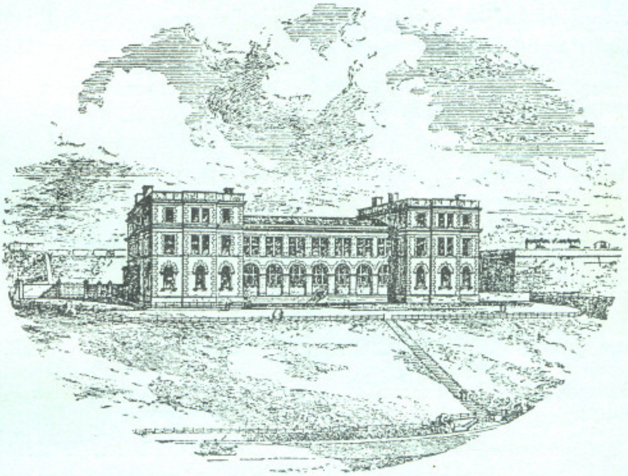
New Series.—Vol. XXI., No. 2—issued March, 1937.
(Completing Volume XXI.)
Price Fifteen Shillings net.

Journal
OF THE
MARINE BIOLOGICAL ASSOCIATION
OF
THE UNITED KINGDOM.



THE PLYMOUTH LABORATORY.

PLYMOUTH
PUBLISHED by the MARINE BIOLOGICAL ASSOCIATION
from whom copies can be obtained at the published price (postage extra)
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THE DIRECTOR, THE LABORATORY, CITADEL HILL, PLYMOUTH
Trade discount of 20 per cent is allowed to booksellers.
Sent free by post to all Members of the Marine Biological Association.
Annual Subscription for Membership, One Guinea.
PRINTED AT THE MAYFLOWER PRESS BY WILLIAM BRENDON & SON, LTD.

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The Habits of the Angler-fish, *Lophius piscatorius* L., in the Plymouth Aquarium.

By
Douglas P. Wilson, M.Sc.,
Naturalist at the Plymouth Laboratory.

With Plate I and 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE Angler-fish (*Lophius piscatorius* L.), also known as the Fishing-frog, Monk-fish, Sea-devil, etc., is notoriously difficult to keep in captivity. It has rarely survived in an aquarium for any length of time and published accounts of observations made from life are somewhat conflicting. Much that has been written about the habits of the species has been based on deduction from the structural features of dead specimens. It seems therefore worth while putting on record the details of some recent observations made at Plymouth, where a number of angler-fishes have been kept alive and in health for periods varying from a few weeks to nearly a year.

Although living angler-fishes are regularly brought ashore by the S.S. *Salpa* very few survive for more than a few hours. It is probable that the soft and flabby nature of the body, particularly of the abdominal wall, exposes the fish to severe internal injuries in the trawl. All survivors have been small and had apparently in some way escaped the usual bruising that takes place when the cod-end is hauled. It is noteworthy that one brought up in unusually good condition was taken in a small Agassiz trawl, an instrument which is much less severe on its captives.

The colour of a healthy angler-fish generally distinguishes it at once from those that are dead or dying. The latter exhibit a fine speckling of pigment that from a little distance imparts an almost uniform chocolate brown appearance to the greater part of the head and back. In a healthy specimen the colour is usually paler and yellower, being often coarsely mottled with light and dark patches, especially when it has presumably come off a gravelly bottom.

With the exception of the first specimen (later referred to as Angler-fish No. 1) all have been kept in a glass-fronted slate table-tank, five feet long, two feet four inches wide, and with a water depth of nearly fifteen inches. The greater part of the bottom was thickly strewn with a gravelly sand containing much fragmented shell (see Plate I): at one end there were a few large rocks. A few small starfishes, Aphrodite, Scaphander Holothuria, and some small fishes shared the tank.

In nearly every instance hand feeding was necessary for the first few weeks, because living fishes of species attractive to angler-fishes were not at the time available. Dead wrasses (generally *Ctenolabrus rupestris*, sometimes *Labrus bergylta*), gobies (*Gobius minutus* and *G. paganellus*), and an occasional gadoid were given. As remarked later some individuals took more readily to this treatment than did others. The fish was always inserted into the angler's mouth head first. If the jaws gripped it, it would almost invariably be swallowed, but very frequently the mouth would be opened as wide as possible and by a convulsive movement the food " coughed " out. Repeated insertions might be necessary before the angler-fish would bite. One or two angler-fishes that were at first difficult to feed seemed to learn through experience and later on gave, on the whole, less trouble.

In order to make observations on the use of the lure living fish were from time to time placed in the tank. If newly caught from the sea, however, they would be too bruised and frightened to react to the angler's lure. Fish netted from a tank where they had lived for some time were better, but even so were generally too scared to behave naturally. Removing the angler-fishes themselves to a tank containing small fishes, which had been living there long enough to be fully accustomed to their surroundings, gave greatly improved results. This tank was twice the length of the angler's own and was strewn with sand; it housed starfishes of several kinds and some Corystes crabs. The angler-fishes were never seriously isturbed by their transference (in a large bowl of water) and would usually at once settle themselves in a sandy hollow and begin to fish.

I should specially like to thank Capt. V. Lord and the crew of the S.S. *Salpa* for the care they have taken with the angler-fishes they have caught alive. Mr. G. M. Spooner has from time to time attended them, and kept notes for me when I have been away, and to him I am also grateful.

HISTORICAL.

The literature relating to angler-fishes and their habits is extensive. From Aristotle onwards the curiosity of naturalists has been aroused, but few writers appear to have watched the fish alive, either in its natural environment or in the confines of an aquarium tank, and many stories of its habits are based largely or solely on imagination. I propose to mention here chiefly those more recent authors who have recorded observations on the living animal.

One cannot, however, ignore Aristotle. His remarks show that he must have spent much time watching the creature through the surface of the sea. He saw angler-fishes stirring up the sand and mud when settling themselves on the bottom ; he saw the dorsal fin-rays used as baits, and the capture of little fishes. He records the unusual thinness of angler-fishes caught after the loss of the tips of their fishing rods. All that later writers can do is to amplify his remarks by filling in the details.

In more modern times a few naturalists have made some first-hand observations. In 1874 Saville Kent kept an angler—apparently for a few days only—in the old Manchester Aquarium. He compared it to a rock, the irregular bordering tags of skin resembling Grantia, ascidians, etc., organisms such as hang down from rocky ledges. The dorsal spines he likened to young Laminaria fronds, and the eyes to acorn-barnacles. He apparently did not see his specimen feed, but supposed that fishes misled by this mimicry would approach near enough to be snapped up : he seems to have doubted stories of angling activities.

Guitel (1891) kept a Lophius, sixty centimetres long, for two months in the laboratory aquarium at Arago. He never saw the lure in use ; it was always folded back out of the way. His fish captured a bass half its own length and two large Sargus fishes when they happened to swim too close above the mouth.

Bigelow and Welsh (1925) record some observations by W. F. Clapp, who frequently watched the feeding habits of this fish at low-tide in Duxbury Bay, Mass. It is described as lying motionless among the eel-grass with the " bait on the tip of the first dorsal ray swaying to and fro over the mouth, either with the current or by some voluntary motion so slight as to be invisible." It was observed to take tomcod (*Microgadus tomcod* Walbaum) which were caught when they swam too near to the bait. The species of angler-fish here mentioned is given as *Lophius piscatorius* Linnæus, but Berrill (1929) has more recently brought forward strong evidence to support an earlier conclusion that the American angler-fish is distinct from the European and should be named *L. americanus* Valenciennes.

Dahlgren (1928), in a popular account of the habits and life-history of the angler, mentions that he has watched numbers of this fish tethered alive in the sea close to the Mount Desert Island Laboratory. He describes how they were there attacked by starfishes and sea-urchins, which ate away patches of their skin. Dahlgren did not see his anglers feed and he definitely states (p. 22) that no one has seen a Lophius feed while confined in an aquarium. " He makes a poor aquarium subject since he refuses all food in captivity, and hence does not live long." Dahlgren points out the paucity of original observations on the use of the lure for fishing since Aristotle made the first statement about it.

The most important recent observations are those of Chadwick (1929), who gives a short, but very accurate account of the feeding habits of angler-fishes in the Port Erin aquarium. He repeatedly saw them use the lure to attract coal-fishes (*Gadus virens*), which they seized and swallowed head first.

Finally one gathers from a popular article (Weller, 1934) that living angler-fishes are occasionally exhibited in the Brighton Aquarium, and that they are there fed on flat-fishes attracted by the lure. The species has also been exhibited in the Zoological Society's aquarium at Regent's Park (Boulenger, 1932) but survived for only a few days, evidently not feeding.

INDIVIDUAL HISTORIES.

During the past two years about ten angler-fishes have lived, apparently in good health, in the Plymouth aquarium. Of these only five have survived longer than a few weeks: some particulars of their histories are given below.

Angler-fish No. 1.

Caught : first week in January, 1935.
Died : 8th April, 1935.
Length when caught : 6 inches.
Length at death : 7¼ inches.

During the first part of its captivity it lived in a bowl strewn with shelly gravel and placed under circulation from a sea-water jet. Later it was exhibited in a small tank in the public part of the aquarium. For the first ten days no food was taken although living *Gobius minutus* and small flat-fishes were supplied. Hand feeding was then resorted to, the mouth being held open while a fish was inserted. While at first it was difficult to induce the angler to accept food, this later became easier, and it was no longer necessary to force open the mouth. This angler was never known to catch prey for itself. A photograph of it, taken within a fortnight of capture, is reproduced elsewhere (Wilson, 1935, Fig. 80).

Angler-fish No. 2.

Caught : 18th April, 1935. Died : 17th March, 1936.
Length when caught : 10½ inches.
Length on 7th November, 1935 : 15 inches.
Length on 10th January, 1936 : 17½ inches.
Length at death : 18¼ inches.

This specimen, like all subsequent ones, was placed in the tank already described (p. 478) as soon as it was brought in. For about the first month it was every two days or so placed in a bowl and removed from the tank for convenient feeding by hand. Later it was allowed to catch living fish for itself. It was often seen to fish with the lure, except during the last few months when it always waited until prey chanced to wander, or was driven, within reach. This angler, like the first, was very docile and easy to handle, never snapping at the fingers when fed by hand. It finally succumbed to disease.

Angler-fish No. 3.

Caught : 3rd September, 1935.
Died : 16th November, 1935.
Length when caught : 8 inches.
Length at death : 10½ inches.

At first fed on dead fish given by hand or forceps, it later refused such proffered food and apparently subsisted on living *Gobius minutus*, which were put into the tank and which it must have caught for itself. It was often seen using its fishing lure and once or twice was observed to catch a goby that came too near. A post-mortem revealed two half-digested *Gobius minutus* in the stomach and unidentifiable remains in the intestine. Cause of death unknown.

This specimen was rather vicious and would snap fiercely at food presented with the forceps ; it was not safe to give food with the fingers.

Angler-fish No. 4.

Caught : 17th December, 1935.
Died : 25th March, 1936.
Length on capture : 11¼ inches.
Length at death : 13 inches.

Unlike the last this fish never snapped when hand-fed and was quite docile. It was very easy to feed, generally accepting dead fish readily when living were not available and rarely " coughing " them out again. It gave very fine displays of its angling abilities, and on it, more than on any other single specimen, my account of this habit is based. It eventually died from the disease that killed No. 2 as well as one other angler-fish not specially mentioned in this paper. This disease was evidently highly infectious ; the skin and underlying tissues of the head swelling rapidly, becoming soft and gelatinous, and finally peeling away to the bone, death ensuing within a few days.

Angler-fish No. 5.

Caught : 29th January, 1936.
Died : 24th May, 1936.
Length on capture : 10½ inches.
Length at death : 12½ inches.

This was first fed by hand on dead fish which were occasionally accepted but more often refused, being " coughed " out repeatedly. There is little doubt that it caught and ate the *Gobius minutus* living in the same tank. It was often seen with the rod held horizontally forwards above the closed mouth as if in readiness to fish, but was never actually observed to catch anything. It died by jumping out of the tank during the night, having been saved from the disease that killed Nos. 2 and 4 by being isolated from them. A post-mortem revealed remains of food, including an otolith in the intestines.

The remaining angler-fishes need not be specially mentioned. They were very useful in checking observations made on these five, and added some details to them. One, caught early in July, 1936, and suddenly dying for no apparent cause about five weeks later, is shown in Plate I. This photograph was taken when it appeared to be in perfect health eleven days before death. At that time it was expected to live for at least several months.

Angler-fishes show strong individual characteristics, especially as regards their habits and reactions. While some are sharp tempered and snap readily at any object, such as a ruler pushed towards them, others are very quiet and docile. Some readily swallow dead fishes placed in their mouths, others do not. Some angle with the lure much more frequently and readily than do others. One or two specimens have made little or no use of the lure, at least while being watched. Certain individuals seemed much more inclined than most to sit about on the rocks at one side of their tank. In short, no two anglers behaved exactly alike.

GROWTH.

In Figure 1 are shown graphically the length increases of the five angler-fishes whose histories have just been given. Except for No. 2 only the lengths at capture and at death are plotted. Frequent measurements were not taken as they were scarcely practicable. It is extremely difficult to measure a living angler at all accurately, especially at the bottom of a tank where the ruler has to be balanced horizontally on the rounded upper surface of the angler's head. The amount of closure of the mouth may make a slight difference. The limits of error are probably an eighth of an inch or a little more either way. For this reason too much reliance should not be placed on the exact slopes of the growth lines as shown. Nevertheless the relatively rapid growth of No. 3 as compared with the others might be due to the fact that it took place when the tank temperature was higher than at the times when Nos. 1, 4, and 5 were kept. On the other hand the rapid growth of No. 2 between 7th November, 1935, and 10th January, 1936, scarcely justifies such a conclusion.

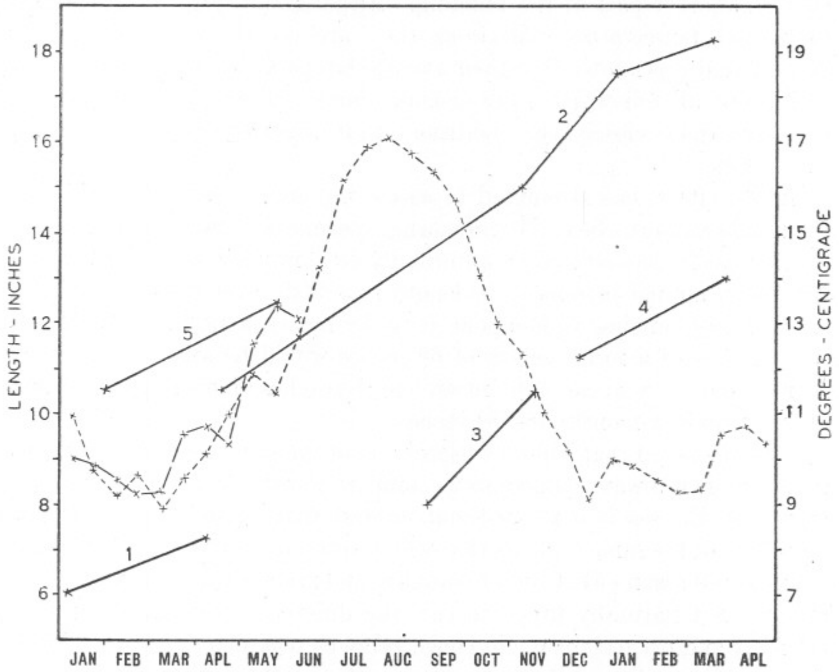

FIG. 1.—Growth of the five angler-fishes mentioned in the text shown by continuous lines. Broken lines represent tank temperatures from January, 1935, to June, 1936. Temperatures from January, 1936, to June, 1935, are plotted on the left and the points joined by longer broken lines. Each plotted point is an average fortnightly temperature calculated from daily readings taken by Mr. A. J. Smith.

Angler-fish No. 2 increased in length by 7¾ inches in almost exactly eleven months, giving an annual increment of about 8½ inches per year. The other four fishes lived for much shorter periods than this, but all appear to have been growing at approximately similar rates.

In assessing the value of these growth data for young angler-fishes kept under aquarium conditions it should be remembered that all were carefully fed and probably on the whole got as much food as they wanted. The temperature curve given is based on regular readings taken in an aquarium tank in another part of the building. Although all tanks exhibit slight individual temperature variations they are on the same circulatory system, and it is known that their average temperatures do not materially differ, but all follow the same general curve. Thus this curve should represent quite closely the conditions that occurred in the angler-fish tank itself.

Fulton (1903) has attempted to assess the growth rate of Lophius in the northern North Sea. By measuring specimens trawled in all months of the year he has estimated, admittedly on somewhat scanty data, that the mean annual increment in length is a little over 6 inches, this for angler-fishes ranging from about 6 to 18 inches long. He considered that anglers of a mean length of 6¾ inches would be approximately six months old; a year later the mean length reaches about 12½ inches, and at two years six months 18–18½ inches.

It will be noted that Fulton's fishes were of the same size range as mine. Although it is always dangerous to compare growth in an aquarium with growth in the sea it is not without interest that his estimate of annual growth is of the same order as that which actually took place in captivity. If one could assume that both his anglers and mine obtained as much food as they felt naturally urged to eat, the difference between his smaller estimate and my records might conceivably be regarded as due to a difference in temperature. Bottom water in the northern North Sea is considerably colder throughout the year than that circulating in the Plymouth aquarium.

MOVEMENTS AND CAMOUFLAGE.

As has been often remarked by other writers angler-fishes are very poor swimmers. They can get along moderately fast by vigorous undulations of their stumpy bodies, but this looks and probably is an exhausting process. Once in mid-water they can plane down gracefully with outstretched pectoral fins, but on the whole they do not swim much, spending the greater part of their time resting quietly on the bottom. The paired fins are used for walking; the pelvics by virtue of their position under the widest part of the head raise the fish off the ground; they are used as legs and are assisted by the pectorals pushing against the ground. The centre of gravity lies between the insertions of the pectorals and the pelvics. When the angler-fish settles down in sand or sandy gravel it digs for itself a small hollow to accommodate the deep rounded underparts of head and abdomen. The pelvics shovel the sand and any pebbles somewhat forwards and outwards and the pectorals push this material away to either side. The fish has remarkable control over the movements of the pectorals, they are used almost like webbed hands. In a few minutes the hollow is made and the angler then backs into it. One or both of the pectorals may flick a few grains of sand over the back. As the fish finally settles down it slightly raises the head and then lowers it rather smartly. By this action water is driven out from under the fish and, flowing away on all sides, spreads out the irregular tags of skin that fringe the lower jaw and sides of the body. The tags then settle neatly on the surface of the sand alongside. At the same time the pectorals spread themselves flat over the ground. In this position the coloured upper surface of the angler-fish is almost flush with the surrounding surface.

The angler-fish has very perfect powers of matching its colour and colour mottlings to the sand or gravel on which it is resting. I consider that once it has settled down and become fully colour-adapted it is more difficult to detect than the average flat-fish, unless the latter happens to be partially buried. Frequently I have been surprised at the time it has taken to discover the whereabouts, in a not very large tank, of an angler-fish known to be there. The disguise produced by the remarkable way in which the colour mottlings take on the tone and texture of the ground is heightened by the presence of the fringing tags, which break up the outline of the body and merge it most effectively with the surroundings (see Plate I).

When an angler-fish is really settled small bottom organisms crawling over it do not seem to cause disturbance. An *Aphrodite aculeata* has been seen to crawl rapidly across the head and eyes without the fish taking any apparent notice.

Certain individual angler-fishes would sometimes sit propped up among the rocks at one end of their tank. It may be that they were attracted by the small fishes (blennies, wrasses) that tended to congregate there, and the habit does at any rate suggest that from time to time they would naturally haunt rocky places in the sea. The suggestion made by some writers that an angler-fish simulates an irregular lump of rock with the tags resembling attached sedentary organisms should not therefore be dismissed too lightly. I am of the impression, however, that in such a position an angler is more readily perceived by other fishes, but the point is one that is difficult of proof.

RESPIRATION.

A peculiarity of the angler-fish and its relatives is the position of the gill-slit, which opens behind the pectoral fins instead of in front of them as in all other fishes. Viewed from above the slits are largely hidden by the pectoral fins, but their innermost and posterior corners open in the axils between these fins and the trunk. In the position in which the angler normally lies, the lower border of each slit is formed by a loose flap of skin, which in the above-mentioned axil is developed to form a somewhat spout-like structure, or perhaps a better comparison is to the lip of a jug turned upwards. The upper part of the slit is formed partly by the base of the pectoral, and partly by a loose flap of skin, lying in the axil, and stretching from the fin to the innermost posterior edge of the slit where it passes into the spout. Except during expiration the spout is covered by this loose dorsal flap of skin and is invisible from above. When expiration takes place the flap is drawn forwards to uncover the spout and with it forms a round hole (see Figure 2 and compare Plate I where the angler is not expiring). The upward curvature of the spout causes the expiratory current to be deflected vertically upwards. The expiratory currents, one from each side, were frequently so strong that the larger angler-fishes disturbed the surface of the water a foot or more above. The vertical deflection ensures that the sand around the lurking angler is undisturbed when it breathes, thus probably reducing to a minimum the chance of detection by its prey.

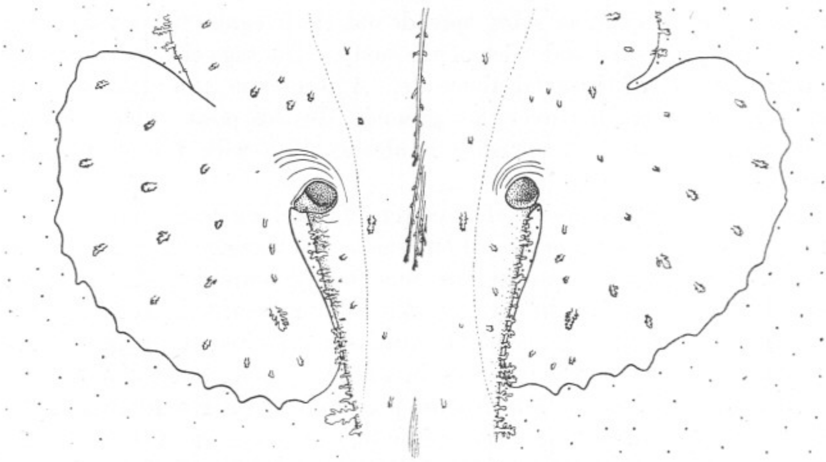

FIG. 2.—A sketch, based on a flashlight photograph, of the gill-slit apertures of an angler-fish during expiration, viewed from above.

When a Lophius is quietly resting there is a long interval between the beginning of one expiration and the next. At a temperature of 11° C. the following times were recorded.

1 minute 25 seconds.
1 ,, 56 ,,
1 ,, 44 ,,
1 ,, 38 ,,
1 minute 50 seconds.
1 ,, 42 ,,
1 ,, 40 ,,

One wonders whether these long intervals may not also assist the fishing, since they enable the angler to keep its body perfectly still while attracting its victims.

A typical respiratory cycle takes place as follows. For most of the period the angler-fish lies still with the mouth closed or nearly so. Towards the end of the period the mouth opens slightly and for some seconds inspiration takes place, the head rising slightly. The mouth is then closed, expiration follows immediately and lasts for a few seconds, the head sinking slowly down again.

While swallowing prey the respiratory rate is increased for several cycles. The resting periods are omitted, and the breathing movements are often more vigorous than usual. Perhaps the swallowing is thereby assisted, or maybe the energy expended in the capture demands an increased rate. On the other hand this increased rate has often accompanied the swallowing of dead fish placed in the mouth and accepted quietly without effort. The movements are genuine inspirations and expirations, not merely discharge of water taken in when catching prey.

Use of the Lure.

There is no doubt whatever that the first dorsal spine, or "rod," with its tag of skin, or "bait"—the whole being known as the "lure"—is used to attract fishes into reach of the mouth. This has not only been seen by Chadwick (1929) and others, but has been repeatedly confirmed by my own observations. An angler when hungry erects the lure immediately any suitable fishes come anywhere near and endeavours to attract one of them close enough to be caught. The lure is quickly jerked to and fro, and as the rod is almost invisible the bait (in my specimens always forked and "fly-like," not vermiform) simulates some tiny creature darting about. An attracted fish rushes up in an endeavour to catch it; the bait is skilfully flicked out of its way just in time and, with a final cast, is dashed down in front of the mouth which may open very slightly. The intended victim, still following the bait, turns slightly head downwards; it is now more or less directly head on to the angler's mouth. The jaws snap faster than the eye can follow, and the tail of the prey is next seen disappearing from sight through the firmly closed mouth.

