during the year ...	20	0	0			
	50	0	0			
				2200	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director at 31st March 1941 plus additions at cost:						
As at 31st March 1945	4150	0	0			
Additions during the year	150	0	0			
				4300	0	0
LIBRARY, at valuation of Mr Ridgill Trout in January 1941 plus additions at cost:						
As at 31st March 1945				16070	0	0
STOCKS ON HAND, as valued by the Director:						
Specimens	600	0	0			
Chemicals	250	0	0			
Journals	400	0	0			
				1250	0	0
SUNDRY DEBTORS:						
Sales of Specimens, etc.	291	12	11			
Ministry of War Transport—Hire of S/S "Salpa"	33	10	0			
Ministry of Agriculture and Fisheries—Fourth instalment of Grant from Development Fund for 1945–6	3512	0	0			
				3837	2	11
PREPAYMENT				14	5	6
GENERAL FUND INVESTMENT, at market value as at 31st March 1931:						
£352. 2s. 3d. Local Loans 3% ... ... (Market value at date £351. 13s. 5d.)				232	7	10

REPAIRS AND RENOVATIONS FUND:						
As at 31st March 1945			438	19	8	
Add: Transfer from Income and Expenditure Account			50	0	0	
Interest on Investment			12	17	10	
						501 17 6
COMPOSITION FEES FUND:						
As at 31st March 1945			299	5	0	
Add: Fees received			63	0	0	
						362 5 0
RESEARCH FUND—MISS N. G. SPROSTON:						
Grant received			420	16	8	
Less: Expenditure			412	10	9	
						8 5 11
BUILDINGS RECONSTRUCTION FUND:						
Transfer from Income and Expenditure Account			800	0	0	
Add: Balance due to General Fund as *per contra*			1400	0	0	
			2200	0	0	
Less: Expenditure			2200	0	0	
						— — —
CAPITAL RESERVE ACCOUNT:						
As at 31st March 1945						21688 8 2
SURPLUS ACCOUNT:						
As at 31st March 1945			4201	0	7	
Add: Surplus for the year, as per Income and Expenditure Account			296	18	6	
						4497 19 1
						£43,105 11 10

C. F. A. PANTIN
O. D. HUNT } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1946 according to the best of our information and the explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & Co.

Prudential Buildings, George Street, Plymouth.
26th April, 1946.

E. T. BROWNE—BEQUESTS FUNDS INVESTMENT at cost:								
£6707. 11*s.* 3*d.* Conversion Loan 3% ... ... (Market value at date £6808. 3*s.* 6*d.*)							6628	9 4
"SALPA" DEPRECIATION FUND INVESTMENTS, at cost:								
£590. 6*s.* 0*d.* Local Loans 3%						506 10 9		
£5256. 15*s.* 4*d.* Conversion Loan 3% ... ... (Market value at date £5925. 3*s.* 7*d.*)						5359 14 11	5866	5 8
REPAIRS AND RENOVATIONS FUND INVESTMENT, at cost:								
£429. 17*s.* 11*d.* Conversion Loan 3% (Market value at date £436. 6*s.* 11*d.*)							438	19 8
COMPOSITION FEES FUND INVESTMENTS, at cost:								
£18. 8*s.* 6*d.* Local Loans 3%						15 15 0		
£339. 2*s.* 8*d.* Conversion Loan 3% ... ... (Market value at date £362. 12*s.* 5*d.*)						346 10 0	362	5 0
CASH AT BANK AND IN HAND:								
Lloyds Bank Limited						394 19 11		
Cash in Hand						38 17 1	433	17 0
RECOVERABLE EXPENDITURE:								
Biological Investigations on Algae:								
As at 31st March 1945			32	5	8			
Expenditure			830	13	3			
			862	18	11			
Less: Grant, etc., received ...			791	0	0			
						71 18 11		
Buildings Reconstruction Fund, estimated amount recoverable under War Damage Act						1400 0 0	1471	18 11
							£43,105	11 10

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1946

	£ s. d.	£ s. d.
To Salaries, including Association's Contributions to Superannuation and War Bonuses ...		8473 13 7
,, Laboratory and Boats' Crews' Wages, including National Insurance, Contributions to Superannuation Scheme, War Bonuses and Employers' Liability Insurance ...		4411 1 3
,, Upkeep of Library		230 19 0
,, Scientific Publications, less Sales		249 1 1
,, Upkeep of Laboratories and Tank Rooms, etc.:		
Buildings and Machinery	126 6 1	
Electricity, Oil, Gas, Coal and Water ...	480 14 4	
Chemicals and Apparatus	297 9 1	
Fire Insurance, Tithe, Ground Rent and Rent of Store	77 3 11	
Travelling Expenses	192 19 5	
Stationery, Postages, Telephone, Carriage and Sundries	370 6 6	
Specimens	204 17 2	
Architect's Fee for Plans for reconstruction of Buildings	400 0 0	
		2149 16 6
,, Expenditure in connection with Motor Fishing Vessel:		
Wages	95 8 10	
Sundry Expenses	70 10 7	
		165 19 5
,, Maintenance and Hire of Boats:		
Petrol, Oil, Paraffin, etc.	19 0 1	
Maintenance and Repairs with Nets, Gear and Apparatus	56 10 2	
Purchase of Materials for Nets, etc., for Sale	62 18 7	
Boat Hire and Collecting Expenses	20 1 7	
Third Party Insurance	5 0 0	
		163 10 5
,, Bank Charges		5 8 6
,, Transfer to Repairs and Renovations Fund		50 0 0
,, Transfer to Buildings Reconstruction Fund		800 0 0
,, War Time Expenditure		
,, Balance, Being Surplus for the Year ...		296 18 6
		£16,996 8 3

	£ s. d.	£ s. d.
By Grants:		
Ministry of Agriculture and Fisheries Grant from Development Fund	14042 0 0	
Fishmongers' Company	500 0 0	
British Association	50 0 0	
Royal Society	50 0 0	
Physiological Society	30 0 0	
Cornwall Sea Fisheries Committee	10 0 0	
		14682 0 0
,, Subscriptions (excluding Subscriptions received in advance)		344 3 11
,, Donation		25 0 0
,, Fees for Tests of Materials		58 11 6
,, Sales:		
Specimens	1213 10 1	
Nets, Gear and Hydrographical Apparatus ...	19 0	
		1214 9 1
,, Table Rents (including University of Cambridge £105; London £105; Oxford £52. 10s. 0d.; Bristol £25; Birmingham £31. 10s. 0d.; Leeds £21; Manchester £10. 10s. 0d.; Leicester £10. 10s. 0d.; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20 and Ministry of Works £104)		528 7 6
,, Interest on Investments		19 8 8
,, Sale of Dr M. V. Lebour's Book		5 0 0
,, Sale of "Plymouth Marine Fauna" ...		7 2 0
,, Balance of Expenditure on War Damage Repairs written off in earlier years Recovered from War Damage Commission		112 5 7
		£16,996 8 3

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by a research vessel and by a motor boat and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

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