As far as I have been able to observe the bait is not actually touched by the victim before it is caught, as has sometimes been supposed. Touching the bait with forceps does not cause a reflex snapping of the jaws.

The moving lure has a strong attraction for healthy hungry fishes of several kinds. Small pollack, whiting, pout, and bass were the species actually observed to be attracted to it, but probably most pelagic fish that capture moving prey by sight would at least swim up to investigate the darting object. Many fishes take a ready interest in moving things. A small angler crawling over the bottom of a tank into which it had just been placed aroused, as a rule, the curiosity of nearby fish, pollack and small dabs swimming towards it, keeping, however, at that time a safe distance away.

Besides the quick lashing motion of the lure just described, some anglers occasionally combine with it another movement. Every now and then the rod is depressed until the bait hangs just in front of and rather below the level of the lower jaw. It is then for a few seconds given a curious vibratory movement, after which the sharp flicking is again resumed, the bait being jerked over wide arcs in various directions.

The second to sixth spines of the dorsal fin are more conspicuous when raised than the lure; they generally bear numerous short tags of skin along their whole lengths, but lack special tags at their tips. I suspect, but have not been able definitely to prove, that they are sometimes used as an accessory lure. I have once or twice seen them waved from side to side when fish, which the angler presumably might desire to eat, were too distant for the lure to be readily visible. It seemed at the time that the angler was endeavouring to seize their attention, but unfortunately on these occasions the fish were newly brought in from the sea and were too damaged to behave normally. These spines are often kept raised, although quite still, when no fish are about. In the sea water-movements might gently wave the tags; on a fish swimming up to investigate, the lure proper would be brought into play to manoeuvre it in front of the mouth, the more vigorous motion of the bait now attracting the fish more than the spines, which in any case could be folded back. As a rule they remain erect while the angler is fishing.

The lure is not invariably used when prey is captured. Very often anglerfishes simply sit quite still until a fish chances to swim near enough. They can be very patient. Individuals vary much in this respect, some using the lure much more than others. When the lure is not in use it is depressed right back between the eyes, while the other dorsal spines may or may not be raised. Some individuals were often observed to direct the lure forwards horizontally across the mouth, keeping it quite still in that position for hours on end. Whether this has indicated hunger, and the rod was in a ready position for instant action, I have not been able to determine satisfactorily, but suspect that hunger may have been the explanation.

Angler-fishes rarely chase their prey. Very occasionally I have seen them crawl towards some newly introduced pollack or similar fishes which they had been unable to attract, only to settle themselves down again and ply the lure from a nearer vantage point. If a fish passes a little to one side an angler may turn its head slightly towards it, but never more than the merest trifle. The movement is so slight that I have never seen a fish alarmed by it. To a practised eye the presence or absence of slight movements of the head and eyes, and other almost imperceptible signs, will show whether an angler-fish is hungry and interested in prey or not.

SEIZURE OF PREY.

The actual seizure of the prey takes place too quickly for the human eye to follow. One moment the pollack is there trying to catch the bait, the next the angler-fish is sinking back with the pollack's tail protruding from its jaws. In between there is a blur of rapid movement which defies analysis by straightforward observation. Certain points, however, seem clear and can be stated.

The angler-fish nearly always strikes when the fish is just in front and a little above the level of the mouth. The latter is almost completely closed, although there may be a slight anticipatory gape. The prey should be more or less head on and approaching slowly, although this is not an invariable rule. When the moment comes to strike it seems that the angler suddenly thrusts itself a short way upwards and forwards with the aid of the pelvic fins braced against the ground. Little assistance appears to be given by the pectorals. At the same instant the mouth opens and presumably the buccal cavity is rapidly enlarged, sucking in water and fish at the same time. The jaws snap and the angler sinks back into its sandy hollow to swallow its captive in more leisurely fashion. The tail slowly disappears between the angler's lips, the fish, which always lies on its side, being drawn in and swallowed head first. The heavy breathing movements that occur during swallowing have already been described (p. 487). As the still struggling fish passes down the œsophagus and reaches the stomach its captor sometimes shivers a little as at a queer sensation.

It is well known that when the mouth of an angler-fish is closed the lower jaw projects a considerable distance in front of the upper. This leaves a well-marked gap between the two jaws. The gap is closed by a flap, pigmented on its upper surface, which is attached below the rows of lower teeth and projects freely backwards towards the upper jaw behind. This flap among other functions seems to play an important part in preventing the escape of prey, especially when a fish has to be turned in the buccal cavity preparatory to being swallowed head first. When a fish has been caught broadside on, and has not been very firmly held between upper and lower teeth, I have watched this flap gradually and carefully worked over the fish, starting from one end or the middle.

Guitel (1891) suggests that swallowing is assisted by the very mobile superior and inferior pharyngeal teeth, which by a to and fro action drag the prey in through the jaws and pass it back into the throat. This may very well be so ; the point could be investigated with an X-ray apparatus.

The angler-fish always endeavours to seize its prey head first, but is sometimes unsuccessful, especially if it strikes at a fish swimming over it from behind forwards, or one that is crossing the jaws at right angles to the body axis. In these circumstances it is quite common for the fish to be seized by the middle of the body, both head and tail projecting from the jaws. The head is usually drawn in first, not without difficulty as the angler's hold must be loosened an instant and there is a chance of the prey escaping. Occasionally the fish may be caught tail first, leaving the head projecting ; this is drawn in—one or two careful gulps may be necessary—and I believe, but cannot be sure, that on such an occasion the fish is turned round within the buccal cavity so as to be swallowed head first.

The few flat-fishes I have seen taken were always caught head first as they were approaching from directly in front. My impression is that greater care is taken to seize flat-fishes in this way and that they are not as much esteemed as round fishes. On one occasion when a small dab was lying across its mouth an angler-fish struck at a young whiting. The whiting was caught by the middle of the body, but in the action the dab was sucked in through the mouth. The presence of the dab obviously disconcerted the angler which seemingly tried to swallow it first while still holding the whiting. After some seconds, however, it released the latter and swallowed the dab, several pronounced gulps being required to get it down. The whiting was caught and swallowed a few minutes later, after which no further interest was shown in food.

The incident just related was the only occasion on which I have seen more than one fish caught simultaneously. I believe that an angler-fish takes care, as a rule, that not more than one shall be seized at once, especially if the fishes be of a fair size relative to itself. It seems too that a captured fish must be completely swallowed before the angler is ready to strike again.

An angler-fish rarely misses ; only once or twice have I seen it happen, the intended victim dashing off in great alarm. An angler does not strike unless capture is a reasonable certainty. Once or twice an angler-fish has released a well-caught fish, probably because it was too large and struggled too violently for it to be swallowed in comfort, the angler perhaps not being extremely hungry at the time.

Amount of Food taken at one Meal.

Lophius has long had a reputation for gluttony that seems to be based only on the size of its mouth, an occasional well-filled stomach, and on the fact that fishes are often found in its buccal cavity when the trawl is hauled. These latter, at any rate, almost certainly got there by accident, for should an angler, in its struggles amid the densely packed cod-end, happen to open its mouth an assortment of creatures will immediately fall through the gape and it will be almost impossible to eject them. Some, indeed, the angler may even be forced to swallow.

In captivity an angler is no more gluttonous than any other fish, and perhaps less so than some. The number of fishes it will take at a meal varies, of course, with their size and the hunger of the angler. Generally speaking an angler that has been feeding regularly will take one or two, occasionally even three, round fishes such as pollack when they are about equal in length to the width of its mouth. It will then refuse food for two or three days, when it is again ready for a meal. It seems to take about two days for the stomach to empty itself of one meal and prepare for the next. Quite often an angler that has been induced to take food on the day following a meal has been sick a few hours afterwards, frequently during the night. The partially digested remains of both meals have been readily distinguishable, one meal being more macerated than the other.

Size of the Fishes taken.

It was quite evident from my observations that the captive angler-fishes much preferred their prey to be on the relatively small side. Out of a number of different sized pollack they would definitely try to select those shorter than the widths of their mouths, and would regularly refuse to strike at those which well exceeded these widths, even though hungry and given excellent chances of catching them. Quite often I have seen a relatively large pollack hover in perfect safety close above an angler's mouth, although a little later smaller fish of the same species would be eaten. In general it can be stated that a fish as long as an angler's mouth is wide is the maximum size normally taken. Very occasionally I have watched an angler swallow a fish larger than this, and no doubt they will take such when more than ordinarily hungry. On the other hand, it is already recorded how angler-fishes will sometimes release large and powerful fish they have seized (see p. 490). There is no question that the act of releasing was always deliberate on the part of the captor ; it always had a good and powerful grip on the prey.

These observations accord with Fulton's remark that " the great majority of the fishes found in the stomachs were small even when the angler was large." Now and again relatively very large fishes are found in the stomachs of angler-fishes : perhaps a really ravenous angler will strike at prey larger than usual, and no doubt individuals vary to some extent in their prejudices as regards size.

SPECIES EATEN.

The angler-fish shows distinct preferences for certain types of fish. There is little doubt that it will eat readily soft-finned round fishes such as pollack, whiting, pout, grey mullet, and clupeoids, while on the whole avoiding species with strong spines or of unusual shapes. A small shoal of gadoids or of clupeoids (such as a bucketful of " brit ") released in its tank instantly evokes excitement and interest, whereas wrasses, sticklebacks, and flat-fishes have in my experience failed to arouse this response. As mentioned previously, flat-fishes are swallowed, but only, I think, when the angler is really hungry and other species are not available—at least this is true for the small angler-fishes I have kept. I have never seen a wrasse fished for or caught, although there is some slight evidence that occasionally they have been taken when no observer was present. On the other hand, dead wrasses, both *Ctenolabrus rupestris* (L.) and *Labrus bergylta* Ascanius, have been repeatedly fed by hand to several young angler-fishes. The slow and hesitating manner in which these and other dead fishes were usually swallowed was in marked contrast to the quick certainty with which naturally seized living fish were dispatched.

Some species have been repeatedly refused; these were *Agonus cataphractus* (L.), *Trigla hirundo* Bloch, *Spinachia vulgaris* Flem., and *Syngnathus acus* L. Several times a suitably sized gurnard has given more than one angler-fish several excellent opportunities to catch it. Once or twice as it was passing within easy reach an angler has made to strike and then hesitated. It was reported to me by witnesses that one angler-fish did seize a gurnard swimming over it amid a shoal of pollack, but that it released it immediately. I once saw a fifteen-spined stickleback caught twice in succession and each time released, the angler-fish taking no further interest in it. The stickleback continued to live in the angler's tank for seven weeks afterwards; it showed no signs of damage, and doubtless owed its life to its hard protective coverings and the stiffness of its body. The same angler regularly swallowed considerably larger pollack.

In addition to the species already mentioned as being readily eaten by my angler-fishes some others were taken from time to time. Chief among these were gobies, *Gobius minutus* Pallas certainly, and possibly also *G. paganellus* L. The shanny, *Blennius pholis* L., was caught once or twice, and on one occasion a Lesser Weever, *Trachinus vipera* Cuv. & Val., was swallowed without ill effect. It happened by accident; the angler in question was lying in wait for a small shoal of pollack and whiting living in the tank into which it had just been put for feeding purposes. These fish were passing close by, but just out of reach, when a net, accidentally dropped into the tank, hit a buried weever some distance away. The weever dashed off in a direction heading for the angler's mouth, approaching from in front; it was seized with amazing speed and immediately swallowed head first, its struggling tail protruding for a few seconds. The angler-fish seemed to suffer no inconvenience from the weever's poison spines and duly digested it before taking further food.

Bass occupy an anomalous position in the dietary of my angler-fishes. There was a shoal of small ones in the feeding tank at a time (January, 1936) when I had two angler-fishes in perfect health. One (No. 2) was about 17½ inches long; the other (No. 4) was about 11½ inches long. The bass were roughly half the length of the maximum sized pollack No. 4 was taking and were therefore suitably sized prey for both. The larger angler would catch and swallow them readily whenever it was given the chance, but the smaller persistently refused to strike at them. On several occasions when the bass were attracted to its bait, and hovered around its mouth in easy position for capture, this angler-fish deliberately folded back the lure into the position of rest and would not resume fishing until they had wandered away. It was quite evident that this angler preferred the pollack also present in the tank, and that it did not want the bass. Had the spiny fins of the bass anything to do with this, and would this angler have eaten the bass had they been still smaller? We can only guess. Guitel, however, records that his angler-fish ate a bass half its own length: was his desperately hungry?

Fulton (1903) has examined and analysed the stomach contents of five hundred and forty-one angler-fishes caught mainly in the Moray Firth, Aberdeen Bay, and off the Shetlands. Nearly half the stomachs were empty and were " shrunken and collapsed, with thick walls, probably showing that a considerable interval had elapsed since a meal had been obtained." The remaining half contained mostly the remains of fishes with a small admixture of cephalopods and crustaceans. Of the fishes about seventy per cent were round fishes, mainly whitings, haddocks, codlings, sand-eels, and herrings with an occasional Agonus, gurnard, lesser weever, Norway pout, and Lumpenus. Flat-fishes comprised roughly thirty per cent of the fish food and of these common dabs were by far the most numerous, solenettes, long rough dabs, plaice and flounders being also eaten. It will be seen that these observations on the stomach contents of anglers caught in the sea agree closely with the conclusions arrived at from the study of living anglers in captivity.

There are fairly frequent records in the literature of sea-birds having been swallowed by angler-fishes. The indications are that the birds are seized on the surface, the anglers coming up below them. Whilst it does not seem usual for angler-fishes to go after their prey in this way they may so behave when very hungry.

SOME REACTIONS OF FISHES TO THE PRESENCE OF AN ANGLER.

When living fishes are put into a tank containing an angler-fish they do not immediately become aware of its presence, and the same remark applies when an angler-fish has been induced to settle down in a tank containing fishes fully acclimatized to that tank. Bottom fishes such as dabs and gurnards have several times been seen resting on an angler-fish large enough to swallow them, sometimes even lying across the mouth without showing awareness of danger. Small pollack have accidentally touched an angler's soft body and not shown signs that they were aware of its nature. In the ordinary way fish rarely or never perceive the angler once it has merged itself with the bottom as already described (p. 485). Even when one of the members of a small shoal of pollack had been attracted away and caught close-by, its companions gave no indications of alarm.

After some time in the tank of the angler, a fish that has not been caught will gradually become aware of the danger to which it is exposed and will then keep well out of reach. Small pout and pollack have survived thus for several weeks until one day, while less wary than usual, or when upset by a sudden fright, they have swum too near and been eaten. Fish aware of an angler are not attracted by its lure. Small pout, wrasses and blennies would circle round food dropped on an angler's back, always keeping at a respectful distance. Food dropped well away from the angler would be rushed for at once, but only once or twice has a rather large wrasse been so bold as to sneak up behind and take food from the back of the angler, and then only from a part some distance from the mouth.

Fish therefore can learn to avoid an angler-fish, but whether they do so in the sea is a matter for speculation. Fulton (1903, p. 199) seems to think that they may: his opinion is that "the rarity of the large fishes in the stomach of the angler probably points to their greater caution than when younger. Experience, no doubt, teaches them more readily to detect and to avoid the formidable lurking trap which forms part of their natural environment." While this may be true it may also be due partly, perhaps mainly, to the angler's habit of avoiding, as a rule, the capture of relatively large prey.

REGENERATION OF THE LURE.

The lure is of such prime importance to an angler-fish that its loss might be attended with serious consequences. Aristotle has remarked on the thin state of anglers that had lost their baits. It is a delicate organ and easily damaged. No doubt it is not essential and an angler-fish might still be able to capture stray fish that chanced to wander near, but in a sparsely populated region this might not occur sufficiently often to keep it well fed. If it is lost, can it be replaced?

I have good reason to believe that this is so. When, a month after its arrival, my first angler-fish was carefully compared side by side with another of exactly the same size freshly caught but dead, it seemed evident that the former's lure was missing. The organ was present and easily seen in the dead specimen, but could not be found in the living fish, although the knob on which it should articulate was clearly present in front of the true second spine. Thereafter, watch was kept for any sign of regeneration. For about the next four weeks, when the fish was kept in a shallow bowl, a careful and almost daily examination was made in a good light, but nothing rod-like was seen. At the end of this period the angler was placed in a small glass-fronted tank in the public part of the aquarium and it was there difficult to observe fine anatomical details with certainty. During the last fortnight before it died close observation was not made, but two days before death attention was attracted by what appeared to be a tuft of fine skin or mucus which seemed to be attached to the skin on the inner side of the right eye ; this had not previously been seen. On removing the fish from the tank after death it was at once obvious that this tuft was none other than a well-formed bait on the top of a fishing rod normal in appearance. The conclusion reached was that the lure had been regenerated—assuming that previously it had had one and lost it in the sea or in the trawl—while the angler-fish had been living in the aquarium tank.

SUMMARY.

1. Young angler-fishes have been kept alive and in health for periods varying from a few weeks to eleven months. They were sometimes hand-fed on dead fishes and sometimes allowed to catch living prey. They grew at an average rate of about eight and a half inches per annum. All had strongly marked individual characters.

2. With pelvic and pectoral fins a slight hollow is made in the sand into which the angler settles itself. Its upper surface is now flush with the ground, and the colour and colour mottlings are closely matched to the surroundings. The bordering tags of skin break up the outline.

3. Breathing movements occur at relatively long intervals. The expiratory currents are discharged in the axils between the pectoral fins and the trunk, and are deflected vertically upwards.

4. When fishing the lure is jerked smartly in all directions. Small fishes are snapped up, one at a time, as they try to catch the bait. They are generally seized and swallowed head first. The second to sixth dorsal spines and their tags possibly function as secondary lures when attracting fish from a distance.

5. The angler-fishes usually fed every two or three days. The largest sized fish taken was, as a rule, as long as the angler's mouth was wide. One or two such fishes would form a meal.

6. Angler-fishes appear to prefer gadoids, clupeoids, and similar soft-finned round fishes to any others. They will eat flat-fishes, but not so eagerly.

7. A lurking angler is not readily detected by other fish. In time, if they are not caught, they become aware of its presence in their tank and keep away.

8. If the lure is lost there is evidence that it is regenerated.

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EXPLANATION OF PLATE I.

Photograph of an Angler-fish (*Lophius piscatorius* L.), 7¾ inches long, resting on the bottom of its tank and fully colour-adapted to its surroundings. It had dug for itself a slight hollow in the sandy gravel and was known to stay in this place for at least six hours. The lure is held forwards, the rod crossing the mouth horizontally. The divided bait, dark in tone, is clearly visible at the middle point of the lower jaw, between it and the light-toned piece of gravel to the right of the umbo of the Nassa shell. The lure is being held perfectly still; no fish are in sight. The second to sixth dorsal spines are depressed.

Technical data: One magnesium flash on the right side. Ilford Soft Gradation Panchromatic plate. No filter. f/44. Taken through the surface of the water: depth about fourteen inches.

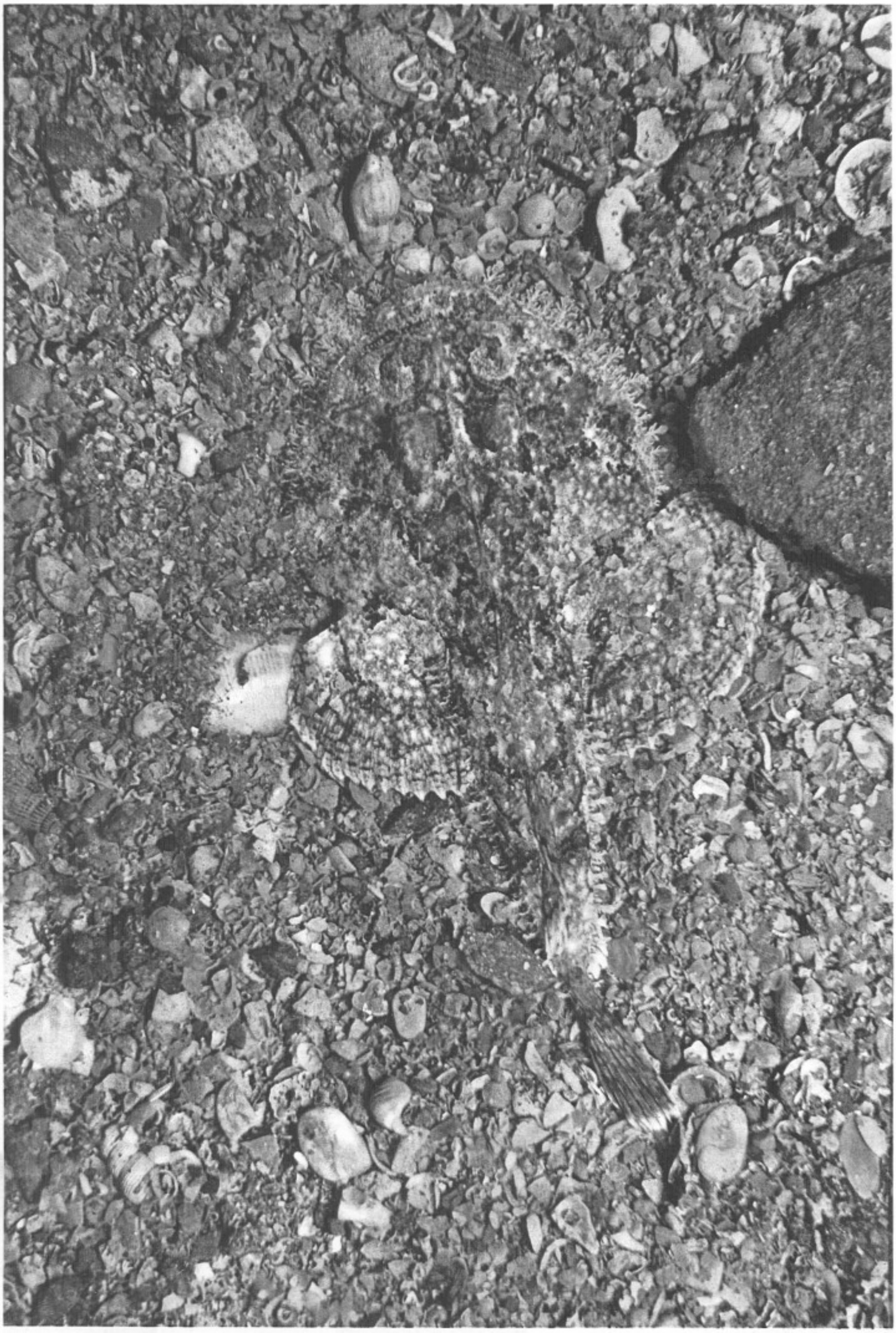

Photo. D. P. Wilson.

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The Learning of Detours by Wrasse (*Ctenolabrus rupestris* L.).

By

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Assistant Naturalist at the Plymouth Laboratory.

With 13 Figures in the Text.

CONTENTS.

PREFATORY.

THERE is probably no branch of biological research which can continue indefinitely without finding itself compelled to take account of the specific behaviour, if not actually the psychology, of the organisms with which it deals. This necessity has already been noticeable even in those departments of study in which attention is concentrated on the more abstract features of organisms, and in which individuals are regarded, as far as it can possibly be managed, as units of a standard type, acted on by independent external forces. No better illustration can be found than the attempts at relating the phenomena of organic structure to the causal agency of natural selection. If further light is to be thrown on this fundamental problem, no subjects are more suitable for the purpose than sexual selection and mimicry. But in both these fields of investigation progress is arrested until considerably more is known of the behaviour of the animals concerned—in the former, of the actual effect which display of sexual structures exerts on choice of mates, or stimulation of coition; in the latter, the whole problem depends on the extent to which the mimetic characters can serve to impose on the sensory discrimination of predators. Lloyd Morgan (1900, p. 311) was one of the first to appreciate how the situation was developing. "Many interesting problems," he wrote, "which are keenly discussed by evolutionists in the light of natural selection presuppose conscious situations which are more or less tacitly taken for granted." Of course, stress need not be laid on the expression "conscious": it is sufficient for the point at issue to put "discrimination responses" in place of "conscious situations."

If behaviour cannot be ignored in the morphological sphere, still less is this possible in the ecological, when problems concerning the distribution of populations, and of relations of individuals to their physical and biotic surroundings, are encountered.

There are two rather different ways in which behaviour characteristics come increasingly to force themselves on the attention of ecologists.

(i) The fixed and regular aspects of behaviour of which account has to be taken, or which at least have to be assumed or are presupposed, may take on an intricate and specific form requiring elucidation by special study. As a clear illustration from animal ecology, one may cite the significance of the factor of "habitat selection" in interpreting the causes of distribution of breeding birds in an area of mixed habitats, as recently shown by Lack (1933). In marine biology similar cases come to notice. The vertical distribution of populations of plankton organisms is evidently to a large extent dependent on the specific behaviour reactions of the animals to the illumination of the water, or other factors in their environment. The availability of food for, e.g. bottom-living fishes, or shore birds, seems to depend more than at first might be expected on the special methods (due to specific feeding reactions) the animals employ to obtain it; so that the *setting* of the food organisms has to be taken into account, in addition to their mere *presence*. To quote one other familiar example —the breeding migrations of many fish are unquestionably regulated by special instinctive responses, and until something more is known about these the whole study concerned with the factors which affect the movements of populations of these species can scarcely progress far.

(ii) Secondly, it may come about that it is insufficient to regard only the fixed and regular aspects of behaviour, but that account has to be taken of the fact that the behaviour of both individuals and communities is modifiable, and, within limits, capable of adaptive, or even progressive, change. It seems that most ecological problems which have to take concern of special features of behaviour are destined to come up against the complicating factor of the *modifiability* of behaviour. Even in the case of the vertical distribution of plankton the effects of physiological adaptation to optical stimulation have to be taken into account, significant shifts in the level of maximum concentration being attributable to this factor (F. S. Russell, 1931, pp. 400–405). In vertebrates this aspect can probably never be ignored for long. The return migration of fish to their breeding grounds, in so far as it is dependent on reactions to environmental stimuli, appears to involve reactions conditioned by the past reactions of the fish. At least there is evidence that this is so in the case of the Pacific Salmon (Rich and Holmes, 1928).

Again, the diets of shore and estuarine birds, some of which can utilize a considerable variety of food organisms, may vary according to the birds' acquired habits. It is a familiar fact that birds may ignore an unfamiliar source of food until discovering it by chance, when subsequently they may take heavy toll of it. This may happen, in the case of shore birds, to an extent sufficient to affect appreciably the mortality of shore invertebrates, and so once again the modifiable aspect of behaviour (of predators) has to be reckoned with, in the study of such a comparatively abstract property (of the food organisms) as the rate of mortality.

Another illustration which has recently come to notice shows the intricate relation between ecology and animal behaviour. The distribution of the Great Grey Seal (*Halichoerus grypus*) population in the South-Western area of England is intimately related to the presence of suitable breeding quarters (Steven, 1936). But whereas in the Scillies the seals lay their pups on open beaches, on the mainland of Cornwall they breed entirely in the interior of caves. Whatever has been the cause of this choice (and it probably resides in the attacks on the stock made in the past by man), it is evident that an acquired habit, or behaviour modification, has to be reckoned with. Since the areas which provide suitable breeding caves are severely limited, and the effect of this limitation is reflected on the distribution of the seal population—for instance, causing an almost complete absence on the south coast—the distribution, therefore, is directly affected by this acquired habit of the Cornwall seals.

These examples may serve to indicate how ecological investigations which primarily deal with the most general aspects of some animal population come to be concerned, firstly, with special features of the animal's behaviour, and, secondly, with the *modifiability of that behaviour*. The second aspect opens up an interesting field for investigation, and it is taken as a starting-point for a line of research of which the present paper is offered as a first contribution.

Viewed on a broad scale, all biological study is seen to have its origin in the observations made on organisms in their environmental setting and in the problems thereby raised. It is not complete until the results of the train of research so instigated are directed back to the observations which provided the starting-point. Unless its direction is adequately orientated with respect to this main circuit, laboratory research is apt to narrow in scope, to settle in water-tight compartments, to become too unnecessarily abstract. We have seen that the problem of the modifiability of behaviour is raised in purely ecological studies, which circumstance at once draws it out from its recess among subjects of predominantly academic interest and brings it within the province of action of the marine zoologist. If any justification is required for research on the subject of the modifiability of behaviour, it is the above consideration on which main emphasis is to be laid. At the same time the claims are not to be overlooked of the intrinsic interest of the subject itself; of its bearing on academic problems such as the evolution of intelligence; of its relation to the subject of development and maturation; of the contribution it can make to the interpretation of learning, and the contacts thus established with general biological theory; and, lastly, of the problems it raises, and should assist in solving, with regard to methods and technique—as yet imperfectly developed—appropriate in the investigation of behaviour.

DETOUR EXPERIMENTS WITH TELEOST FISH.

With a view to making some contribution to the study of the modifiability of behaviour in Teleost fish, it was decided to utilize the method known as "detour" training as a basis for experimental work. The value of this method has been pointed out by E. S. Russell (1931) who, applying a technique made familiar by Köhler in his classical work on chimpanzees, undertook experiments with the freshwater stickleback (Gasterosteus). The capacity of the fish was tested for reaching a food object by a roundabout path. The food, presented inside a glass pot, was easily visible through the glass, but could only be reached if the fish made a detour round through the opening of the pot. At the start the fish attempt to reach the food directly, and may spend a long time swimming at the pot before eventually finding the opening by chance; but after continued repetition they come to acquire the habit of swimming straight to the opening. In the same way they come to adopt an efficient method of escaping from the pot, an action which at first presents difficulties.

We have evidently here to deal with a behaviour modification of an adaptive type which may be placed in the category of "learning," if this term is used in a fairly general sense. The animal "learns" to develop a response which enables it to overcome an obstruction in its path to a food-object, which functions as the immediate "goal" of its activities. The acquired efficient response has to grow out of several discrete movements, which are at first given independently of each other.

The main problem is to discover how this change in behaviour, this development of a more efficient response, is to be interpreted : what, in fact, are the necessary conditions for its occurrence, and how it is related to the fish's neural organization. The state of the theory of learning in general is such that there is no ready interpretation of the phenomenon. The " learning " of detours is actually a simple form of maze-learning, and presents many features in common with that shown in " puzzle-box " situations, in which the learned response involves the performance of certain movements in a correct order. It is noteworthy that neither in maze-learning, nor in other kinds of problem-solving, does present knowledge extend far enough to make possible an adequate interpretation of the learning process. On the one hand straightforward accounts in physiological terms of a strictly mechanistic type cannot absorb all the facts ; on the other hand a theory, such as that of the " gestalt," which majestically ranges over the facts, travels too far beyond those at present available, and, further, is too comprehensive even to have acquired a precise formulation.

The difficulty is augmented by the fact that most of our existing information on problem-learning is derived from higher vertebrates which, it might be said, exhibit the phenomenon in too complex a form. We require to know more of the behaviour of vertebrates lower in the scale which are capable only of the elementary types of problem-learning. With such animals—and here it is that Teleost fish come in—simple situations can be presented which allow of adequate experimental control.

Russell's experiments were carried far enough to give some suggestive indications (1931, p. 408). He established the fact that the fish are normally able to learn simple detours ; that the correct solution was first found by chance, and that at first the activity of the fish is undirected, at least in respect to the obstruction ; that change in behaviour occurs with repetition of the trials, marked by a change from undirected to directed activity, and by a sudden fall in the learning curve ; and that, associated with the acquirement of the efficient response, the pot appears to acquire some sort of significance from the aspect of the fish, as though some change in sensory organization had occurred.

But the question still remains—how did the performance of the correct movements, at first brought about accidentally, become " stamped in " ? The suggestion is implied that it comes about as a result of change of sensory organization, of which the fish's reactions to the pot itself give evidence. The fish comes to sense a certain relation between objects in its surroundings, and adjusts its movements accordingly. This is in harmony with the " gestalt " viewpoint. But there is no claim that the experiments are adequate to serve the difficult function of demonstrating the validity of this interpretation. Nevertheless, the results can perhaps be said to be suggestive ; and it should be realised that if this interpretation of detour learning can, by further experiment, be shown to hold, a considerable step forward will have been made in the study of the sensory capacities of lower vertebrates.

The experiments described below aimed at procuring detailed observations on the fish over the whole course of training, in order to find what relations could be established between the final learned response and the various behaviour reactions given in earlier stages. For instance, it was important to enquire how far successful *methods* of making the detour, perhaps at first arrived at fortuitously, determined the method by which the learned response was performed. Again, were there, it was asked, any features of behaviour in earlier trials which determined whether a learned response would be established or not ? The simplest type of detour was chosen and a record kept of all movements of the fish against a time scale throughout the trial. The records were subsequently subjected to analysis, and, where possible, quantitative data were abstracted. The main features which emerged are discussed in the second half of this paper, after the experiments have been described. It may be noted that the procedure adopted in this investigation resembles somewhat that of the field naturalist, who first sets out to record as minutely and impartially as possible the behaviour, whatever it may be, shown by an animal under observation, and subsequently works out the most important features of the mass of details as a whole ; rather than that of the experimentalist, tackling a clear-cut problem, who arranges his experimental conditions so that a definite answer is given one way or the other. In elaboration of these experiments it should be possible to harmonize the best of both methods.

METHODS.

General procedure. The fish used in these experiments were small, immature specimens of the Rock Wrasse (*Ctenolabrus rupestris* L.), from 5 to 7 cm. in length. This species readily adapts itself to captivity and lives well in tanks of restricted size. It soon gets over the effects of any shock that may be induced by capture in a net or disturbance of its tank. Altogether the species proves an excellent experimental animal.

For the whole of the time during which it was subjected to experiment, each fish was kept isolated in a rectangular glass dish (size either 42 × 24 × 12 cm. or 36 × 28 × 15 cm., internal dimensions). Preliminary experiments were made on three fish (A, B, and C) in the early part of 1934, in two dishes set up inside a larger tank (in the main laboratory) screened from excessive light. The remaining nine fish (D1 to 9) investigated together in the later months of that year were kept in a darkened room.

the dishes ($36 \times 28 \times 15$) lying in a row on a long table, screened from each other with strips of cardboard. The dishes were provided with air circulation.

The fish, in each case, was allowed to get thoroughly accustomed to its surroundings, and to take food off a piece of thin wire. After being placed in the experimental dish it was never fed in any other manner. Prior to the feeding an electric light of moderate intensity was switched on. In the main experiment the lighting of the room served as a signal—and probably actually acquired this association—that feeding was about to take place. It was found that the fish very soon came readily to associate the wire with food and gave positive reactions to the observer when he approached the dish. They followed movements of the hand when this was passed over the tank, and also were closely attracted to the pipette used from time to time for picking up debris accumulated in the dish. Any shock reactions given at first soon disappeared, and they soon became indifferent to such extraneous stimuli as may have reached them (e.g. vibration from footsteps in neighbouring passages). These facts are emphasized to show that feeding responses, at least, were free from inhibitions which might have interfered with the experiments.

After an adequate period had been allowed the fish for settling down, experimental feedings were started. The fish now never fed except in a situation in which it had to surmount a certain obstruction: it now always had to take an indirect route to reach the food. Whatever type of obstruction was used the procedure at each feeding followed along the same lines. The fish was enticed to a particular corner of the dish, and at the same time the obstruction (in most cases the arrangement of glass plates described below) was carefully lowered into the tank. The food, still presented at the end of a thin wire, was then transferred to an appropriate position, and left hanging in the water on its wire support. The fish was able to detect the food by sight, but was in such a position that it could not directly reach it. Actually, it had either to enter a pot or pass round a glass plate. A stopwatch was set going as soon as the fish began to swim towards the food, and a record of the observed movements of the fish was taken. The observer's head and shoulders were in the fish's range of view, but it was found that the fish was too absorbed in its attempts at reaching the food to be affected even by quite considerable movements on the part of the observer. For precautionary measures, however, the observer kept still all through the trial, as nearly as possible in the same relative position with respect to the dish. As soon as the food was taken, the obstruction was removed, and the fish once more left in a clear tank. Two such feedings, on an average, were given to each fish in one day. After a time it was possible to reduce the amount of food given at each trial to a very small quantity, so that as many as five feedings could be given in one day before the food ceased to attract.

The food, for the most part, consisted of the muscle of freshly killed prawns. This was now and again varied with small pieces of squid.

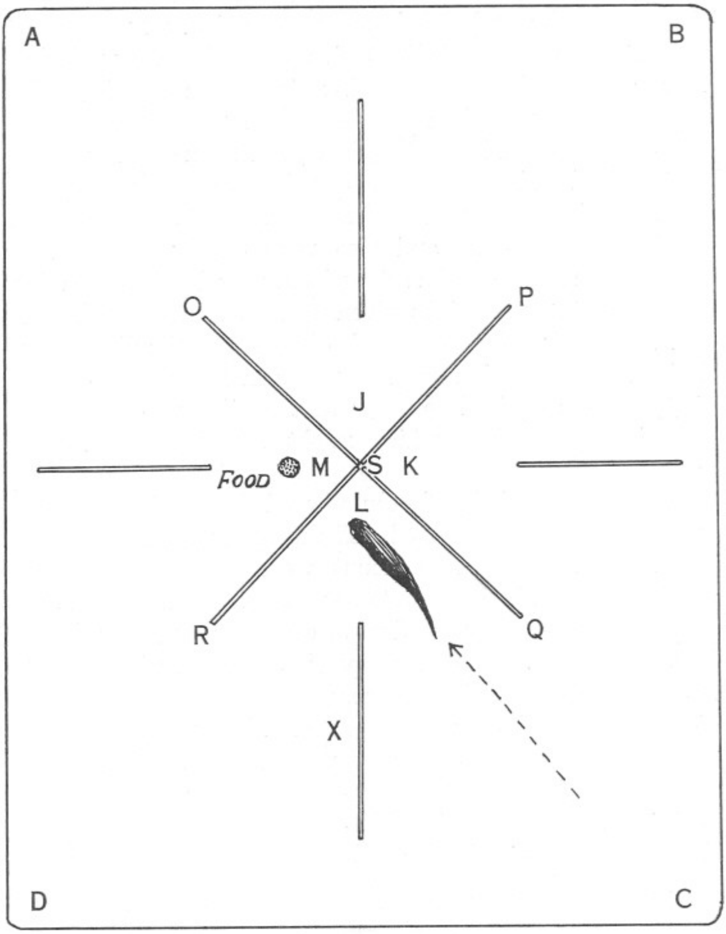

Fig. 1.—Diagram of the arrangement of glass plates used in training the fish. See text, p. 505. ×⅓.

A, B, C, D marks the inner edge of the glass dish. J, K, L, M, S, and X are positions to which special reference is made in the accounts of the experiments. O, P, Q and R mark the positions of the edges of the four central radiating glass plates.

Apparatus. The only special apparatus that requires description is that employed to furnish the fish with a detour path. In the majority of experiments here described it consisted of a special arrangement of glass plates (the glass 2 mm. thick) set in a pattern shown in Fig. 1. These plates were held in a wooden frame made to fit over the top of the dish (Fig. 2). At each feeding the loaded frame was lowered into the dish, the glass plates then forming a sort of maze restricting the directions in which the fish could freely move. In Fig. 1 a number of positions in the horizontal plane are marked by letters, and it will be convenient to use this lettering for describing positions in the dish. The plates OS, PS, QS, and RS were each 8·6 cm. wide. The side plates were fixed so as just to protrude into the square O, P, Q, R.

With this apparatus both the position of the food and the starting position of the fish could be varied in different ways. The symmetrical arrangement of the plates also permitted an easy exchange from right to left, such as is required in testing transfer of learning. In practice, the food (except in the case of fish B) was always placed during training at the position M, and the fish started from the neighbourhood of C. The fish thus had to circumvent the edge R; and in doing this had to make a detour of some 6·5 cm. If the glass plate had a clear surface, or even if its edges were marked with a black line, this simple detour was quite enough to test the fish's capacities to its limits. The other portions of the "maze" served their purpose during tests on fish which had learnt to make a detour of the plate R S.

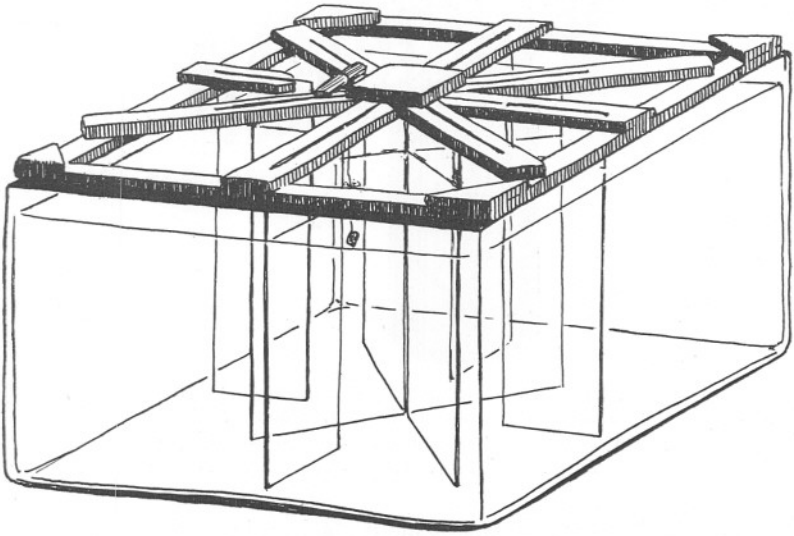

FIG. 2.—Optical view of glass dish with the wooden frame, holding the glass plates, in position. See text, above.

The wire supporting the food was lightly held on a piece of wood resting on the frame in the position shown in Fig. 2. A loop was made in the wire in such a way that the wire fell naturally into a vertical position when placed on the support.

Another piece of apparatus used consisted of a glass tube fixed horizontally on a weighted upright support (Fig. 3). The tube, 10·2 cm. in length, and of 3 cm. internal diameter, had an opening on the side placed uppermost, near the closed end. Through this opening the food, suspended on a wire, was lowered, and thus came to rest inside the tube 8·5 cm. from its open end. The support was painted black and the glass tube covered by a heavy black meshwork, roughly painted on. The extent of the tube was thus made visibly conspicuous, though the food could still be seen through the meshes. The fish could not reach the food except by passing through the open end of the tube.

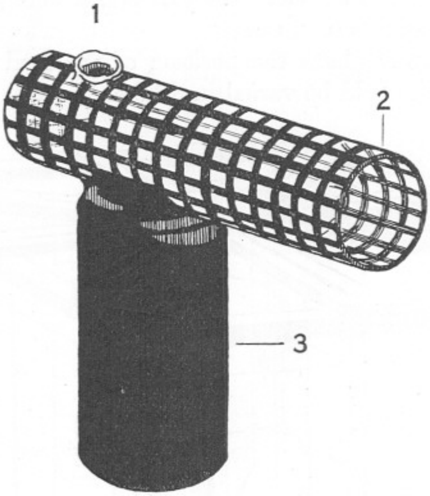

Fig. 3.—Sketch showing the tube, painted with black meshwork, presented to fish D9. See text. × $\frac{2}{5}$.
1. Hole through which food wire was inserted.
2. Mouth of tube. 3. Weighted support.

DESCRIPTION OF EXPERIMENTS.

I. Detours Necessitating Entry into a Glass Receptacle.

E. S. Russell (*loc. cit.*) has adequately demonstrated that fishes are capable of learning to find their way into a pot, either of clear or somewhat opaque glass, whereas their first reactions lead them to attempt to reach the food directly.

An important characteristic of this type of detour experiment is that the obstruction is more or less easily visible and the indirect route can be in some sense "surveyed" by an animal with adequate powers of vision. The possibility is offered that the pot or tube may become viewed as an object, and both the food and the way of access to it sensed in relation to the object as a whole. This evidently happens in the case of higher mammals, and may well happen to a greater or lesser extent in that of teleost fish. Russell found that the fish, after training had progressed, came to give special reactions to the pot itself, as though it had acquired a new significance in their world. This at least indicates that the fish were capable of sensing the pot as an object.

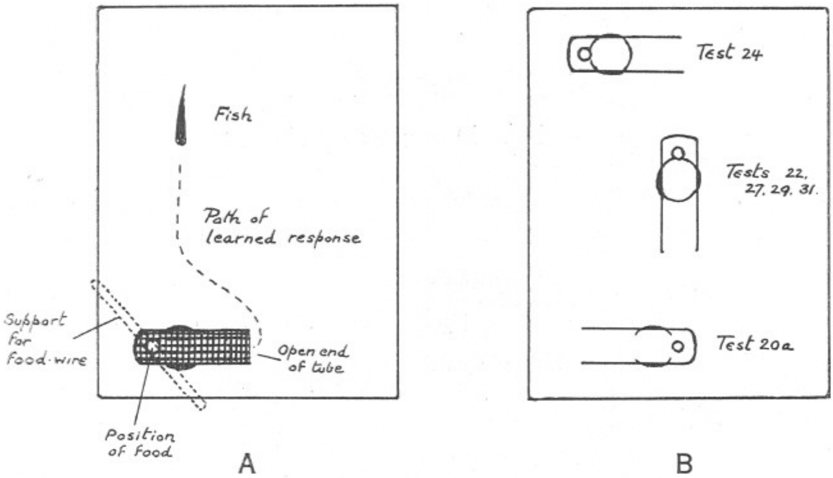

FIG. 4.—Diagrams of conditions presented to fish D9. ×⅛.
A. General conditions under which training took place. B. Three alternative positions of the tube given in the tests indicated.

Since the wrasse proved capable of learning a more difficult type of detour, more suitable for procuring the type of data required, it was not considered necessary to repeat the pot experiments. One fish, however, was given the meshed tube described on page 506 (Fig. 3). The tube with its black support could not have failed to provide a conspicuous object, and the meshwork marked the glass obstruction in a conspicuous manner.

Fish D9.

Length: 5½ cm.

After 8 days in the dish the fish had settled down and took food readily off the wire. The pot was then introduced (Nov. 23): the fish showed "apprehension" and could not be enticed closer than to 5 cm. of the new object. The pot was removed and replaced the next day. Two feedings were then given (Nov. 24) as close to the pot as the fish would approach, now about 3 cm. The pot was now left in the dish until Nov. 26, when feedings were given both over it and close by its side. The inhibitory influence of the pot was now disappearing. The pot was then left in the dish, and next day it was possible to give the first trial feeding, the pot now having no inhibitory influence at all. Thus the latter was overcome in four days.

For the first day (Nov. 27), when three experimental feedings were given, the pot was left in the dish, but subsequently it was removed after each trial. It was always placed in the same position in the dish near corner D, in the position shown in Fig. 4a.

The fish was attracted to the far side of the tank. The baited wire was then lowered into the hole on the upper side of the tube, and hooked over a wooden support resting on the corner angle of the dish (Fig. 4a). The stop-watch was set going as the fish passed the middle of the dish in the direction of the food.

A modification, however, of this procedure had to be introduced after a dozen trials. The pot, by then, had become such an attraction in itself that the fish now often entered it before there was time to introduce the food at all. So the food was now placed *inside* the tube before the latter was lowered into the tank. It now lay on the bottom of the tube near its closed end, and, incidentally, was now in a more inconspicuous position.

The duration of the trials are given in Table I. These figures serve to indicate the rapidity with which the fish came to develop an efficient performance.

TABLE I.

FISH D9. DURATION OF TRIALS.

Date.	*Serial No.*	Duration of trial.	Remarks.
Nov. 27	*1*	7′ 18″	
..	*2*	3′ 04″	
..	*3*	5′ 43″	
28	*4*	2′ 25″	Entered tube a second time.
..	*5*	2′ 18″	Investigated opening before [food introduced.
29	*6*	1′ 59″	
..	*7*	0′ 49″	
..	*8*	(4′ 51″)	Not adequately attracted [by food.
30	*9*	0′ 26″	
Dec. 1	*10*	3′ 05″	
3	*11*	0′ 36″	
..	*12*	1′ 29″	
4	*13*	0′ 32″*	Food now introduced with pot.
5	*14*	0′ 11″*	Efficiency now attained.
..	*15*	0′ 27″*	
..	*16*	0′ 13″*	
6	*17*	0′ 10″*	
..	*18*	0′ 12″*	
Dec. 7	*19*	0′ 11″*	
..	*20*	0′ 14″*	
..	*21*	0′ 16″*	
..	*22*	(Test)	
10	*23*	0′ 14″*	
..	*24*	(Test)	
..	*25*	0′ 14″*	
..	*26*	0′ 08″	
..	*27*	(Test)	
12	*28*	0′ 09″*	
..	*29*	(Test)	
..	*30*	0′ 19″*	
..	*31*	(Test)	
13	*32*	0′ 09″*	
..	*33*	0′ 17″	
..	*34*	0′ 09″*	
..	*35*	0′ 14″	

Any doubts as to whether the pattern on the tube prevented vision of the food inside were quickly dispelled during the first trial. For two periods, each of about $\frac{3}{4}$ minute, the fish made persistent attempts at reaching the food object through spaces between the meshes. It worked actively all round the closed end of the tube. It even snapped at the glass from below. Its behaviour was perhaps remarkable when it is remembered that only two days previously it was still nervous of approaching the pot.

More than seven minutes passed before the fish eventually reached the food in this first trial. After some fruitless efforts at reaching the food directly, it spent some time swimming irregularly around the pot, with occasional excursions into other parts of the dish. But it was a long time before the fish came right opposite the opening of the tube ; for the latter

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* Food already inside the tube, lying on the bottom, when the tube was lowered into the tank. All trials after *13*, except *18*, *26*, *33*, and *35*.

lay rather high in the water and the fish tended to swim at a lower level. It was not until 7′ 13″ that the fish's movements brought it immediately abreast of the opening, and that for the first time could it have had an open view of the food. It would not have been surprising if the fish had now displayed hesitancy. Viewed from the opening, the food had a bizarre visual background of radiating and intersecting black streaks, which may well have obscured the outlines of the food object in the fish's visual field, even if the pattern did not itself exert an inhibitory effect. The fact is, however, that *the fish swam straight into the tube and snapped at the food without the least hesitation.*

The next few trials were performed in a similar manner, the fish swimming into the tube the first time it happened to come opposite the opening. It never again took so long as on the first occasion, and would doubtless have given still better results if it had not shown a tendency to swim round underneath the opening.

There were early signs that the fish was beginning to acquire some familiarity with the apparatus in which it was fed. After trial *4* it swam into the opening a second time. At the beginning of *5* it swam up to the mouth and looked inside, before the food was introduced. Again, at the beginning of *6*, it swam up to the opening and inserted its head into the tube. But in both these trials, once the food had been introduced, the fish still persisted for some while in its attempts at reaching the food directly, and took over two minutes to make the detour.

In trial *7* for the first time the fish reached the food in less than a minute. Trial *8* is unsatisfactory, as previous to it the fish had been accidentally disturbed, and when the trial was given it did not appear to be at all strongly attracted to the food. It was still probably in a certain state of inhibition. The length of duration of *10* is to be attributed to disturbing influences. There was some delay in presenting the food, and during this interval the fish swam into the empty pot at least twice on its own "initiative." There was also a second observer present. Apart from these two trials, a reasonably steady improvement in efficiency of performance may be seen.

An important factor in the increase of efficiency was a reduction in the time spent in attempts at reaching the food direct. This suddenly fell to 5″ in trial *9*, and, though the next three trials gave 1′ 30″, 20″, and 36″ respectively, it suddenly became negligible from *13* onwards. From this point the fish no longer spent any time in attempting to reach the food direct through the glass.

Trial *13* marks a point of rather sudden improvement. After this trial an efficient response can be said to have become established. From *14* onwards the fish rarely even swam to the closed end of the tube where the food lay: as it passed towards the tube, at a distance of about

10 cm., it diverted its course somewhat to the left to bring it to the open end.

It is to be noted that this main step in the progress of learning also coincides with a modification in the experimental conditions referred to above—from *13* onwards the food was inside the tube when the latter was placed in the dish. It is possible that this change exerted an effect on the course of learning; but if it did so, the effect was a favourable one. It is noteworthy that the main difference involved was that the food was made *less* conspicuous—probably invisible except at close quarters—and so may not have held the same attraction as before. It is therefore possible that there was less to distract the fish from its growing tendency to move to the open end of the tube, but if this were so, the fact is certainly noteworthy. If not, then the sudden improvement has to be regarded as an independent feature of the learning process (e.g. as in fish D5, pp. 528, 550).

When the original conditions were repeated (trials *18*, *20*, etc.) there was no difference in the fish's performance from that in other trials.

During the efficient period (*14* onwards) the fish, as has been stated, rarely even visited the closed end of the tube. In the best performances it swam straight to the opening, and in, without hesitation. But it still on occasions swam round the pot once or twice, having missed the opening first time.

Certain tests with the pot placed in different positions were made. The positions are shown in Fig. 4. Thus in trial *20a* the pot was turned round so that its opening faced corner D. The fish took its usual course, swimming straight to the left-hand end (left, that is, from the position of the fish) and made persistent efforts to get into the tube at this point. The trial was abandoned at 1′ 30″. Trial *24* provided a mirror image of the normal situation. The fish again tried the left-hand side first, but this time did not persist in attacking the end: it swam to and fro and reached the food in 37″. Both these tests indicate that the fish had acquired the habit of *moving to the left-hand side of the tube*, whatever its position, rather than to distinguish the open long arm of the tube from the short closed arm.

Four tests were made with the pot standing in the middle of the dish, the opening facing towards the observer. The fish was started on the left-hand side. In the first two (*22*, *27*) the fish swam round and round the tube and did not enter it even when coming abreast of the opening. Both tests were abandoned, after 3′ 30″ and 2′ 15″ respectively. However, both *29* and *31* were solved readily (10″ and 30″). It is possible that the different relation to the electric light, and so a difference in the illumination of the interior of the tube, was responsible for the failure of the first two tests. One can at least conclude that the position of the tube relative to its background and to the angle of approach of the fish was still of importance.

These details of the performances of fish D9 are given to illustrate the type of result obtained with wrasse when the arrangements seem to supply optimum conditions for learning. The obstruction is easily seen, while at the same time the food remains visible ; there is only one indirect route, which can probably be readily surveyed by an animal with adequate powers of vision ; the task of discovery of the indirect route is well suited to the natural exploratory behaviour of wrasse. It emerges, however, that this type of detour problem is not well suited to the sort of analysis we wish to undertake. The fact that there is really only one method of solving the problem is a severe limitation, and the efficient response is arrived at too rapidly to allow of comparisons between its separate components.

II. Detours necessitating Passage round Partitions of Glass.

With the apparatus described on page 504 it was possible to try out a detour of another type—one in which the obstruction is invisible or only figures very obscurely in the fish's visual field. Other varieties of glass plates can always readily be substituted, such as ones with their surface marked in some way so as to render it conspicuous to the fish. The apparatus also allows of other modifications of experimental procedure and is thus conveniently adaptable.

The results of the preliminary experiments, with fishes A and B, showed that wrasse are capable of learning to get round a plain glass obstruction effectively, although an efficient response is acquired with difficulty and precariously maintained. Fish A was presented with the problem subsequently given to other fish, of group D, but since other conditions differed somewhat, caution must be used in making detailed comparisons between the performances of A and other fish.

The experiments on fishes D1 to 8 were carried out simultaneously under comparable conditions. D2, 3, 4, and 5 were given an obstruction of plain glass, as in the case of A. With D1 and 6 the plate was edged with a black strip, 5 mm. in width. D7 and 8 were presented with a glass plate of similar dimensions, but with its surface marked with a meshwork of scratched lines. The lines on this plate were ruled at 5 mm. intervals, with the aid of a glass-cutter. Though made as firm as possible, and very noticeable in the air, they did not show up very conspicuously under water.

In all these cases, during training, the food was presented at M (Fig. 1), and the fish started from corner C.* A detour of 6·5 cm. to the left had to be made.

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* Except fish B.

Fish A.

Length 6·5 cm.

Jan. 4, placed in experimental dish standing in an empty tank in the main laboratory, under conditions referred to on page 502. For 12 days fed with Mytilus and pieces of Polychaete worm off the end of a wire, until it had become thoroughly habituated to this method of feeding and its conditions in general.

Jan. 16, first experimental feeding. Jan. 16–Feb. 10, 67 experimental feedings given. Feb. 10–14, interval during which fish was moved from the tank and water renewed. Feb. 14–March 3, 67 experimental feedings given. March 4–19, interval during which dishes were disturbed. March 20–22, 11 further experimental feedings.

Trained to plain glass obstruction, detour 6·5 cm.

The experiments on this fish constituted the main part of the preliminary investigations, carried out between January and March, 1934. For the first fortnight there was no indication that the fish was acquiring any increased efficiency in its performance, but eventually it developed a stable learned response, working leftward along the glass until reaching the edge.

The general course of learning is shown graphically in Fig. 5, in which a curve is given representing the duration of successive trials. As is usual with these "learning curves," its course is very irregular until the learned response is stabilized, when it remains at a uniform low level. The averages of groups of five successive normal trials are as follows (trials which are called "tests," in which the conditions are altered in some particular respect are not included in these figures):

Date.	*Serial No. of trials.*	Average duration.	Date.	*Serial No. of trials.*	Average duration.
Jan. 16–18	*A 1–5*	7′ 52″	Feb. 14–16	*B 1–5*	2′ 03″
18–22	*6–10*	5′ 38″	17–19	*6–10*	1′ 17″
22–23	*11–15*	2′ 26″	19–20	*11–15*	0′ 38″
24–25	*16–20*	5′ 03″	20–21	*16–20*	0′ 14″
25–29	*21–25*	6′ 16″	23–24	*24–28*	0′ 16″
30–31	*26–30*	1′ 36″	24–25	*29–33*	0′ 11″
Jan. 31–Feb. 1	*31–35*	1′ 29″	26–28	*34, 43, 44, 48, 49*	0′ 11″
Feb. 1–2	*36–40*	1′ 09″	March 1	*50, 53, 55, 57, 58*	0′ 12″
2–3	*41–45*	0′ 32″	2–5	*59, 62, 64, 65, 66*	0′ 12″
3–5	*46–50*	0′ 37″			
5–6	*51–55*	0′ 31″	March 20–21	*C 1–5*	1′ 02″
7–8	*56–60*	0′ 48″*	21–22	*6–10*	0′ 12″
8–9	*61–65*	0′ 18″			

First series (trials *A1* to *67*). In the early trials the fish found considerable difficulty in reaching the food, and the average duration of the first 24 trials was higher than in any other fish. To start with, there was a conspicuous contrast between two alternating phases of behaviour: the movements were partly directed towards the food, resulting in the fish keeping close to the glass; partly random with respect to the food, resulting in the fish swimming away to various parts of the tank. These two phases alternated continuously; the attraction of the food always returned when it had been lost temporarily. But it was only the first 7 trials that were characterized by this behaviour. After that the fish

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* Includes one "bad" performance of 2′ 27″.

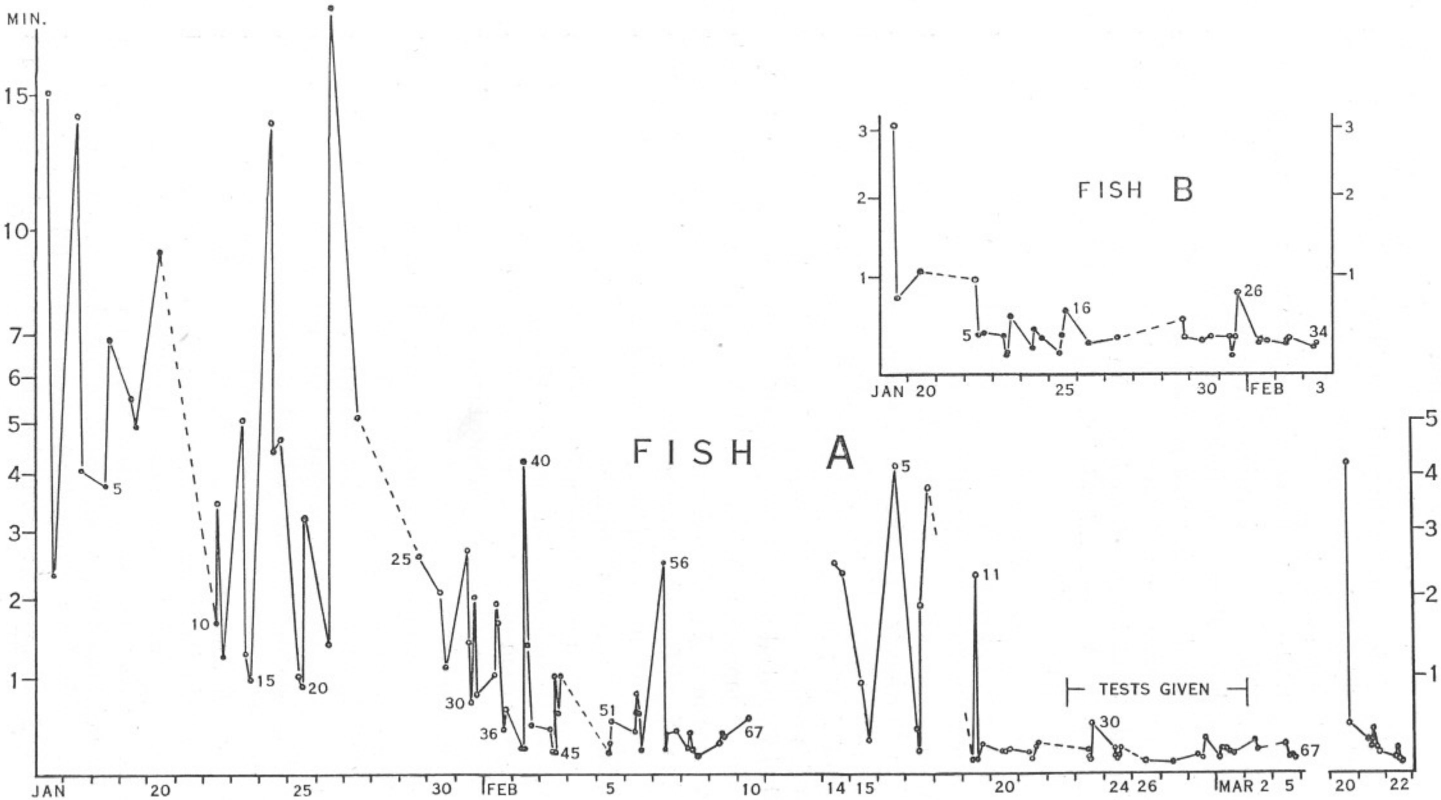

FIG. 5.—Learning graphs of fishes A and B. The duration of each normal trial feeding is plotted on a logarithmic time scale, and lines drawn between successive points. The line is broken when an interval includes one whole day on which no feedings were given. Serial numbers of the trials are placed at intervals along the graph.

was, on the whole, remarkably persistent in attacking the glass, even though the trial lasted several minutes. This was the first noticeable change in the fish's behaviour.

Another 18 trials passed without any further indication of improvement in efficiency. The average duration still showed no sign of decreasing. Trial *23* lasted over 19 minutes, during which time the fish gave no signs of having acquired anything, except the loss of the tendency to swim right away to other parts of the tank. It is all the more remarkable, therefore, that shortly after this a definite improvement became apparent. The curve (Fig. 5) shows a decided fall in its mean level at the point marked by trials *25* and *26*.

Analysis of the results shows that at this point two changes in the behaviour occurred simultaneously which together made for a marked improvement in efficiency. (1) At this point there was the first real drop in the time spent at the start of the trial in attempting to reach the food directly. Previously these times had fluctuated a good deal and were sometimes very long. For trials *19* to *23* they still maintained the high average of 2′ 20″ ; but in the period *24* to *29* they had dropped to 1′ 05″. (2) At this point the fish for the first time displayed a tendency to bear steadily leftwards down the glass, and this tendency was maintained.

The next " improvement " came at *36*. The fish from this point onwards firstly, often moved straight down the glass leftwards as soon as it had started moving left, and, secondly, succeeded in passing the edge *at the first attempt* four times out of five. With respect to the latter feature no further improvement was shown.

Further stages in the acquirement of a more efficient response were as follows. By *45* the leftward movement had come to be almost invariably a sideways movement along the glass, wheeling movements round the edge having become virtually eliminated (see below). At *55* the tendency to move straight down the glass as at the first leftward movement was almost established, and at this point the second marked drop occurred in the time spent in attempts to reach the food directly.

The learned response involved a swimming leftward along the glass in a more or less continuous movement until the edge was reached, the fish " feeling " its way round by making constant contact with the surface. In this movement the fish was orientated either at right angles to the glass, or, more usually, making an angle of 45°, having turned half-left. In either case the food was in the range of vision of the right eye. With regard to the process by which this response was established, one point deserves comment. During the first 25 trials, when the fish only succeeded in getting round the edge by lucky random movements, two methods of accomplishing the feat were equally frequent. Either (*a*) random working over the surface happened to bring the fish to the edge and so sometimes on and round, or (*b*) it happened to swim to the left and got round in a wide sweep. At *26*, as has been seen, there was a sudden tendency shown to work down the glass in a continuous movement; that is to say, an efficient response began to develop out of method (*a*). Method (*a*) may be said to have started to acquire significance. But at the same time method (*b*) had been learnt in some measure, the fish sometimes turning sharply to the left and a further sharp right wheel bringing it round the edge. For a time, then, there was an antagonism between two methods. Eventually the response developed from (*a*) predominated—as in all other fish subsequently trained under the same conditions—and by *44* method (*b*) was practically eliminated. This antagonism no doubt hampered and delayed the smooth course of learning. It is possible, however, that the successful accomplishment of the trial through method (*b*) may have been partly responsible, through a "transfer of learning," for an improvement in method (*a*) shown at *36*, after which the fish normally got round at the first movement down the glass, having learnt to swim left for an appreciably long stretch.

A further complication occurred with respect to method (*a*), the movement along the surface of the glass. This was normally accomplished by the fish keeping more or less at right-angles to the glass, or turned half-left, the food being viewed through the right eye. But the first attempts in reaching the food after the first leftward movement were often made at an angle of 45° to the glass, the fish orientated *half-right* and the food in the field of *both eyes*. A certain antagonism between these two positions had therefore to be overcome. This was more clearly shown in fish B (p. 519).

In view of these complications, it is not surprising that the process of learning was long and not by any means straightforward. The action was learnt in a precarious way. Nevertheless the results obtained from other fish show that an efficient performance can be established before there is any stabilization of the actual movements performed or in the orientation adopted, and demonstrate that variation in the methods of making the detour *need* not set up antagonisms which impair the acquisition of a learned response.

Second series (trials *B1* to *67*). After an interval of four days, during which the fish was subjected to disturbance, trials were renewed. The fish proved to have lost a good deal of ground, but it was not long before it regained the efficiency acquired during the first series of trials.

The tendency to move leftwards was retained from previous training, but at first the fish was inclined to travel only for a short distance down the glass. A change came at *5*, from which trial onwards it always carried on so as at least to come close to the left-hand edge. A further rather sudden change came at *10*, after which the fish only rarely failed to pass round the edge in its first leftward movement. After *10* there is only very slight general improvement in the action of moving leftwards.

Another retention from previous training relates to the time spent at the glass opposite the food before the first leftward movement. This period was short from the start of the second series, but there was a sudden and quite marked improvement after *9*. The average duration from trials *5* to *9* was 11″, while for subsequent groups of 5 trials the values were as follows : 7″, 6″, 7″, 5″, 5″, 5″, 4″, 3″. The change at *10* coincided with the improvement noted above with respect to the continuity of the leftward movement.

When the learned response had been thoroughly established, some experiments were made to test the extent of organization of the action. The experimental conditions were modified in certain respects, and the effect on the fish's behaviour observed. These " tests " are described below.

Third series (trials *C1* to *11*). After an interval of 15 days from the completion of the second series, trials were renewed on March 20 to 22. The first took over 4 minutes ; but after this trial the fish rapidly improved. Trials *2* to *6* averaged 0′ 21″, and *7* to *11* averaged 0′ 10″.

Tests in which sight of food was interrupted. In trials *B35* and *36* a prism was placed against the back of the glass, near the edge, in such a manner that, as the fish passed leftwards, the sight of the food was cut off without the intervention of an obvious partition. In the first trial the fish hesitated twice at the edge of the prism, but went round successfully the third time. In the second trial it went straight round first time. Thus it appeared that, for perfect performance of the detour response, the food need not be visible all the time.

In trial *38* a piece of mirror was placed at right angles to the glass, again cutting off the view of the food, and, instead, presenting the fish with a reflection of itself. The fish solved the trial perfectly successfully at first leftward movement. Similarly when the test was repeated (*39*). In the next trial, however, it stopped in front of the mirror and behaved as if its reflection had been detected. Trial *41* was once more performed efficiently ; and trial *42*, by contrast, resembled *40*, the fish reacting energetically to its reflection.

These few trials showed definitely (1) that the fish was sensitive to its mirror reflection, and may be induced to react to it. But (2) in spite of this fact, the learned action may proceed normally, as in *38*, *39*, and *41*, although the vision of the food object is replaced by the mirror reflection. The impetus of the learned action is evidently strong enough to overcome the attraction of the mirror reflection. These tests, then, serve to show that it is not merely inessential that the food be in sight all the time, but the action has strong enough impetus to progress in spite of distractions.

Tests in which the detour was extended. In these tests the fish had to pass two partitions instead of one. It was started from K, instead of from L. The results are given below. In all eight trials the fish reached the food by working to the left. It thus passed first from K to L, and then had to perform the normal course to which it had been trained, from L round to the food.

Average of previous 9 normal trials (L to food): $10\frac{1}{2}$ secs.

Trial No.	K to L.	L to food.	Total duration (secs.).
45	8	14	22
46	92	28	120
47	264	15	279
51	12	8	20
52	11	10	21
54	8	11	19
60	16	7	23
*61**	(24)	(12)	(24)

It will be noted that the fish gave an excellent performance on the very first test, and with the outstanding exceptions of the second and third tests, showed that the conditions presented no special difficulty. The passage from K to L was made in the same manner as the learned response from L to food, and was performed as rapidly. The lapse in trials *46* and *47* involved a temporary inability to pass from K to L, and it is interesting to note that just previously the fish had been given a long unsuccessful trial from J, following which a temporary instability in its response appears to have resulted. It is, however, the efficient performance of six out of eight tests that is significant, and serves to show how a learned detour response can serve to facilitate greatly the response to a detour of greater complexity.

These tests gave a hint that the fish had acquired a tendency to move to the left rather than towards the right when meeting an obstruction, for when at K it worked toward Q rather than P. Two tests in which the fish was started from J gave further evidence of this. From this position it could reach the food either by passing one partition to the right, or three partitions to the left. One of these tests (*45a*) was unsuccessful. The fish did not reach the edge O at all, and the trial was eventually abandoned. The other (*61*) was performed successfully in 2′ 31″, the fish *working round to the left*, and eventually reaching the food by the most roundabout route. The fish had evidently acquired such a strong tendency to move leftwards that it was unable readily to adapt its movements to conditions representing the mirror image of those to which it had been trained.

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* Part of longer trial.

Fish B.

Length 7 cm.

Jan. 2, placed in experimental dish in an empty tank in the main laboratory, under conditions referred to on page 502. For a fortnight fed with Mytilus and pieces of Polychaete worm off the end of a wire, until it had become thoroughly habituated to this method of feeding. It took food somewhat more readily than fish A, which was investigated at the same time.

Jan. 17–18, first trials with the glass partitions, which however proved unsuccessful, the fish showing increasing " panic " on repeated contacts with the glass.

Jan. 19–Feb. 8, 48 experimental feedings.

Trained to plain glass obstruction, with short detour of 4·1 cm. Later transferred to detour of 6·5 cm., as presented to most of the other fish.

The fish proved more energetic than A, and at first was much disturbed on making contact with glass partitions. It was trained to a very simple detour. A plate of 8·3 cm. width was interposed between it and the food, the course on either side of it being left free. It had thus to pass sideways 4·1 cm. either to the right or the left.

The learning curve is given in Fig. 5. The averages of groups of five successive trials are as follows :

Serial No. of trials.	Average duration.	*Serial No. of trials.*	Average duration.
1–5	1′ 15″	*21–25*	0′ 18″
6–10	0′ 20″	*26–30*	0′ 25″
11–15	0′ 19″	*31–34*	0′ 15″
16–20	0′ 25″		

After only 5 trials a level of efficiency was reached, and no further improvement was shown. A constant method of solving the trial was adopted. The fish first spent a little time in attempting to reach the food directly. It then began to bear to the right, all the time keeping orientated towards the food. It continued steady rightward movement until reaching the right-hand edge of the glass, passing which it swam straight forward to the food. Except for one of the earliest trials, it always made the short detour in this manner. The variations in the durations of the trials were largely due to variation in the time spent before bearing to the right. Once it had started sideways movement it almost invariably continued until the edge was reached.

The constancy of the level of efficiency after trial *4* is noteworthy. Though there was room for improvement, none was shown after this trial.

After 34 trials, the fish was given a longer detour, of the same type as that to which other fish were trained from the start. The only difference lay in the fact that it had to move round by the right instead of the left. (Food presented at K, fish started from near corner D.) After 14 trials had been given the fish began to grow lethargic and training had to be discontinued. Nevertheless some significant results were obtained.

The average duration of groups of successive 5 trials was as follows :

1–5	0′ 46″
6–10	0′ 36″
11–15	0′ 52″

The effect of the previous training was at once apparent. No random movements were made from the glass ; there was strong tendency to move down the glass to the right, the fish keeping orientated towards the food ; and the first three trials were performed by the method previously learned. At the same time, however, the fish showed some hesitation in moving continuously down the increased length of glass. There seemed to be a limit to the distance it would readily withdraw from the food. This hesitation did not decrease : rather it led to new reactions which upset the stability of the response.

From the fourth trial onwards it began to make turns towards the right, and to work down the glass at different angles. In some trials it reverted to the original behaviour, but these were rather less efficiently performed than others. Probably on account of a certain confusion in behaviour thus introduced, the duration of the trials, after first declining somewhat, became distinctly longer than when the fish was first presented with the 6·5 cm. detour.

Fish D2.

Length : 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 11, seven feedings given. Oct. 12, frame with glass plates tested in the tank ; fish took food readily just after in spite of the disturbance. Oct. 13–Nov. 13, 45 experimental feedings.

Plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is shown in Fig. 6. The average duration for successive groups of five trials is as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	2′ 18″	*26–30*	1′ 14″
6–10	2′ 19″	*31–35*	1′ 0″
11–15	6′ 36″	*36–40*	2′ 51″
16–20	3′ 44″	*41–45*	2′ 30″
21–25	2′ 22″		

The experiments on this fish were abandoned, when, after 45 trials, it seemed farther off establishing a learned response than at the start.

This fish was decidedly " nervous " in the early stages, and tended to give shock reactions to the glass partitions in a manner not observed in other individuals. For some time it was only possible to give one trial a day. This effect, however, had worn off by trial *10*, and the fish's behaviour was thence normal.

For the first few trials the fish showed a strong tendency to move to other parts of the dish, though it repeatedly returned towards the food. From trial *4* onwards, however, this tendency was only shown in a modified form or appeared only after the trial had lasted a considerable time. From this point the fish worked steadily, often actively at the glass, and was unusually persistent in its attacks on it.

With regard to the failure to establish an efficient response, certain features are worthy of notice. The earlier trials were mostly solved by the fish giving a left-turn, swimming left, and right-wheeling round the edge. The left-turn movement was thus apt to lead directly to a solution. During trials *3* to *12*, 10 such left-turn moves were made, and no less than 6 were effective in this way. Yet this movement suddenly dropped out at this point. The same thing happened in the case of other fish which did eventually acquire an efficient response and is commented on at a later stage.

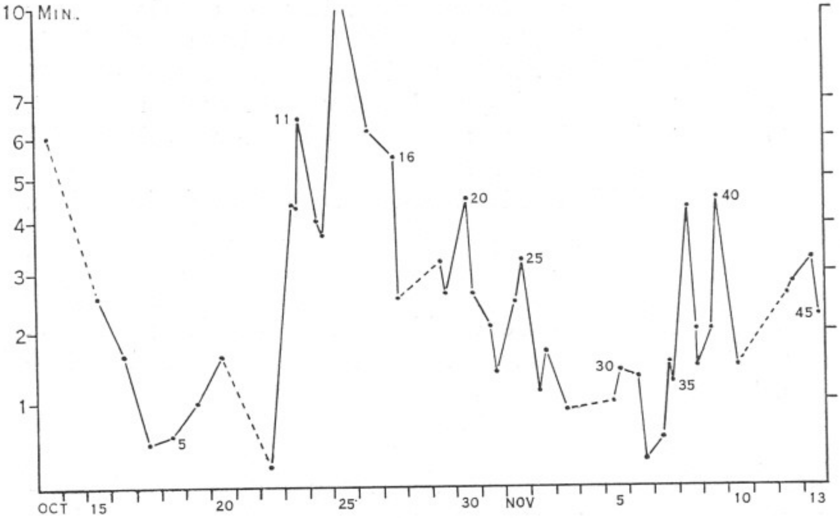

FIG. 6.—Graph of duration of trials of fish D2. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

For a period, between trials *25* and *35*, some improved efficiency was shown. Though, in the main, there was gradual improvement from *14* onwards, trials *17* and *26* mark two stages in which there was comparatively sudden change. The first point marks the complete disappearance of all random movements away from the glass, and at the same time the frequency of leftward movements along the glass (after the first) increased. The second marks quite a sudden permanent reduction in time spent in attempts to reach the food directly, another sudden increase in frequency of leftward movements, and withdrawing movements from the glass (which had been a conspicuous feature of some earlier trials) quite suddenly disappeared.

The improvement was not maintained and a marked " lapse " occurred after *35*. The trials now show an increase in time spent in attempts to reach food directly, before any leftward movement, a decrease both in *frequency* of leftward movements (after the first) and in their *efficiency*. There was also a return of withdrawing movements from the glass. It is interesting to note that the decrease in efficiency of leftward movements set in while their frequency was still increasing (trial *29*) ; the lapse was thus to some extent forecast.

The performances during the last 10 trials, though comparable in duration with those of the earlier, differ in some other respects. Notably, there was no return to making random movements away from the glass, or to making left-turns. If the fish had " learnt " nothing else, it had acquired the habit of working persistently at the glass. Its responses to the situation, though relatively ineffective, had become more stabilized

Fish D3.

Length : 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given. Oct. 13–Dec. 13, 83 experimental feedings.

Trained to plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 7. It will be seen that after trial *10* the curve sinks to a low level from which it sharply rises at intervals, representing intermittent inefficient performances. After *42*, inefficient performances become more frequent, until at *51* a bad spell sets in during which the durations of the trials are even greater than at the start of the experiment. Towards the end efficiency is increasing considerably, and the fish is well on the way to establishing an effective response when the trials are eventually abandoned.

From *16* to *42* there was a spell over which the times averaged 12″, if three intermittent " bad " trials, which stand out in marked contrast to the others, be omitted. During this period, then, the fish had produced an efficient response, on which, however, it appears to have had a precarious hold. The explanation of this, as well as some understanding of the bad lapse that set in, is forthcoming when the observations on the fish's behaviour are examined.

A peculiarity of the behaviour was the exceptional activity shown at the start of the trial. The fish set at the glass with a burst of energy, which, however, waned after half a minute or so. Unless it had passed the edge in this opening period of activity, the fish settled down to steadier, but still persistent, attempts to reach the food through the glass.

FIG. 7.

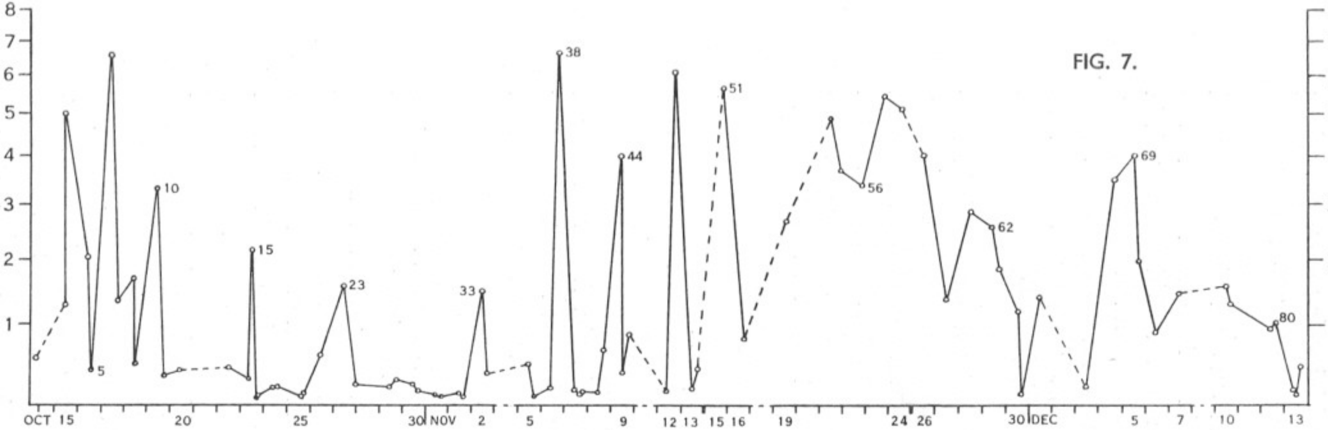

FIG. 8.

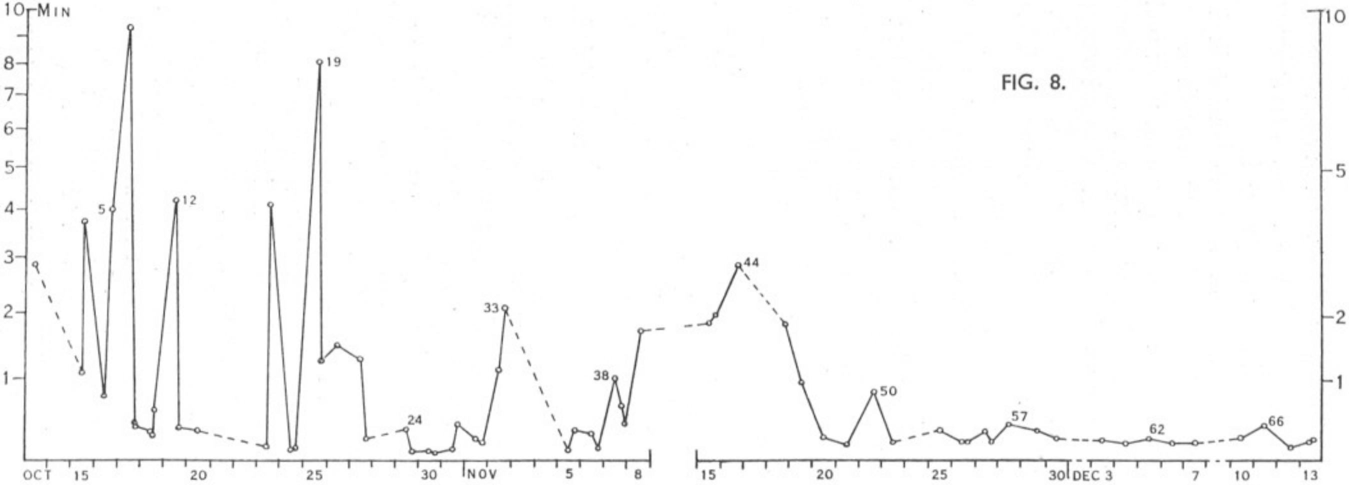

Fig. 7 (above).—Graph of duration of trials of fish D3. Fig. 8 (below).—Graph of duration of trials of fish D4.
(A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

Another peculiarity was that the fish never made random movements away from the glass to other parts of the tank. It held persistently to its attempts at passing the glass obstruction. During the opening period of activity it was, from the start, inclined to work leftwards along the glass keeping orientated towards the food (as with fish B, p. 518). When less active it was less inclined to bear leftwards. The success of the trial, therefore, depended a good deal on the success of the efforts of the first half-minute. Several of the fish in early trials spent some time in attempting to pass straight to the food before bearing to one side. In the case of D3 the duration of this period was at a minimum level as early as the 4th trial.

The features of the behaviour shown in early trials might well have been expected to work together towards a rapid acquisition of an efficient response. And to a large extent this proved to be so. The one drawback, which was never adequately overcome, was the decrease in activity after the first half-minute. If the trial lasted beyond this period it was likely to be prolonged considerably. The conspicuous intermittent " bad " performances were due to this cause.

Compared with that of other fish, the behaviour was remarkably uniform and invariable. Also there was a decided indication of a cycle of responses repeated in each trial, if prolonged. The more energetic opening " attacks " on the glass at the start led the fish to bear left in a very short time and to bear left far enough to get near or reach the edge round which it had to pass. Working up and down the glass it was liable frequently to reach the edge during the opening period. All the time the fish kept approximately orientated in the direction of the food. As activity decreased the extent of glass traversed also decreased, and the fish settled to a quieter " attack " on the glass in the middle region of the plate. The occasions on which it came as far left as the edge R now became less frequent, and the chances of achieving a solution decreased considerably. It was not, as a rule, until the trial had lasted some while that any other movements were given. These consisted in sharp turns either to the right or the left. It is noteworthy that all the first 6 trials were solved as a result of a complete or partial left-turn. But the success of the left-turn movement, as in the case of other fish, did not lead to the establishing of this method of solution. After trial *6* the left-turns were almost entirely of a partial kind, and they soon became merged in the general leftward movement along the glass. As to right-turns, the fish had a spell of these in trials *3* and *6*, but only very occasionally in other trials.

The short durations of *9*, *11–14*, and *16* onwards were the result of the edge being passed during the more active spell. The fish, however, took some time to acquire the habit of reaching the edge, and passing it, in one continuous movement.

The bad lapse which set in between *40* and *50* was associated with an entirely new feature which appeared for the first time in *48*. In that trial the fish began repeatedly to withdraw straight back from the glass. This movement was quite a " useless " one and tended to check leftward movement. It figured largely in trial *51* and from *53* onwards, when it was regularly given after the first half- or three-quarter minute. In *54*, for example, the fish spent over 4 minutes continuously moving backwards and forwards in the middle region of the glass without once getting near the edge.

It might at first sight be supposed that the development of this useless habit was responsible for the lapse. But it is probably more true to say that it developed as *a result* of the lapse, being a symptom rather than a cause. Trial *44* can be said to mark the beginning of the lapse : the fish took 4 minutes to reach the food, but during the time did not give the withdrawal movement at all. The inefficiency of the performance resided in the fact that the fish showed disinclination to move leftwards, and, when it did so, to move far enough.

The improvement towards the end of the series was marked by a reduction in the time spent in making withdrawal movements, and the increased tendency to make half-left turns towards the edge R. Most of the later trials were solved by the latter movement.

Four tests were given with the squared glass substituted for the plain glass (see p. 561).

Fish D4.

Length : 4 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given, food taken with exceptional eagerness. Oct. 13–Dec. 13, 69 experimental feedings.

Trained to plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 8. The averages for successive groups of five trials are as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	2′ 35″	*36–40*	0′ 29″
6–10	2′ 07″	(Interval)	
11–15	1′ 08″	*42–45*	1′ 53″
16–20	2′ 44″	*47–52**	0′ 22″
21–25	0′ 42″	*53–57*	0′ 17″
26–30	0′ 11″	*58–62*	0′ 15″
31–35	0′ 46″	*63–67*	0′ 15″

In spite of the fact that several good performances were given during the first 20 trials, and that trials *25* to *28* were performed exceptionally well, it was a considerable time before a consistent response was established.

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* Trial *48*, on consideration, omitted. Fish sluggish, behaviour abnormal.

The fish worked at the glass energetically, and was apt to make sudden darts. Its movements were rather variable. In early trials it sometimes turned left and swam into the region of corner D, and on five occasions reached the food by swimming up from this corner. It also showed a tendency to make right turns, which sometimes took it into the region of corner C, and in four trials it moved from there into K.

The movements which took the fish round the edge R to the food varied considerably. Sometimes the fish kept orientated towards the food, withdrawing along the glass surface obliquely leftward ; sometimes it turned partially to the left, keeping the food within range of vision of its right eye ; sometimes it turned left and wheeled round the edge. And there were modifications of these three main methods. It is noteworthy that, after *12*, the third movement proved an effective method of solving the problem. Yet for a long time it was only occasionally attempted.

In spite of the variable quality of its reactions to the obstruction, the fish, after *23*, gave a series of performances in which its methods were consistent (the first of those enumerated above). At first, too, it seemed to have established a consistently *efficient* response, but lapses set in. By Nov. 7–8 the fish appeared definitely to be in sub-normal health, and after *41*, the series of experimental feedings was interrupted. Trials were suspended until Nov. 15, during which period the fish was fed normally in an ordinary manner, off the wire.

When trials were resumed (*42*) the fish had recovered normal activity. Trials *42* and *43* were solved in just under two minutes, both by the third method. The fish, then, had lost the previously established tendency to make the detour by method 1. But, at the same time, it had retained certain features from its previous training. (i) It had come to move leftwards almost immediately, never spending more than 8 seconds in attacking the glass in the original position ; and (ii) it had come to keep up a persistent attack on the glass not making any movements away to other parts of the tank.

As indicated by the figures for the duration of the trials, a sudden change came at *47*, which marked the beginning of a series of efficient performances. A learned response can now be said to have been established : the sudden improvement is noteworthy. It is also of interest to note that the variable quality of the fish's responses, which had reappeared after *43*, persisted for some time after efficiency was established. The method of solution was not stabilized until efficiency had been attained. The significance of this feature is discussed on page 551. Towards the end the left-turn-and-right-wheel movement tended to predominate.

Fish D5.

Length : 5 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 13, eight feedings given. Oct. 15–Dec. 13, 102 experimental feedings.

Trained to plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 9. The averages for successive groups of five trials during training are as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	11′ 36″	*21–25*	0′ 36″
6–10	5′ 51″	*26–30*	0′ 13″
11–15	3′ 18″	*31–35*	0′ 14″
16–20	0′ 48″	*36–39*	0′ 12″

Before the 40th trial an efficient learned response was securely established, and after this various tests were performed on the fish. In spite of apparently hopeless efforts in early trials, this fish emerged as the most proficient performer of those trained to the plain glass obstruction.

The earlier performances were outstandingly " bad." The fish was excessively disposed to wander over various parts of the tank, particularly in the right-hand part, and only eventually reached the food when it happened to move round near it. After twelve trials had been given it seemed no nearer a learned solution of the detour than at the start, and appeared to be a hopeless case. Yet by the 18th trial it was well on its way to acquiring an efficient response, which was established from *24* onwards. An improvement came with comparative suddenness, following on a remarkable change in the fish's behaviour. The change may be said to have dated from the end of *13*.

The manner of the fish in early trials contrasted sharply with that of fish D4. Its movements were characteristically leisurely and it was not subject to more violent bursts of activity. In contrast with fish D1 (p. 531), however, it had little tendency to persist in working against the obstruction, but constantly reacted by turning and swimming away from the glass to some other part of the tank. However frequently it might return in the direction of the food, this lack of persistence remained. The solutions of the early trials were more conspicuously fortuitous than in the case of any other fish. Of the first twelve, five involved swimming up from corner D, in three the fish swam in an arc between R and D from the front of the tank, and in three an approach was made from corner A. Only in two (*5* and *9*) did the fish keep at all close to the glass in moving leftwards round the obstruction, in both of them turning left and wheeling round to the right. No habit was developing which could provide a basis for a learned response.

Trial *13* progressed on the same lines as the previous inefficient trials. The fish had had three short spells at the glass, when random movements brought it into the right side, and thence to the back part of the tank. It moved round again to corner C, and, 2′ 15″ from the start of the trial, moved up to the food in the original position. It then behaved in a changed manner: it bore leftwards, keeping close to the glass, continued till the edge was reached, and passed the edge at 2′ 25″, snapping at the food immediately after. It had never made the detour in this manner before.

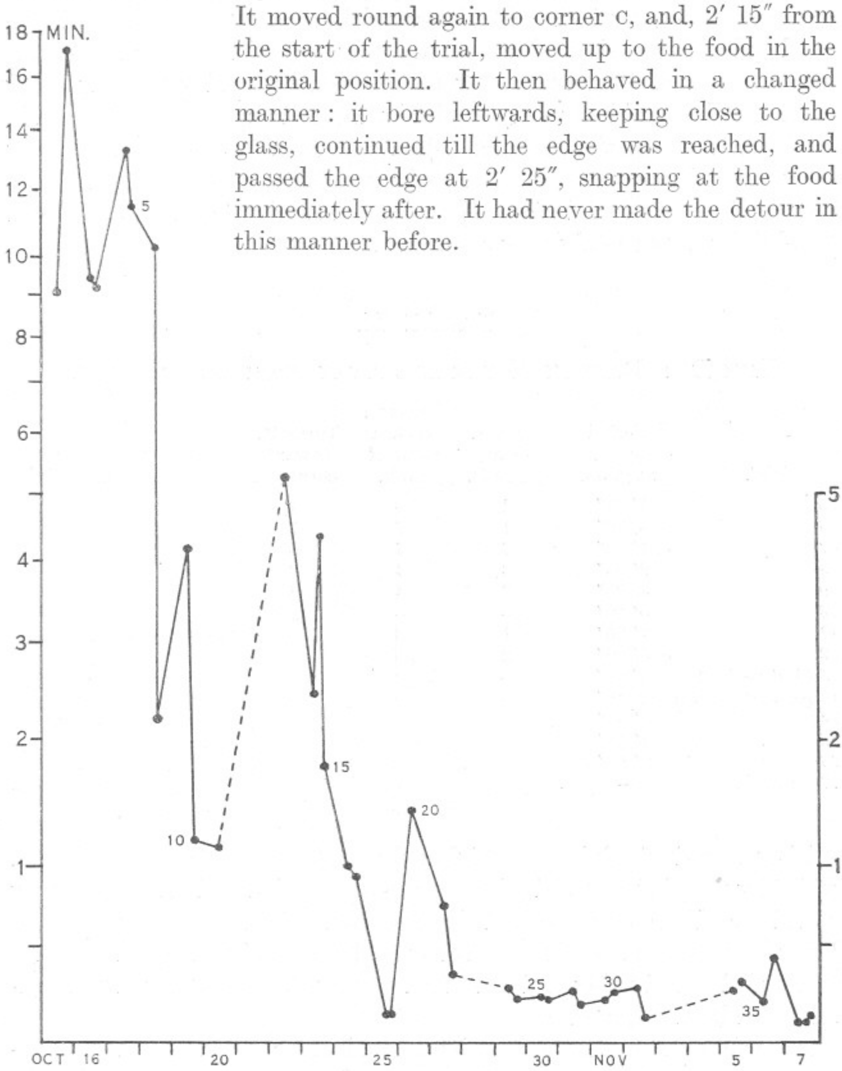

FIG. 9.—Graph of duration of trials of fish D5 during training. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

The type of behaviour shown at the end of *13* persisted in all subsequent trials. Though *14* was not solved until over 4 minutes, the whole of the period was occupied with leftward movements along the glass. Though the fish had still to learn to work more continuously leftwards and to desist from minor withdrawing movements, the contrast between this performance and preceding trials was most striking. And the changed behaviour was permanent. Persistent working over the middle and leftward side of the glass almost completely replaced other movements. The reaction of turning sharply to right or left and swimming away from the glass suddenly and completely dropped out. The data given in Table II illustrate this feature. Moreover, turning movements of any sort were only very rarely given. Only two full left-turns were noted in the whole series of trials from *14* to *39*, and no right-turns at all. Even half-left turns were only very occasional.

TABLE II.

FISH D5: RANDOM MOVEMENTS AWAY FROM OBSTRUCTION.

Trial.	Period spent at glass.	Turns L. toward corner D.	Turns L. toward front of tank.	Turns R. toward corner C.	Remarks.
5	1′ 47″	1	–	4	
6	8′ 10″	1	7	7	
7	c. 7′ 00″	7	7	4	
8	2′ 05″	3	4	2	
9	4′ 05″	3	4	3	
10	0′ 30″	–	–	2	
11	1′ 05″	1	3	–	One withdrawal.
12	c. 4′ 00″	2	5	3	
13 (first period)	0′ 42″	–	2	1	
13 (second period)	0′ 10″	–	–	–	
14	4′ 20″	–	–	–	Several withdrawals.
15	1′ 44″	–	–	–	,, ,,
16	0′ 58″	–	–	–	
17 onwards	–	–	–	–	No withdrawals after *21*.

The method of solving the trial achieved for the first time at the end of *13*, by working leftwards close to the obstruction and finding the way round the edge R, characterized all subsequent trials. It has to be noted, however, that the actual movements which took the fish round the edge still varied considerably, and continued to vary after efficiency in performance had been acquired.

After the change of behaviour, it was not long before a marked improvement in the efficiency of the fish's performance became noticeable. Trials *18* and *19* both were solved in less than 10 seconds. After *21*, trials were consistently good. The steady improvement is indicated by the figures given in Table III. It will be noted that leftward movements increased both in frequency and in efficiency.

TABLE III.

Improvement in Performance of Fish D5.

Trial Serial No.	Total duration.	Leftward movements per min. (i) Total per min.	(ii) Un-successful.	(iii) Successful.	Ratio unsuccessful : successful—(ii) over (iii).
14	4′ 21″	1·6	1·4	0·2	6
15 to *20*	5′ 13″	3·3	2·1	1·1	1·8
21 to *39*	4′ 18″	7·2	2·8	4·4	0·6
Period of Maximum efficiency. Normal trials, between *80* and *101*	1′ 36″	11	2	9	0·2

Tests.

Food presented on the right. From *40* onwards certain tests were performed on the fish which were intended to throw light on the nature of the learned response. One series of ten, carried out at regular intervals between *40* and *58*, consisted in presenting the fish with, so to speak, a mirror-image of the conditions to which it had been trained. The food was presented at K, and the fish had to move to the right round edge Q. The results are summarised in Table IV.

TABLE IV.

Fish D5: Tests in which Food was presented on the Right of the Dish.

Test Serial No.	*Trial Serial No.*	Duration Test.	Normal trial.	Remarks.
A 1	*40, 41*	13′ 00″+	0′ 10″	
2	*42, 43*	0′ 26″	[2′ 43″]	
3	*44, 45*	0′ 22″	0′ 28″	
4	*46*	0′ 10″	0′ 12″	
5	*47, 48*	1′ 02″		
6	*49, 50*	0′ 31″	1′ 02″	
7	*51, 52*	1′ 53″	1′ 36″	Very marked tendency to withdraw appears.
8	*53, 54*	10′ 00″+	0′ 17″	
9	*55, 56*	14′ 00″+	2′ 25″	Again marked tendency to withdraw.
10	*57, 58*	4′ 15″	0′ 25″	,, ,, ,, ,,

The times marked with a plus sign indicate that the trial was abandoned before the fish reached the food.

In all cases the test trial was given first, followed by a normal one. An unfortunate result of the tests was that the normal performances were somewhat upset, one conspicuous bad habit developed in the former—that of withdrawing repeatedly from the glass—being transferred to the latter.

Nevertheless one or two definite points emerge. In the first place, the performances of the tests are seen to fall sharply into groups. (1) The fish proved quite incapable of giving adequate rightward movements, and the behaviour in the tests differed conspicuously from that in the normal control : these tests include *1*, *8*, *9*, and *10*. (2) There was no significant difference in the performance on the two sides, and the learned behaviour can be said to be completely transferred : viz. trials *2* to *7*. The fish thus exhibited two quite distinct behaviour patterns under the new conditions.

Secondly, the fact that the fish was capable of exhibiting transfer of learning without having to learn the new detour anew is worthy of notice. Tests *2*, *3*, and *4* were all performed as efficiently as could have been expected were transfer of learning a reality. Also it may be noted that the first test was all but solved in an extremely short time, the fish just failing to pass the edge at 5″ (after which it never moved to the right again).

A " bad " habit, involving the useless movement of withdrawing repeatedly from the glass for a short distance, appeared first in tests *1* and *7* and was again shown in the normal trial which followed the latter. The movement became conspicuous in trials which followed, and a series of normal trials had to be given to train it out. After *67* normal efficiency was re-established. Evidently, then, the tests set up a certain instability in the fish's behaviour.

Fish started from other parts of dish. Between *74* and *102* the tests consisted in starting the fish from some part on the right-hand side of the tank, the food placed in the normal position. The fish thus had to make a longer detour, and two courses were opened to it, either round to the right and up to food passing edge o, or round to the left. It was found that the fish sometimes took one route, and sometimes the other. The main feature shown was that the passage round to the right took, on the average, a longer time, and evidently presented greater difficulties, than that to the left. This is seen from the figures given below, derived from combining all the tests, and averaging the times spent in reaching the food from three starting-points. A large difference is seen between the rightward and leftward courses. Evidently, then, the learned response had established a facility for leftward movement.

TABLE V.

FISH D5 : COMBINED RESULTS FROM TESTS IN WHICH THE DETOUR WAS EXTENDED.

The figures denote average of time taken to reach food from the positions indicated.

From position . .		BF	EB	
		2′ 22″ ——→	1′ 41″	Rightward movement.
	0′ 46″ ——→	0′ 31″ ——→	0′ 09″	Leftward movement.
From position	BF	FC	GC	

The end part of the rightward course, round the edge O, resembled a mirror-image of the normal conditions (passage from GC). It is therefore comparable to the conditions presented in the first series of tests, in which the fish had to make a passage round Q. It may be noted that the fish's behaviour in the first two trials (*73* and *79*), in which it had to find its way round O, compared with its behaviour in the former tests. On the first occasion it failed to get round O at all, showing no inclination to bear to the right. The second showed complete transfer, the performance being accomplished efficiently in 10 seconds.

The interpretation of the process of learning exhibited by the fish is further considered in the discussion (pp. 549–552).

Fish D1.

Length: 5½ cm.

Sept. 25, transferred to experimental dish; P.M., took food. Sept. 27–Oct. 11, seven feedings given; soon came to take food readily. Oct. 12, frame tested in dish; disturbance sets up fright reactions in the fish, which would not take food immediately after; but fish took food readily two minutes later. Oct. 13–19, seven feedings. Oct. 20–Dec. 7, 61 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black strip, ½ cm. wide. Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 10. The average duration for successive groups of five trials is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 07″	*26–30*	0′ 48″
6–10	3′ 33″	*31–35*	1′ 05″
11–15	4′ 19″	*36–40*	2′ 26″
16–20	0′ 55″	*41–45*	2′ 21″
21–25	2′ 28″		

The fish was characteristically a steady worker, moving slowly and deliberately. It never exhibited any marked bursts of activity. From the start it showed a tendency to work persistently at the glass, and never moved off to the right-hand side of the tank.

The only movement it made away from the glass involved a full left-turn and passage to corner D or to the front of the tank. During the earliest trials, twice did the fish swim up to the food from corner D, and on three occasions a full left-turn followed by a right-wheel took the fish round the edge R. But after the 6th trial the left-turn movement suddenly dropped out of the fish's repertoire and was only given on one other occasion during the next 36 trials.

As the above figures indicate, the fish failed to establish a learned response. There were two periods in which improvement appeared to be coming, but the promise was not fulfilled. And this in spite of the fact that the fish's behaviour was perhaps more stereotyped than in any other

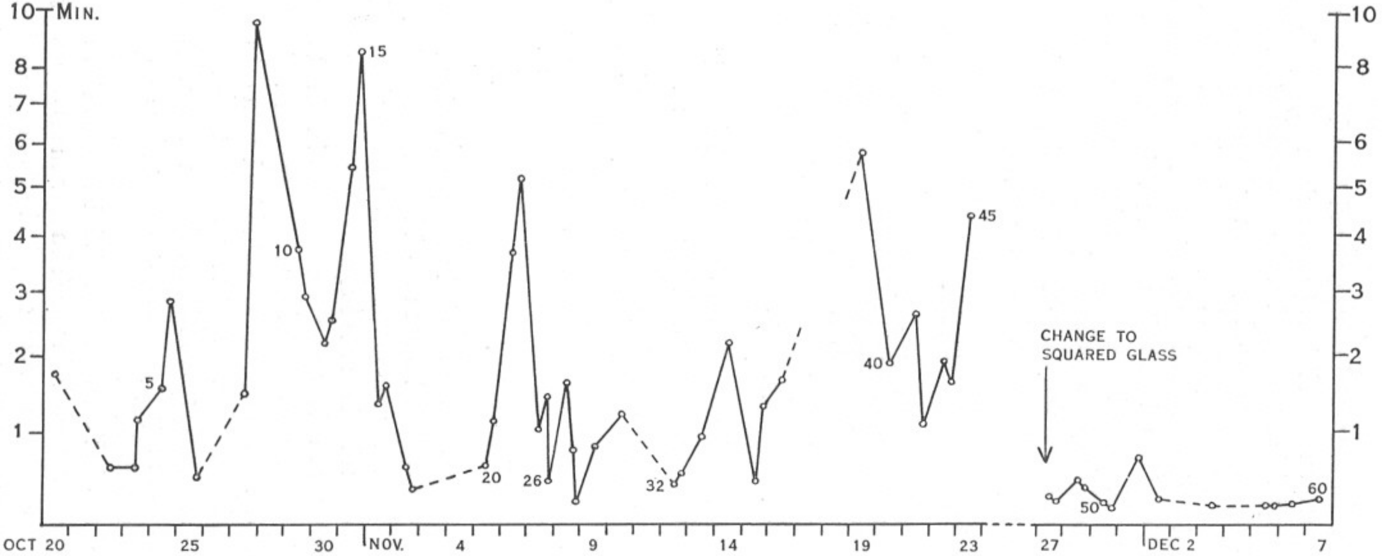

Fig. 10.—Graph of duration of trials of fish D1. Note the sudden change to an efficient performance when squared glass was substituted for plain glass (see p. 561). Two normal trials given the latter period were abandoned unfinished at 3 minutes.

fish. With the exception of the left-turn movements mentioned above, it kept remarkably uniform throughout. The fish settled into a habit of reacting to the obstruction in a certain manner which eventually led to its passing the edge. Yet the performances did not consistently improve.

Some tests were performed on this fish in which the plain glass was replaced by another on which a meshwork of fine lines had been scratched (p. 511). The results were striking, the fish giving a series of perfect performances, showing that something had been learned during the first 45 trials. These results are dealt with on pp. 560–561.

This fish gave no evidence that the black edge of the glass had any effect in facilitating the passage round the detour. Neither were any special reactions given to the band, nor was the fish induced to perform movements different from those given by other fish against plain unbordered glass.

Fish D6.

Sept. 25, transferred to experimental dish: P.M., took food with gentle coaxing. Sept. 27–Oct. 18, 13 feedings given. Oct. 19–Dec. 13, 75 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black stripe, ½ cm. wide. Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 11. The average duration for successive groups of five trials is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 34″	*41–45*	1′ 04″
6–10	4′ 12″	*46–50*	1′ 05″
11–15	5′ 18″	*51–55*	0′ 45″
16–20	4′ 58″	*56–60*	0′ 44″
21–25	3′ 28″	*61–65*	0′ 40″
26–30	1′ 06″	*66–70*	0′ 42″
31–35	0′ 58″	*71–75*	0′ 54″
36–40	1′ 08″		

The durations thus settle down to a uniform average level of about ¾ minute. This comparatively high value is due to the fact that the fish learned the alternative circuitous path to the food, moving to the right and passing three partitions (Fig. 1, partitions Q, P, and O). D6 was the only fish to give this curious result.

It is of special interest to examine the early behaviour to discover the steps which led to the acquisition of the response. Careful analysis of the movements made by the fish during early trials has shown certain features which can only be summarized here.

(i) From the start the fish had a tendency to react to the glass by making sharp turns to the right or left. The first four trials were solved as a result of a left turn; in two cases the fish wheeled widely round the edge, in two it swam into corner D and up to the food from that point.

FIG. 11.

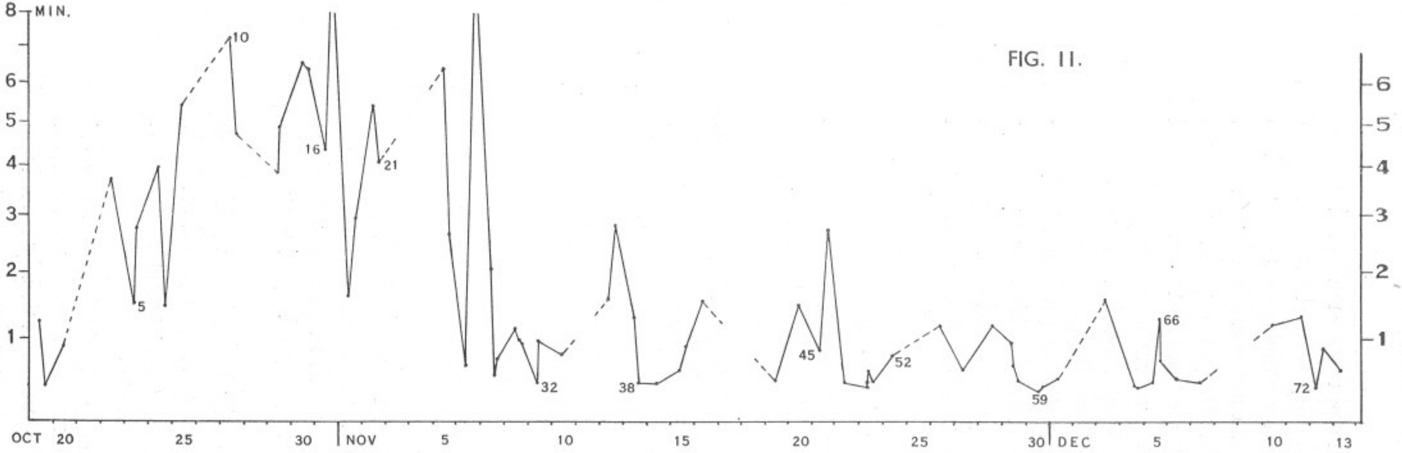

FIG. 12.

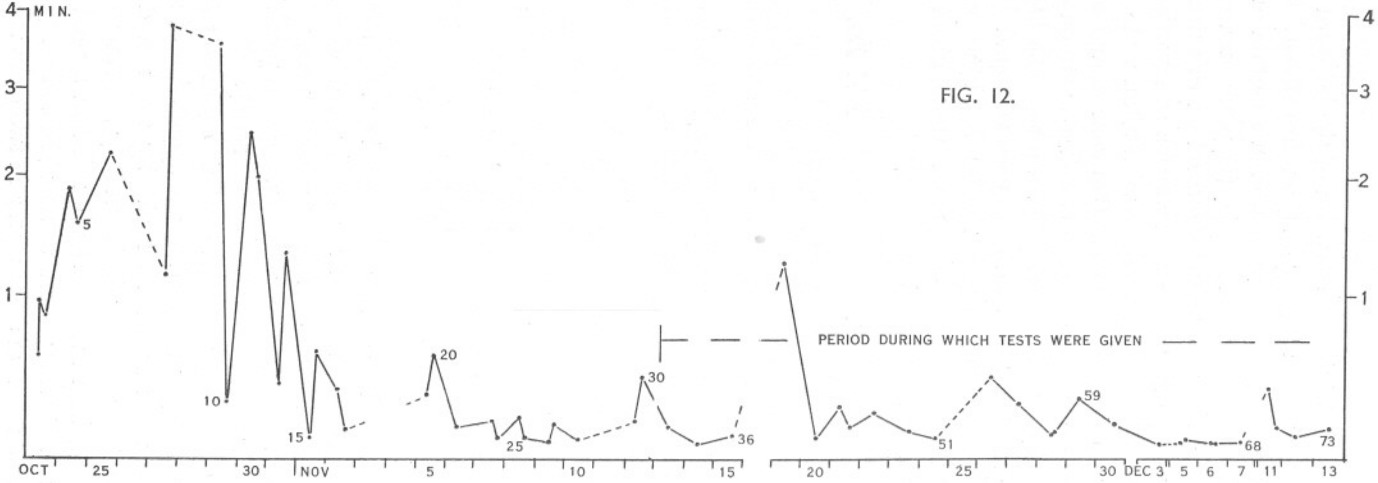

Fig. 11 (above).—Graph of duration of trials of fish D6, which acquired the habit of making the detour by the roundabout route.

Fig. 12 (below).—Graph of duration of trials of fish D7. From Nov. 13 onwards various tests were regularly given: only the normal control trials are given in the graph.

(ii) A new feature of behaviour appeared in trial *4*: the fish began repeatedly to withdraw from the glass along the line of its approach (i.e. back in the direction of corner C). This trait persisted and came to be an outstanding peculiarity of the behaviour of this fish, normally characterizing the opening period of almost all trials from *4* onwards.

(iii) Left-turn movements, occasionally given in early trials, were very successful in leading to a solution. Yet they became less and less frequent, and virtually disappeared after trial *13*. Several other fish showed this feature. Right-turn movements were more frequently given than left turns, and their frequency, if anything, increased. This feature was not shown by any other fish. It is evidently connected with the fact that the right-turn movement became associated with the withdrawing movement mentioned above.

(iv) Almost as soon as the withdrawing movement appeared, right-turn movements became associated with them. The effect was that the fish now frequently turned past edge Q into the region K. Other fish in early trials occasionally found their way into this compartment, but none so persistently as D6. From this position the fish almost always passed farther to the right, round into region J. Here it once again found only a single partition between itself and the food, and further movement to the right usually took it round the edge O. From trial *5* onwards the fish normally reached the food from this side of the tank.

(v) Finally, the fish showed exceptional disinclination to bear leftwards along the glass partition in its first assaults. This movement in fact was only given on three occasions during the first 10 trials (as contrasted with some 40 full turns). On first making contact with the glass opposite the food, the fish began withdrawing movements almost at once, and soon found its way into compartment K.

The tendency, then, to withdraw and bear right (in spite of the success of left-turns in the earliest trials) resulted in the fish working round the tank to the right and approaching the food from the direction of A. Trials *5*, *6*, *8*, *9*, *11*, and *13* were solved in this manner. Moreover, from this point onwards this course was invariably taken, and came to be followed with increasing efficiency.

It was some time, however, before any real improvement could be noticed. The time taken to reach compartment K varied from 5″ to over 4 minutes, and frequently the fish moved back round Q. Occasionally, too, it would pass back into K after reaching J. The time spent in circumventing edge O varied from 31″ to 3′ 39″. Eventually, a rather noticeable improvement came suddenly at *23*. From this trial onwards the course was followed continuously: only on one occasion (*25*) did the fish move back from region K. The passage from Q to P was now performed with very little hesitation, the time taken not exceeding 13″, and falling to an average level of 10″, gradually decreasing to 6″. The time spent in making the passage round O for a period of 20 trials did not exceed 35″, with a minimum of 9″. Efficient performances of total duration between 25″ and 40″ became increasingly frequent.*

As time went on the fish became increasingly adept at threading its way round the glass obstructions, until it was not far short of acquiring a complete co-ordinated response. It is probable that, with repetition, co-ordination of successive motor responses was occurring to some extent. Just before trial *46*, during a delay in the presentation of the food, the fish was observed to swim round the whole course in about half a minute, though there was no food present. At trial *56*, and again on the last day that experimental feedings were given, the fish swam the whole course on its own initiative in the minimum time of 25″.

Certain tests with this fish deserve notice. In the first place it was found that the black border on the glass plate SR could be removed without the least effect on the reactions of the fish. From trial *50* onwards plain glass was always used. In view of comparable evidence from fish D1 (p. 533), it may be inferred that the existence of this band does not aid the fish in perceiving the glass plate as an object.

Secondly, valuable evidence was obtained that the passage round the glass maze to the right was not dependent on influences external to the dish—for instance, such impressions of objects beyond the maze as may have figured in the fish's visual field. In trial *59* the frame was reversed, the fish started from A, and the food presented at K. The relations of the fish and food to the maze were thus unaltered, but the fish had to swim away from the light and towards the observer. The fish gave an exceptionally efficient performance, reaching the food in 22″. The same conditions were repeated next trial (*60*) and again the fish traversed the route with little hesitation, reaching the food in 25″. Further, it was found that, in normal trials, the position of the light could be varied without any effect on the fish's response. Evidently then, the fish's movements were made relative to the food and frame and were independent of features external to it.

With this fish, learning as it did a comparatively long detour, unusual opportunities were afforded for examining the learning of different parts of the route. If backward association occurred (see p. 553) it might be expected that the last part (passage round O) would be acquired first, and

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* Viz.:

Serial No. of trials.	Number of efficient performances.	*Serial No. of trials.*	Number of efficient performances.
21–30	2	*51–60*	6
31–40	4	*61–70*	6
41–50	4		

the efficient performance of movement into K acquired last, only after the passage round P and O had become a fully co-ordinated movement. Analysis of the records shows no indication of any feature of this sort.

The route is conveniently divided into three sections. (1) Start of trial to passage round Q; (2) passage round Q to passage round P; (3) passage round P to passage round O. All through, the second section was more quickly and efficiently traversed than either of the others. The average times (in secs.) for successive five trials after *25* were 10, 9, 8, 6, 8, 9, 6, 6, 7, with no abnormally long times to overweight the average value. The corresponding times for the passage from P to O (3) were 64, 27, 21, 33, 27, 21, 20, 22, and 34. It appeared evident that the closer proximity of the food when the fish reached position J acted as a hindrance to the efficient passage round O. Again, though both for a time varied considerably from one trial to another, the duration of the final passage from P to O was all along somewhat greater on the average than that from the start to Q (section 1). The final section of the detour therefore presented greater difficulties than any other. And though the efficiency of performance of the different parts increased in rather too fluctuating a manner to show any definite precedence for any one, it can at least be said that the latter section was certainly not learned in advance of the rest.

Fish D7.

Oct. 10, transferred to experimental dish from another similar dish. Oct. 13–Oct. 22, 7 feedings given. Oct. 23–Dec. 13, 73 experimental feedings.

Trained to glass marked with meshwork of fine lines (p. 511). Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 12. The average duration of successive groups of 5 trials during uninterrupted training is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 10″	*16–20*	0′ 25″
6–10	2′ 13″	*21–25*	0′ 10″
11–15	1′ 17″	*26–30*	0′ 12″

This fish proved a good subject. It worked actively and persistently, was not easily distracted, and was not given to making erratic movements. It seldom made any movements away from the glass to other parts of the tank, and on the rare occasions when it did so, it soon returned to the glass.

During the first three trials the only reactions given after continued failure to reach the food direct were full turns to the right or left. Each of these trials was solved in under a minute as a result of the first full left turn.

A complete change of behaviour was shown in the next four trials, which were less successfully performed : the fish now worked close to the surface of the glass, and showed but little tendency to turn to the side. It eventually worked its way round the edge R. During these trials the first indication was obtained that the fish detected the lines on the glass, for its passage down the glass was jerky, and it appeared definitely to move from one square to another.

In the trials that followed there reappeared a tendency to give full turns, predominantly to the left. Between trials *10* and *20* a steady improvement took place, and *21* marks the onset of a spell of uniformly efficient performances.

The period of improvement was marked by an increase in both frequency and efficiency of left-turns, right-turns and other movements dropping out. The method by which the fish passed round the obstruction was constant from *9* onwards : it turned full-left, swam left, and wheeled to the right round the edge. This response became established.

There are two noteworthy features in connexion with this learned response. Firstly, the response is one which *other fish, trained to the plain glass, proved incapable of establishing,* although all performed several early trials successfully *by this manoeuvre* (see p. 548). Secondly, the fish soon came *to give the left-turn movement on its first passage up to the food before first coming in contact with the obstruction.* This never occurred in the case of fish trained to plain glass. The fish turned left regularly on reaching a point 2 to 3 cm. distant from the glass ; and this may be taken as a good indication that it detected the pattern of lines at this point. No doubt the pattern also served as a guide to the edge of the glass, and enabled the fish to wheel right at the correct moment. At any rate, the contrast between the behaviour of this fish (together with D8, p. 539) and that of other fish is a striking fact.

Tests in which food was presented at K. Between *31* and *52*, eight tests were performed in which the conditions presented a mirror-image of those to which the fish had been trained (as with D5, p. 526).

TABLE VI.

TESTS WITH FISH D7.

Food presented at K, fish started from D.			Plain glass.		
Nos. of trials.	Duration.		*Nos. of trials.*	Duration.	
	Test.	Normal.		Test.	Normal.
31, 32	0′ 26″	0′ 10″	*45, 46*	1′ 34″	0′ 15″
33, 34	0′ 25″	0′ 05″	*47, 48, 49*	0′ 09″, 0′ 18″	0′ 09″
35, 36	0′ 08″	0′ 08′	*50, 51*	1′ 31″	0′ 07″
37, 38	1′ 44″	1′ 15″	*54, 55*	0′ 20″	0′ 18″
39, 40	0′ 06″	0′ 07″	*56, 57*	0′ 34″	0′ 07″
41, 42	1′ 40″	0′ 16″	*60, 61*	0′ 09″	0′ 10″
43, 44	0′ 05″	0′ 10″	*64, 65*	0′ 24″	0′ 08″
52, 53	0′ 16″	0′ 25″	*67, 68*	0′ 21″	0′ 06″
			72, 73	0′ 18″	0′ 10″

The performances of the fish were, on the whole, essentially comparable with the normal tests performed immediately after, and indicate an almost complete "transfer of learning."

Tests in which plain glass was substituted for squared glass (Table VI). Ten of these tests were given between *45* and *72*. The durations of performances varied somewhat, but were on the average considerably higher than the normal control tests. Only two were performed as efficiently as the normal. It is evident that the fish found the conditions more difficult; yet the performances are clearly much better than if the fish had had no previous training. The level of the first five trials is somewhere about that of the 12th in the main series: there is, then, some sort of "transfer."

As regards the method of solving these tests, it is of interest to observe the difference made by the absence of the scratched lines. Whereas in the normal trials the fish now invariably turned left before reaching the glass, in the tests it always swam straight into the glass. It then spent a longer or shorter time working close up against the glass, sometimes delaying considerably before bearing leftward. Sooner or later, however, the fish would suddenly turn left and continue, wheeling round the edge. The variations in the times of the tests depended mainly on how long it took the fish to make a full left-turn.

It is of further interest to note that the method of solution of the tests with plain glass was (*a*) identical with the method learned during training to the squared glass, although (*b*) the method was never regularly adopted by the various fish trained to plain glass, evidently presenting considerable difficulties in the normal course.

Fish D8.

Sept. 25, transferred to experimental dish.
Oct. 23–Dec. 13, 77 experimental feedings.
Trained to glass with meshwork of fine lines, as was D7. Detour, 6·5 cm.

The curve depicting the duration of trials is shown in Fig. 12. The average durations of successive groups of five trials during uninterrupted training is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	6′ 22″	*16–20*	0′ 48″
6–10	5′ 12″	*21–25*	0′ 33″
11–15	1′ 25″	*26–30*	0′ 20″

The manner of this fish differed considerably from that of D7. In early trials it was more active, and a good deal more erratic in its behaviour. More prone to make full turns away from the glass,

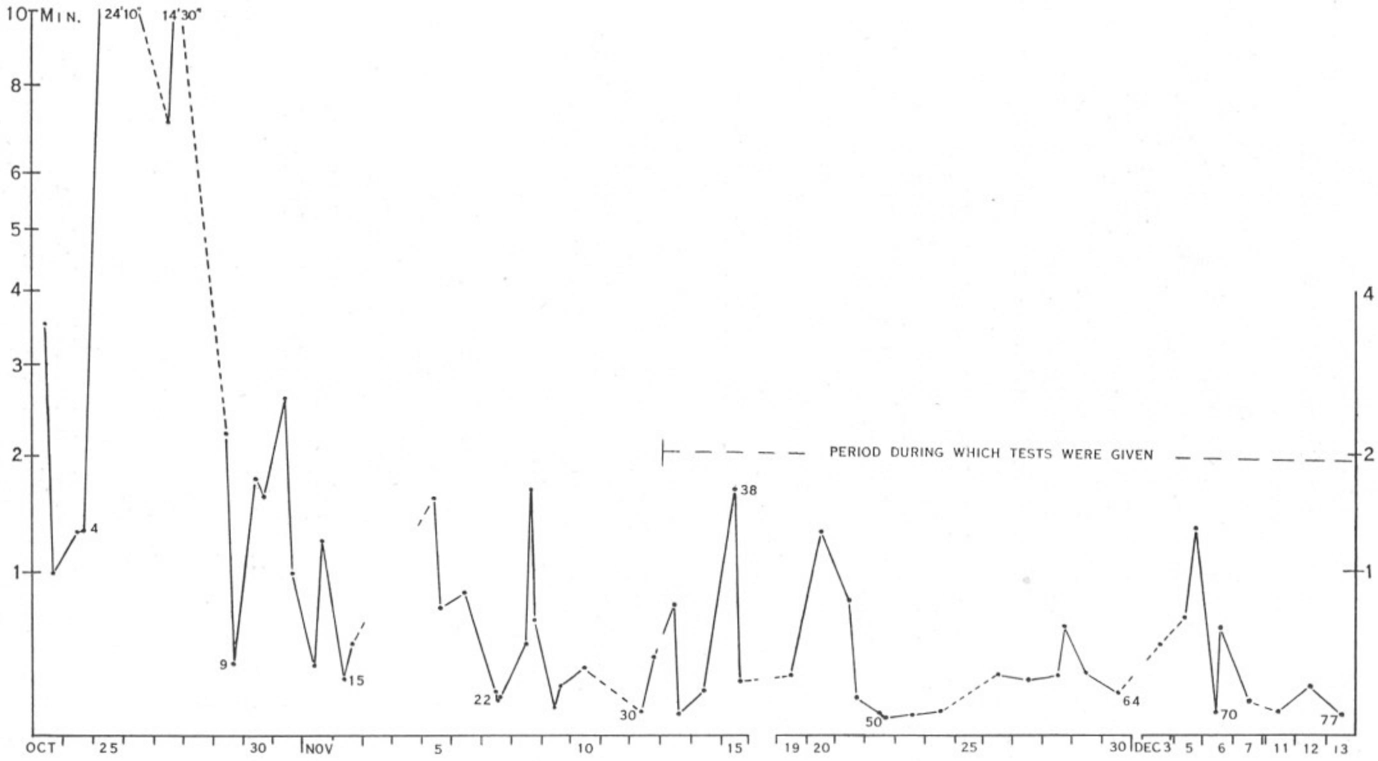


FIG. 13.—Graph of duration of trials of fish D8—as in Fig. 12.

it frequently swam off to other parts of the tank. All through it proved a more unreliable performer, and would doubtless have been long in acquiring a learned response to plain glass.

In spite, however, of this "temperamental" difference, this fish acquired a learned response of the same kind as D7, and the course of learning was in many ways similar, though less regular. The value of the results from this fish lie in the way they tend to duplicate the results from D7, and in the support they lend to inferences derived therefrom.

The solution of the first five trials was fortuitous : the fish happened to reach a part of the tank (region of corner D) from which there lay an uninterrupted path to the food. The trials which followed, however, came to be solved by a complete movement, starting with a left-turn and a right-wheel round the edge. It was this movement, which, as in D7, was established as a learned response : all solutions were effected by this means from trial *6* onwards.

As has been mentioned, the fish was much inclined to give sudden turning movements away from the glass. After giving one of these it often continued to swim right away from the glass. It became unusually inclined to wander over the tank, especially as the trial progressed. This tendency led to two excessively long trials—*5*, which holds the record of 24′ 51″, and *7*, which lasted 14′ 30″. Wandering movements, however, decreased greatly after *7*, and virtually dropped out after *12*.

Among the reactions given to the glass turning movements predominated. The fish was even less inclined to make lateral leftward movements along the glass than was D7. After *11* they virtually disappeared altogether. Withdrawing movements were rare.

A marked improvement came about at the stage of trials *11* to *13*. Before *11* no trend of improvement of performance can be observed. At this stage, however, several indications of a change occurred almost simultaneously. (1) *12* was the last trial in which the fish spent any time away from the glass ; (2) after *12* turns were all to the left ; (3) after *13* the time spent in attempts at reaching the food directly fell to a level minimum ; (4) frequency of left-turns showed two sudden increases, one between *11* and *12*, the other between *13* and *14* ; (5) behaviour became standardized from *12* onwards—leftward movements were now definite left-turns.

The subsequent progress was more gradual than in D7, and the fish continued to give occasional lapses. When, at *31*, tests were started, the fish had not acquired the same uniform level of efficiency as had D7 by this time. The acquisition of the same learned response was, however, well on its way, and the fish was beginning to turn left immediately, before touching the glass.

Tests in which food was presented on the right. Between *32* and *56* a similar set of tests were performed as on D7. Probably because the learned response had not been adequately established, this fish did not show such complete "transfer of learning" as D7. Also, the times of the "normal" tests were rather too erratic to justify close comparisons of the tests and their controls. Nevertheless, one feature may be pointed out. The first test showed the fish wellnigh incapable of adapting itself to the changed conditions. It worked persistently at the glass attempting to reach the food directly. It frequently turned to the left, but showed no tendency to turn right. Eventually, after 6 minutes, it reached the food by sheer accident. The next four tests, however, were performed differently, and the performances much resembled those of the corresponding normal trials, showing good "transfer." Though still showing some inclination to turn left, and still spending a longer time before bearing to the right, the fish solved the tests adequately by turning right and left-wheeling round the edge. In *6* and *10* the test was inefficiently performed, but *7*, *8*, *9*, and *11* were done in short times, only slightly worse than the control.

The contrast between test *1* and the four which followed is reminiscent of a similar contrast shown by fish D5, on which comment has already been made (p. 529).

As far as the extent of "transfer" is concerned, if allowances are made for its less reliable behaviour, D8 tends to bear out the features shown by D7.

Tests in which plain glass was substituted for the squared. The fish reacted in a similar manner as D7, but found the test considerably more difficult. Nevertheless, as in D7, it made the detour more readily than if no previous training had occurred; and, again as in D7, the mean of the first five tests fell at the same level as represented by trial *12* in the main series. Other results agree closely with those given above for the other fish. The fish never turned left before striking the glass; the solution was reached by the same method as that to which the fish had been trained; and the variations in the times were mainly dependent on how long it took the fish to turn left.

III. SUMMARY OF THE PERFORMANCES OF INDIVIDUAL FISH.

DETOUR OF 6·5 CM.

Plain glass obstruction.

Fish A. *Efficient learned response*, after 25 trials in which no evidence of improvement was seen. The main steps in progress came at trials *26*, *36*, and *54*.

Response re-learned after a short interval during which the fish was subjected to disturbance. Main improvement at trial *10*.

Fish D5. *Efficient learned response*, though early trials produced the most inefficient performances of any fish. Important sudden change of behaviour, from which point onwards rapid improvement occurred.

Fish D6. *Unexpected efficient response by indirect route.* Glass obstruction with black band at its edges, which was found to make no difference.

Fish D4. *Efficient learned response* eventually established, after the first period of improvement had been nullified by a bad lapse. Early on a consistent method of solution was adopted, but it was not established. In the later response the actual movements of the fish still varied.

Fish D3. Efficient response not established, though this appeared eventually to be coming on when the trials were abandoned at the 83rd. Response nearly established much earlier on, but a very striking lapse set in.

Fish D2. No response established in 45 trials, though one period of steady improvement was passed through.

Fish D1. No response established in 45 trials, though at one time it looked as if one was developing. This fish was a steady worker, and its behaviour remarkably uniform. A change to the squared glass obstruction after trial *45* produced a striking effect, showing that something had been acquired.

Glass with Meshwork of Scratched Lines.

Fish D7. *Efficient response established.* Note that the method was different from any established, or even partly established when the obstruction was plain glass.

Fish D8. *Efficient response established*, as in D7, but not so readily. This fish a more erratic performer.

Fish D1. *Efficient response given* after change over from plain to squared glass. (Evidence of similar phenomenon in case of D3.)

DETOUR OF 4·2 CM.

Plain Glass.

Fish B. *Efficient response* soon established. When transferred to the 6·5 detour, gave an efficient response at first, but lapsed badly.

DETOUR OF 8·5 CM.

Glass Pot with Black Meshwork.

Fish D9. *Efficient response* soon established.

CONSIDERATION OF WHAT IS IMPLIED BY THE TERM "EFFICIENT RESPONSE."

The training, it is important to remember, involved not so much the acquisition of an altogether new response, but the *modification* of a strongly established natural response—the movement towards a closely situated food-object. The fish had to acquire the habit of moving round to one side to reach the food instead of swimming straight at it. It is necessary, before the method of acquisition of this habit can be discussed, to examine what is known of the basic response, whose presence is a fundamental condition to the subsequent modification of behaviour. Consideration shows that it is not such a simple act as may at first appear.

(i) It is clear that the simple feeding response—the movement up to food-object preparatory to snapping at and swallowing it—is guided by the visual sense. Ample evidence for this has been procured. The olfactory and gustatory senses are evidently brought into play at close quarters, but this fact is irrelevant to the present discussion. The fish can be dependent on its optical receptors alone in discriminating the food-object at a distance, and in controlling its movements towards it. The response which is to be modified is a visual response directed with relation to the " object " which we must suppose is represented in the fish's visual field.

(ii) The movement which the fish performs, though it may be a simple forward motion straight ahead, implies a motor co-ordination of swimming movements. As a simple fact of observation, if the food-object moves, the fish will adjust its movements to the correlated change in its visual field. The ability to do this has been ingrained or acquired during the fish's normal life, and exists before the experiments are started. A high degree of capacity to co-ordinate its movements is possessed by the fish at the outset of the investigation. We can therefore further add that the movements which make up the whole response are directed towards keeping the fish orientated in the direction of the food-object, as forward motion is maintained.

(iii) If an attempt is made to summarize the component events in the series which comprises the response, at least the following must be found significant. (*a*) Food object is somehow differentiated in the total pattern of stimulation of the optical receptors. (*b*) Direction of movement is altered to bring this visual object into a certain relative position ; and (*c*) movement is continued and direction is adjusted, so that the visual object maintains its relation, but becomes increasingly larger. (*d*) Contact is established, swallowing actions bring the food into the fish's mouth, etc.

Further attempting to express these events in terms of neural activity, we may re-write them as follows. (*a*) Stimulation of retinal cells, giving rise to an excitatory pattern in the sensory centres of the brain. (*b*) and (*c*) Discharge of motor activity in response to the new excitatory pattern and in adjustment to it. (*d*) Culmination of swimming movements, accompanied by a new gustatory situation with resulting motor discharges bringing about snapping and swallowing.

The neural co-ordination is adequate to the task of producing a unified action (as it appears to observation), involving the integrated activity of the whole fish. If this neural integration is a reality, then it is evident that something has been left out : only the *main* neural events have been mentioned. Coincident with these are doubtless other, subsidiary, though maybe none the less important, neural reactions. Since the activity of the whole fish is involved, something is going on, whether of a stimulatory or inhibitory nature, in the neural pathways not concerned in the main reaction. It is to be inferred that these are of a kind which secure an integrated pattern of neural activity through the whole fish's body, and that habit will have established the most adequate possible. Among the subsidiary reactions those of the visceral system are no doubt important, assisting to maintain the " food perception " situation, and making ready for the discharge of digestive and gustatory reactions. On the whole, in a healthy fish, they will have come to be such as to maintain an appropriate harmony throughout the body, as well as to maintain an appropriate tension which will ensure that the animal reaches its objective in a normal effective manner. If the fish is temporarily frustrated in its movements this neural tension will be maintained. It is perhaps not going too far to postulate that nervous discharges are such that a state of physiological equilibrium is achieved at the culmination of the act, and that, if the movements are frustrated, new nervous discharges will originate maintaining the state of neural tension for a longer or shorter time, until the culmination is reached.

In short, since the activity of the whole fish is involved, the neural processes concerned are seen to be of a complex nature. Mere interference with the performance of the normal reaction will show indications of this complexity. The apparent simplicity of the act is typical of organic systems in general : they degenerate into a welter of complexity when their functioning is obstructed.

Attention has been drawn to the possibilities of subsidiary neural activity. This may play an important role in establishing physiological " states " with which are associated psychological states such as " satisfaction." It is quite possible that the association of motor responses with states of this type may lead to their establishment at the expense of others without such association. In problem learning a basis may be found for interpreting Thorndike's Law of Effect (p. 547).

(iv) To direct observation, at least, the response has the appearance of a unified action. If analysis reveals a complex of nerve reactions, it is evident that some account must be taken of the manner in which the elements of the complex are co-ordinated. No doubt in the main this co-ordination is developed by the type of neural association that has been revealed by the work on conditioned reflexes and responses. Association may be responsible for establishing, or maintaining once established, processes such as the following. (*a*) The linking of certain sensory or excitatory patterns with certain motor reactions—thus a change in the position of the food-object in the visual field may come readily to bring about a corresponding change in the direction of the fish's movement. (*b*) The linking of successive motor reactions ; a certain reaction A may tend to make for an increased readiness of B, so that the performance of B becomes linked to that of A, irrespective of what changes may be going on in the centres of sensory excitation. (*c*) Certain motor reactions may well, as Washburn (1928) suggests, become associated with certain physiological states, akin to those which accompany emotional states in higher animals. (*d*) If the food-object is kept in the same relation to other objects in the sensory field, the response may acquire an association to these.

Co-ordinated elements in the neural activity of the fish are clearly of first importance in maintaining the unity of the response against influences which tend to disturb it, or in the development of a more " complex " response if the conditions are modified. Various of these processes may play an effective part in the establishment of an efficient response when the fish, as in these experiments, has to make a detour to reach the food.

The main point to be stressed is that when an obstruction is placed in the fish's path, and when the fish has re-established what we describe as an " effective " response adapted to the new conditions, the change that has taken place essentially involves a re-adjustment of the disturbed balance. If new co-ordinations come to be established, it is on the basis of those which existed at the outset.

Consideration of the nature of the " natural response " has thus inevitably introduced the conception of an " acquired " response adapted to altered external conditions. The features that should characterize an efficient acquired response are already apparent. The two primary observable criteria are as follows. (i) It is performed with a minimum of hesitation and maximum of integration—approximating to as uniform an act as the particular individual fish is capable of giving. (ii) The efficiency of performance is stabilized, and a uniform series of rapid times is shown in the learning curve. Applying the first criterion to the special conditions of the experiments described above, we have regarded the following characteristics indicative of an efficient acquired response : (i) immediate turning leftwards away from the obstruction ; (ii) persistent leftward movement for a certain distance, far enough to take the fish past the obstruction and leave it an open path to the food ; and (iii) the whole response performed as one continuous act.

DISCUSSION OF LEARNING SHOWN.

CONSIDERATION OF THE LEARNING IN THE LIGHT OF CURRENT THEORIES.

In this section we have to enquire how far the above results are explicable in terms of certain hypotheses which have been brought forward to interpret learning phenomena of the type with which we are concerned. Generally speaking, these hypotheses, even though they may have been dignified by the name of Laws, are at best generalizations which apply under certain conditions within certain limits. Consequently it should be understood that if the application of any to our present results is criticized, it is not to be implied that the hypothesis itself is attacked. The conditions may not have been suitable for the phenomena which it generalizes to have become manifested. What is intended, however, is that the relevance of these hypotheses should be tested in relation to the actual cases of learning which were observed.

THE "LAW OF EFFECT."

It is perhaps most appropriate to treat first an explanation—or rather an approximation to one—which originated from the pioneer investigator in this field, and with certain obvious modifications might well apply generally in spite of the various criticisms that have been levelled against it. The essence of Thorndike's " Law of Effect " is that when, at first, an animal is unable to give an effective response to a situation which evokes action, and gives varied movements of a " trial and error " nature, after a time movements will become established which lead to a *state of satisfaction*, at the expense of others which do not. Successful movements are thus " stamped in " for the very reason that they have been successful, while " useless " movements become " stamped out " because they fail in this respect. Thorndike's own method of formulating this hypothesis is open to the obvious criticism that he is confusing physiological and psychological terms, but it seems that this difficulty can be removed by replacing the term " satisfaction " by one indicating some correlated state of neural (? and humoral) excitation. It seems quite feasible to maintain the Law of Effect on a purely physiological level.

It is supposed, then, that successful movements, by some process of association, are stamped in through their connexion with states of neural excitation accompanying the "attainment of the objective"—achieving a means of escape, reaching a food-object, or whatever it may be. It is, of course, only a first step towards anything that may be considered an *adequate* interpretation ; but it is worth while to examine our results and see if they show any indication of complying with this hypothesis. If they do not, there are no grounds for pursuing this line of interpretation any further.

Each fish's performance has been critically studied, and an attempt made to trace any possible influence of successful movements in early trials on the performance of trials which follow, and on the development of any effective response that may be formed. It would be laborious, and unnecessary, however, to recount the details of this examination ; for much of the data has to be set aside as of "neutral" character. We shall confine consideration to the main features which have emerged.

(1) Data have been abstracted showing the relation between methods of solution achieved in early trials and the increase in efficiency of subsequent performances. It is seen (*a*) that successful solutions in early stages do not necessarily result in the establishing of the reactions which have led to that solution : that, moreover, methods of solution may suddenly become established which have been rarely or never given before, or, if attempted, have been relatively unsuccessful. (*b*) Also the occurrence of successful solutions does not necessarily lead to an increase in the efficiency of subsequent trials, and increase in efficiency can occur when previous performances have been too varied to give any grounds for expecting immediate improvement.

The frequent early success of the "left-turn" reaction, and its failure to provide the basis of an established response, provide the best instances.

In fishes D1, 2, and 3, the left-turn movement was given from the start, and led to a solution more readily than any other response to the obstruction. Yet it did not lead to a learned response. In the first two fish it dropped out in a surprising way. In fish D4 the movement, on the whole, proved very effective ; yet for a long time was only occasionally given, and did not appear at all frequently until an efficient response had been learnt by another method.

These four fish are considered together, as they did not develop a learned response within the first 45 trials. It is important to notice, however, that D3 quite early on came to give many highly efficient performances, though the efficiency was not established ; yet the successful trials showed no influence of the early successful left-turn movements. D4 eventually learned satisfactorily, and will be considered again below.

Among those fish which succeeded in acquiring an adequate response comparatively quickly, at any rate D7 and 8 (with the squared glass obstruction) established a response on a movement that had been successful from the start—the " left-turn " movement, in fact. In other fish the situation is more complicated, owing to the fact that more than one type of solution proved effective in the period before efficiency had been achieved. But these provide interesting test cases. Each of them will be considered separately.

Fish A, after it had begun to show improvement, was for a time, so to speak, torn between two conflicting methods of solution—the left-turn-and-right-wheel as opposed to the sideways movement down the glass. The latter, before long, predominated. While there is nothing of special significance in this case taken by itself, it shows agreement with all other instances in the fact that, when the obstruction is of plain glass, the left-turn-right-wheel movement fails to become established in spite of its effectiveness.

It also leads us to the case of fish D6, in which, during the earlier trials, two, and only two, methods of solution were achieved. One of these, again, was the left-turn movement ; the other was a withdrawing followed by a right-turn taking the fish into the right-hand regions of the tank, from which it eventually approached the food on the far side. The former movement was not often given, but, when given, led at once to a solution in six cases out of eight. The latter led to a solution after a much longer interval, and by a more circuitous route : *yet it became an established response*, the other completely dropping out after trial *12*. In this case, then, where the fish solved the trial by two alternative methods, the most laborious and, at first, inefficient was established at the expense of one that was far simpler and quicker.

The performances of D4 and 5 are considered below illustrating other phenomena of importance. In them it is seen most clearly that efficiency of performance can be established in absence of uniformity of the actual movements given. In other words, learning can still come about even *before a definite predominance has been established between alternative methods of solution.*

It seems definite enough, from the above evidence, that, in so far as the " success " of certain movements leads to their affecting the performance of subsequent trials, certain types of movement (e.g. particularly the left-turn movement) are far less effective in this respect than others.

(2) The case of fish D5, supported in some ways by D4, is of sufficient importance to warrant a more detailed résumé. This fish, it will be recalled, produced the best learned response to plain glass, although its early performances were the worst given by any of the fish (pp. 526–528).

It was prone to wander about the tank, and for the first 12 trials, during which it showed but slight inclination, if any, of tendency to improve, the solution was usually arrived at by the fish eventually *happening* to get into the part of the tank in which a free path to the food was possible. In trials *1*, *3*, *7*, and *8* it swam to the food from corner D; in *2* and *4*, it swam up from the back (region A); in *11* and *12* it swam round the edge after withdrawing to the front of the tank. Only in *5* and *9* was a solution given involving a continuous movement from the original position—a left-turn-and-right-wheel movement, as it happened. At *13*, however, it eventually solved the trial for the first time by working leftwards down the glass, making frequent contact with it until the edge was reached. The striking feature is that from now onwards all trials were solved by a method resembling this one. The chance methods, and the one given in trials *5* and *9*, dropped out completely.

The main characters of the new adopted method of solution were (i) that the fish bore leftwards and made contacts with glass as it did so, and (ii) that it never withdrew from the glass for more than a short distance in the movements that led to the solution—in fact, it gave up altogether making random movements to the other parts of the tank; and (iii) complete right or left turns no longer feature in the fish's response to the glass obstruction. Though, within these limits, the fish's movements still varied considerably, there is decidedly enough in common between these solutions to contrast them with all those given previously. It may be noted that a conspicuous change in the fish's behaviour coincided with the onset of a rapid increase in the efficiency of the response. Are these two effects to be related?

It may well seem that an interpretation on the lines of the "Law of Effect" can be applied. As a result of "trial and error" behaviour, the fish, at the end of trial *13*, happened to hit on a "satisfactory" method of solution. This method of attacking the problem became in some way "stamped in," so as to affect the behaviour of all subsequent trials. It so happens that it perhaps did so more effectively than might have been expected; but this fact would enhance rather than vitiate the argument.

It may at once be asked why the solution of *13* should have had such significant effects as contrasted with the solutions of previous trials. For the moment, however, let it be assumed that this has happened, so as to give the theory an adequate chance. We must consider in somewhat greater detail what the effects actually were.

From trials *14* to *23* learning progressed rapidly. The habit of making random movements away from the obstruction suddenly disappeared after *13*. The only vestige remaining was seen in a tendency to make occasional short withdrawing movements from the glass obstruction, but this tendency had almost completely vanished by *21*. The fish persistently worked at the glass, and showed increasing inclination to bear leftwards, until eventually getting far enough to the left to pass the edge and reach the food. Both the frequency and efficiency of leftward movements increased.

But, though the general method of tackling and solving the problem was now constant, *the actual movements involved in the solution still varied considerably*. Thus in *13*, *14*, *15*, *17*, *19*, and *20* the fish kept more or less orientated to the food, withdrawing a little before passing the edge: in *18*, *23*, and *25* it had made a half-left turn and was orientated towards the edge of the glass; in *21* it passed the edge without withdrawing at all. Good performances (marked by shortest times and least hesitation) did not depend on the method of solution. It was not until after *25* that the method had become approximately constant. It is apparent, therefore, that the fish acquired the habit of giving an efficient performance *before* the actual movements whereby it was effected had become stabilized. Such stabilization as was attained came later.

Evidently, then, whatever had become " stamped in " at trial *13* was not the actual movements involved. It appears, therefore, that in so far as the Law of Effect may be said to hold good in this case, it did not act by the establishing of certain specific motor responses. If the solution of *13* produced any permanent effects, these must have been of some other type. To this question there will be occasion to return later.

Interesting supporting evidence is derived from fish D4. This performer, after a considerable period of erratic behaviour (during which, however, some excellent trials were performed), eventually acquired a satisfactory stable level of efficiency. The most conspicuous feature in the development of this response is that, as in fish D5, but in an even more marked way, the actual method of solution continued to vary long after efficiency had been attained.

Consistently good performances were given between *49* and *69*, in which successive 5 trials averaged 22″, 17″, 15″, 15″ respectively. Three distinct methods of solution, however, persisted. The efficiency of the general response, therefore, did not depend on the stabilization of the motor reactions involved.

There is little indication in this fish that the " Law of Effect " was operating to any extent; but if some process of this type was responsible for establishing the response, the same conclusion must be drawn as above—it did not act by establishing specific motor responses.

These examples have been considered in some detail as they illustrate most clearly features of which indications were secured in several other fish.

It is to be concluded, then, that if movements which lead to solving the trial cause any neural changes of a " stamping in " nature, these are not connected with the motor paths. The possibility must not be overlooked, however, that such changes may affect that part of the neural mechanism which is involved in the co-ordination of sensory stimuli. This point will be taken up afresh after other evidence has been considered.

The Connexionist and Associationist Hypotheses.

Attempts at interpreting learning phenomena in terms of the physiological properties of nerves and nerve reflexes lead first to a somewhat elementary type of interpretation which may be distinguished as the " connexionist " hypothesis. It is based on the premise that a neural connexion once made is more readily available on another occasion. To what extent this generalization is justified is not by any means clear, in spite of the fact that it has been widely held. Perhaps the recent demonstration of " facilitation " phenomena in neural reactions of certain invertebrates by Pantin (1935, 1936) provides the best experimental data so far available. It is sufficient, however, for the present purpose to accept the fact that this effect may truly occur in the central nervous system of vertebrates, and that the hypothesis could be justified on purely physiological grounds. Now, if this is so, it is evident that a type of learning will result, due essentially to a facilitation of certain nerve connexions, accompanied perhaps by inhibition of others. This will have come about merely through repetition of the behaviour-act.

The question, however, whether detour learning is adequately interpreted on these lines is another matter. In the first place no facilitation effect is to be expected unless the reactions given in successive performances reach a certain level of uniformity ; and it has been seen above that improvement in the fishes' performances did not wait upon standardization of response. More serious still is the obvious difficulty that wherever one out of several alternative responses has to be established, something more is required—something that takes into account the fact that a certain response (or group of responses) is more appropriate than others in the " success " of its outcome. It is at any rate clear that unless the fish performs the same sequence of movements in the solution of each trial, the process of facilitation does not, so to speak, have a chance.

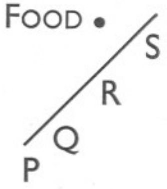
As an illlustration the case of D6 may be cited. The movements of this fish were unusually stereotyped. After the twelfth trial the same sequence of movements was given in each trial : the fish passed round to the right and reached the food from the far side of the tank. With successive trials the speed and efficiency with which the course was covered gradually increased. Thus the total time taken over the trial fell from an average of five minutes to a final level of about 45″. Now this increase of efficiency after trial *13*, once the habit of taking the path had become established, could well have been due to the facilitation of motor connexions, tending to integrate the sequence of movements. But—and this is the crucial point—facilitation could scarcely have had anything to do with the original " choice " of the particular route taken, as opposed to other possible responses—in other words, with the first acquirement of the habit.

Of the fish given the plain glass obstruction, fishes D1 and 3 afforded the most ample opportunity for the working of this process, as they tended to react in a uniform manner. Nevertheless, no efficient response was established in either. On the other hand, the performances of fishes D4 and D5 varied a good deal, and would scarcely have permitted neural facilitation to play more than a very subsidiary role. Yet both developed an efficient response.

It is quite unnecessary to dwell at any further length on the inadequacies of a simple connexionist interpretation. The facilitation of neural pathways cannot itself account for much, unless considered in conjunction with a related process—the *association* of contiguous pathways.

The association of motor pathways can be conceived as occurring in a manner characteristic of conditioned reflexes. If a conditioning process is at work, and if no assumptions are to be made that go beyond legitimate inferences from experimental results in this field, it is not a difficult matter to deduce the course that learning process, in these cases, should take. There is only one way in which a straightforward conditioning process could have produced the effective detour response : namely, through a linking of certain of the independent motor reactions, at first given at random in response to contact with the obstruction, by backward association with the primary reaction of swimming up to the food.

The established unconditioned response *A* (given to situation *A*) with which others may become associated is the final swimming-towards-and-snapping-at-the-food from a position P, clear of the obstruction. The first step will be that the fish in position P (situation *A*) becomes habituated to swim straight to the food from this point. " Being in position P " thus becomes, by a short step of backward association, conditioned to the final movement to the food. Carrying the process back a step farther, " being at Q " (situation *B*) becomes associated with movement to P (response *B*); similarly from a position R the fish will come to move to Q. Finally, the process of association will be carried back to the starting-point, S, where the fish first encounters the obstruction ; and of various responses the fish may at first give in this position that one will eventually become



established which leads it to position R, then on to Q, then on to P, and so round to the food.

The course of learning, then, would take the form of a process of backward association. The observable effects should be clear enough : for the end part of the detour would be learned first, and the beginning of the final integrated response established last. The experimental results can yield crucial evidence on this point. If they show no indication of the above deduced effects, then learning by motor association must be ruled out of question.

It is not suggested that this interpretation is either one to be expected or one which suggests itself as plausible. A little consideration will show a certain artificiality, as well as raise doubts on whether its application, if permitted by the facts, would not raise more difficulties than it removed. Nevertheless, were there indications that the learning progressed in this way, an opening would still be left for the possibility of a fairly straightforward explanation in terms of conditioned response, and it is obviously necessary, for the discussion which follows, to consider every aspect.

For the purpose of investigating this point the fish's response was conveniently divided into three phases ;—(i) movements against the glass immediately opposite the food, in attempts at reaching the food direct ; (ii) leftward movement taking the fish down the face of the glass plate (or parallel with the face) to its far edge ; (iii) rounding the edge of the glass plate. When the most efficient integrated response had been acquired the first phase was reduced to two or three seconds, and there was no return to this position once leftward movement had started ; the second phase involved a continuous movement down the glass as far as the edge without hesitation ; the third phase involved movement round the edge as soon as the fish had reached this position. The acquirement of efficiency in each of these phases of the response was open to examination.

The interpretation being tested necessitates, strictly speaking, that acquirement of efficiency in the third phase should precede *any* general increase in the second, and that the second and third phases be performed as one unified act before there emerge any signs of increase in the first.

The results obtained were altogether different. Acquirement of efficiency, both in the response as a whole (as the learning curves indicate) and in the separate phases, proceeded irregularly. But there was no question of progress in one of the two earlier phases being arrested while efficiency developed in a later. On the whole, increase of efficiency in all three phases progressed together, often sudden improvements in one coinciding with improvement in another.

But it is still possible that secondary influences may have caused a certain increase in efficiency of the earlier phases while the latter were as yet imperfectly integrated. It is therefore still necessary to examine whether later phases show any sign of merely being *in advance* of the earlier. In the Appendix (p. 568) is summarized such data as bear on this point. It is seen that not even here is there the least indication of the effects which the hypothesis of backward association requires. For instance, efficiency in the case of fish D5 was established in the first, second, and third phases consecutively—in a forwards, not backwards, direction. The special case of fish D6 is particularly illuminating: the fish found the greatest difficulty over the last section of its circuitous detour, and never, to the end, really acquired efficiency in passing it.

It is therefore quite evident that the learned responses were not being built up in a backward direction from the completion of the trial. This rules out the possible interpretation that learning was effected by a process of backward conditioning.

We reach, then, the conception that processes involving the facilitation and association of *motor* paths could not have produced the effects observed in our cases of detour learning. Any attempted interpretation on these lines proves inadequate. It will be noted that the evidence here brought forward is quite different from that which had already led us to reject the possibility that successful solutions served to " stamp in " the specific movements involved.

Thus one conclusion which has emerged, reached by two independent lines of argument, is that the development of an efficient response to the obstruction was *not* primarily a matter of the linking up of certain movements, i.e. of establishing a motor habit.

IMPROVEMENT IN PERFORMANCE DUE TO CHANGES IN " SENSORY ORGANIZATION."

Learning which involves the affector processes.

The methods of interpretation hitherto considered have one important feature in common: they take no account of possible changes in the *affector* processes concerned in the fish's response. We have merely considered the possibility of associations having become established on the *effector* (motor) side—as a result either of repetition, or of association with some general neurological state produced by relief of tension, or of backward association from the final successful movement. As these possibilities have been ruled out, attention must now be turned to the main alternative interpretation.

Some of the more familiar learning phenomena in animals belong to a class in which the animal, to speak in ordinary language, comes to " detect " certain relations in its surroundings to which it was previously indifferent. In strictly physiological terms, it is in the affector processes of the response that the essential change occurs. If there is a change in the responses given, it is because a new state of central excitation has arisen, and the new state of excitation produces a new response.

Elementary examples are provided by certain simple conditioned reflex and response experiments. In some, a newly applied " stimulus " (or " stimulus complex ") acquires the excitatory properties of another stimulus through association with it. The former, " stimulus " A, may formerly have had no conspicuous motor effect, or it may have produced a definite response which is inhibited and replaced by that primarily produced by the latter (unconditioned) " stimulus " B. One aspect of this phenomenon is that a change occurs in the excitatory effects of " stimulus " A.

In other cases, rather less elementary, the animal, giving primary response X to " stimulus " A, is conditioned to give that response to B, but to react negatively to C even when A and C are combined. These are the familiar " choice "experiments, from which the " multiple choice " experiments are a special development. Usually a particular visual object of a certain colour, size, or shape, is associated with the primary " stimulus," i.e. food-object, while another object of contrasting colour, size, or shape, is set against it, often (though not necessarily) associated with a primary " stimulus " causing a negative response. But " stimuli " of a visual nature are not the only ones on which such responses can be built ; similar results are obtained involving auditory, tactile, gustatory, and other sense receptors. By such experiments the capacity of the animal is tested for " discriminating " colours, shapes, tones, and various other " sensory " properties. The aspect of this choice-experiment conditioning which we have here to note, is the fact that the animal comes to " detect " a certain contrast, or, more generally, a certain relationship, in its sensible environment, by which, as far as the particular reaction under consideration is concerned, it was primarily unaffected. From the fact that no *new* motor reactions are involved, it is evident that the development of these various conditioned responses is primarily a sensory, or, more strictly, an *affector* phenomenon.

The work of Bull (1928–1934), Herter (1929, 1930), and others, has fully established the ability of teleost fish to develop conditioned responses of various types. With this knowledge, one may enquire whether detour learning, and, more particularly, the manner in which it has been found to occur, is predictable ; and if not, what additional factors or conceptions have to be introduced in order to account for it.

If attempts are made to find the points of comparison between detour learning and typical conditioned response effects, or to express the former in terms of conditioned reflexes, it is soon found that the problem is by no means straightforward. If it had emerged that the detour learning occurred by a process of backward association, the phenomena might have been considered directly comparable, the detour learning appearing as a chain-reflex (or, more strictly, chain-response) effect. But this has been shown not to be the case (p. 554). If, on the other hand, the detour learning compares with the conditioned response in depending on a specific change in the affector processes, then it differs in certain important respects, which at once place it on a higher level of organization, or at least of complexity. The main difference is that a new and more complex motor response develops, and not merely a change over to an alternative response previously given by the animal in other circumstances. If this is to be explained on the grounds that the animal comes to detect some "new" relationship in its surroundings (e.g. spatial and functional relations between itself, the obstruction, and the food-object) in the same sense as this may be said to occur in choice-conditioning, the situation is not in any way simplified. In choice-conditioning the "new" relationship, which the animal, so to speak, is conditioned to detect, is always a straightforward contrast providing stimuli which the sense receptors of the animal are directly capable of analysing.* But the relations which the animal would have to "learn" to detect in acquiring an efficient detour response must evidently be of a more subtle kind, and it would appear that considerable ability for producing a differentiated field of sensory excitation would have to be conceded to the animal. There would appear to be a more highly developed capacity for co-ordinating sensory impulses than might be expected, or than our present knowledge would entitle us to assume.

While, then, conditioned response experiments do not, at first inspection, provide a ready interpretation of detour learning, they do nevertheless demonstrate certain phenomena which are significant for our purpose. The first of these is that associations between nervous paths, at first functionally disconnected, may develop in an orderly and predictable manner; the second is that such associations may develop centrally in that region of the central nervous system which functions in co-ordinating the impulses transmitted by the peripheral receptors. They provide a certain neurological basis for pursuing an attempted interpretation of detour learning as an affector phenomenon.

The affector processes which initiate any given response include both events which occur peripherally in the sense receptors, and those which occur centrally in the sensory centres of the central nervous system. There is first a process involving an analysis of external energy-exchanges into aggregates of unit stimuli, and secondly a re-synthesis of the aggregates of impulses reaching the sensory centres. The mechanisms underlying these complementary functions constitute the affector system. That a distinction should be recognized between sensory analysis and sensory

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* See below, p. 558.

synthesis seems inevitable not merely on morphological grounds, but also as an outcome of the conditioned-response work. The conception, in fact, is derived from Pavlov :

> " . . . the nervous system possesses on the one hand a definite analysing mechanism, by means of which it selects out of the whole complexity of the environment those units which are of significance, and, on the other hand, a synthesising mechanism by means of which individual units can be integrated into an excitatory complex. Thus in studying the nervous activity of the cerebral cortex it is necessary to deal with two . . . distinct phenomena, one involving a neuro-analysis and the other a neuro-synthesis."*

This generalization was intended to apply to Mammalia—vertebrates possessing a cerebral cortex. Nevertheless other vertebrates, as well as some invertebrates, possess centres in the central nervous system associated with afferent nerves and it appears from simple observation that the function of sensory organization—hence neuro-synthesis—is possessed by these animals, however limited that function may be. At the very least it is possessed by teleost fish, which prove capable of producing many of the conditioned reflex phenomena demonstrated in mammals.

Accordingly—to return to the learning problem—if a change occurs in the affector processes, this may involve either the process of neuro-analysis or that of neuro-synthesis. Changes of the first category could involve little more than an alteration of the threshold of excitation of the sensory receptors, though such changes might conceivably have far-reaching effects on behaviour. The second type includes other cases in which a change in the central excitatory complex results. Such could arise through the development of a new neural association. One of its essential features is that it occurs through causes independent of the process of neuro-analysis : it may occur although the external conditions, the stimulation of the sense organs, and the impulses transmitted by them, remain identical.

Since mere changes in the threshold of excitation of the sense receptors could not possibly account even for the most elementary conditioned reflex, to say nothing of detour learning, we may proceed straight away to consider the latter as due to a change in the process of neuro-synthesis. That we are justified in assuming that changes can occur at this stage may be seen by referring back once more to the more elementary conditioned response effects mentioned above. It has been pointed out that these are to be regarded as affector phenomena, occurring centrally, which is the same thing as saying that they involve the process of neuro-synthesis.

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* *Conditioned Reflexes*, trans. by G. V. Anrep, 1927, p. 110.

As the change in question is a matter of association of formerly independent nerve-paths, it may be accepted that the process of neuro-synthesis may be modified, under certain conditions, through certain changes which are of the nature of neural associations.

This conclusion has obvious significance in relation to our problem. It may be asked why it was not introduced at the start of the discussion, or at least in the section above (p. 552) dealing with the associationist hypothesis. The fact remains, however, that the type of modification that appears necessarily involved in detour learning is somewhat different, in some respects more complex, than any indicated by conditioned response experiments. It was not justifiable to attempt this line of interpretation before others, which had the appearance of being more straightforward, had been tested.

The first stage of the analysis of our problem brought us to the significant conclusion that the learning shown was not primarily a matter of the development of a motor habit. Having seen that ample precedent exists for doing so, we have now to proceed to test the hypothesis that the learning has resulted from a modification in the process of neuro-synthesis, i.e. in the manner in which the sensory impulses are integrated.

It will first be necessary to consider a body of evidence of a positive character that at least encourages us in pursuing this line of interpretation.

Effects of visible changes in the surroundings.

The evidence now to be discussed illustrates perhaps the most important feature which has emerged during the course of the experiments, namely, that *changes in the details of the conditions presented to the fish were capable of exerting marked effects on the course of learning*. The changes in question concerned visual characteristics of a type the fish proved able to detect, i.e. affected its responses. Also, their *only* effect on the fish was through the visual sense : they did not in any way directly influence the response movements, or require *different* response movements, as would, for example, spatial re-arrangement of the apparatus, or changes like the setting up of currents in the water. If, then, an influence on the response, or cause of learning, could be detected, it could only have been a secondary influence of the changed pattern of sensory stimulation. The significance of this consideration will be seen later.

(i) As described above, some of the experiments were made with the glass obstruction marked with a meshwork of fine lines. The lines, scratched with a glass-cutter, half a centimetre apart, did not seriously interrupt the view through the glass. Fishes 7 and 8 were presented with this "squared" glass from the start. The former proved a good subject and was not long in acquiring an efficient response, which developed during the period between trials *10* and *20*. From *21* onwards a series of uniform efficient performances was given, averaging some 11″. This was rather quicker than fish D5, the outstanding performer among the seven fish presented with plain glass. Fish D8 showed more erratic behaviour all through, but eventually became as efficient as D7. Unlike the latter, it showed, to start with, strong tendency to wander over the dish, and for some time its performances fluctuated considerably. There is little doubt that this fish would have encountered great difficulty with a plain glass obstruction, and would probably have ranked with those fish that failed to establish an efficient response.

The evidence points strongly to the fact that the detour round the "squared" glass obstruction was more easily learned than in the case of the plain glass. This might well have been expected, since the fishes showed unmistakable signs of "seeing" the pattern on the glass, fine as the lines were. The evidence for this statement is of two kinds. (i) In early trials the fish often worked close against the surface of the glass: in moving leftwards, they usually moved jerkily from one line to another, in a manner never observed when the glass was plain. (ii) In the acquired response the fish turned leftwards before reaching the glass, at a point about 2 cm. distant, as though they had acquired the habit of bearing away from the obstruction as soon as the pattern came into focus: and this was in strong contrast both with the behaviour of other fish presented with plain glass, and with tests on the same fish when plain glass was substituted for squared. Evidently, then, the obstruction was marked with visible characteristics, and it is scarcely surprising that the fish was more effectively enabled to make the detour.

TABLE VII.

Performances of Fish D1 in Later Trials.

Trial No.	Obstruction.	Duration of trial.	Average of five successive trials.	
36	Plain glass	0′ 28″	*36–40*	2′ 26″
37	,, ,,	1′ 20″		
38	,, ,,	1′ 41″		
39	,, ,,	5′ 47″		
40	,, ,,	1′ 55″		
41	,, ,,	2′ 39″	*41–45*	2′ 21″
42	,, ,,	1′ 07″		
43	,, ,,	1′ 58″		
44	,, ,,	1′ 38″		
45	,, ,,	4′ 25″		
46	**Squared glass**	**0′ 18″**	*46–50*	**0′ 19″**
47	,, ,,	**0′ 15″**		
48	,, ,,	**0′ 28″**		
49	,, ,,	**0′ 22″**		
50	,, ,,	**0′ 14″**		
51	,, ,,	**0′ 11″**	*51, 53–56*	**0′ 19″**
52	Plain glass	3′ 0″+*		
53	**Squared glass**	**0′ 43″**		
54	,, ,,	**0′ 16″**		
55	,, ,,	**0′ 12″**		
56	,, ,,	**0′ 12″**		
57	,, ,,	**0′ 12″**	*57, 59, 60*	**0′ 14″**
58	Plain glass	3′ 0″+*		
59	**Squared glass**	**0′ 13″**		
60	,, ,,	**0′ 16″**		

* Abandoned before a solution was achieved.

But more significant still, perhaps, is the fact that the learned response given by these two fish was of a *distinctive type*, differing from any acquired by the fish which learned to surmount the plain glass obstruction. Both fishes, D7 and 8, made the detour by turning leftwards, before touching the glass, swimming left, and wheeling round the edge in one movement. This manoeuvre, as has already been pointed out, was given by all fish during early trials. In spite of its effectiveness, as again has previously been emphasized, it was never established, sometimes dropping out of the fish's repertory in a striking manner. Where, in short, the obstruction was plain glass, the left-turn movement proved impossible to establish. Yet it provided the effective response in both fish trained to " squared " glass. The conclusion seems unavoidable that the marking on the glass made for this significant contrast. This is made all the more certain by the fact that essentially the same movement is given to an obstruction which has striking visible characteristics, such as the pot presented to fish D9.

The experiments with fishes D7 and 8 thus indicate that the meshwork marked on the glass, endowing it with a visible property, (*a*) rendered the detour learning easier, and (*b*) influenced in a marked way the character of the learned response.

(ii) The experiment of substituting the plain glass for squared glass was made in the case of fish D1. This fish, in spite of the uniformity of its behaviour, had shown no signs of establishing a learned response. The result, as may be seen from Table VII, was remarkable.

On the very first occasion the squared glass was introduced a response of marked efficiency was given, and this efficiency was maintained. The average level of the duration of the trial fell to below 25% of its previous value. That no sudden permanent change had taken place, affecting behaviour in both conditions alike, is shown by the results of trials *52* and *58*, in which plain glass was used again. In both of these trials the fish proved incapable of making the detour before the trial was abandoned at the end of three minutes. Here, then, the pattern on the glass made all the difference between a laboriously attained solution, and one approaching maximum efficiency.

A similar test was made with fish D3, and the results, as far as they go, are comparable, if not so striking. At the time this fish was tested it was beginning to show gradual improvement, after a period of very inefficient performances. The figures are given in Table VIII.

TABLE VIII.

TESTS WITH SQUARED GLASS ON FISH D3.

Plain glass.		Tests with squared glass.	
Trial No.	Duration.	*Trial No.*	Duration.
69	4′ 01″	*70*	0′ 11″
71	1′ 59″		
72	0′ 55″	*73*	0′ 16″
74	1′ 29″	*75*	0′ 45″
76	1′ 35″		
77	1′ 19″	*78*	2′ 26″

The first three tests showed a marked reduction in duration as compared with the normal controls, particularly the first. What is also of interest is that the behaviour during the tests differed appreciably from that normally shown by the fish. Most notably, there was a complete absence of withdrawing movements, which characterized all other trials. The fourth test (*78*) showed a bad lapse, and might appear to vitiate the results. It must be noted, however, that in this trial the difference in behaviour was conspicuous all the time, and the solution was eventually reached in a manner similar to that in the other tests, and quite unlike that shown normally.

The effect, then, of replacing plain glass by the squared glass, is that the detour is more readily accomplished. This is brought out in a striking way in the above records from the performances of fish D1. At the same time, as indicated by fish D3, the mode of behaviour during the trial, and the method by which the solution is reached, may be affected.

(iii) During the course of the experiments incidents were noted from time to time which indicated that features in the visible surroundings of the fish influenced the behaviour. In one case quite a trivial feature was responsible for so affecting the fish's response that the efficiency of performance was altogether impaired. This incident, which occurred in the training of the first animal investigated (fish A), is worth recording in detail.

During the second series of trials with this fish, after an efficient method of solution had been re-established, unexpected failures occurred in three trials, in which the fish failed to get straight round the edge of the glass first time. It was then noticed that a strip of white paper inserted into the groove supporting the glass plate (see description of apparatus, p. 505) was protruding a little from the groove, and ended a little short of the edge of the glass. For the purpose of testing whether the presence and position of the strip of paper had any influence on the extent of leftward movement of the fish, the paper was re-adjusted and made to protrude *beyond* the edge of the glass. The fish was again tested and now gave a perfectly efficient performance. Tests were continued, amounting to seven altogether on this particular day. The results are given below in Table IX. Situation A denotes that the edge of the glass lay beyond the edge of the paper, and B that the edge of the paper protruded beyond the edge of the glass.

TABLE IX.

Performances of Fish A, 23.2.34.

Situation.	Performance.
A	2 unsuccessful moves before frame removed at 20″.
B	*round first time (at 11″).*
B	*round first time (at 8″).*
A	3 unsuccessful moves before frame removed at 20″.
B	*round first time (at 7″).*
A	5 unsuccessful moves before eventually reaching food at 45″.
B	*round first time (at 30″, but fish by now not hungry).*

It seems clear enough that the position of the edge of the paper was responsible for the fish's failures. This suggests at once that the fish was using the visible protruding strip as a guide to the position of the invisible edge of the glass. Be this as it may, a further test showed that the learned response itself was not at all dependent on the presence of a white paper strip. The next day the white paper was replaced by light brown paper fitted well into the groove so as to be invisible from below. There was therefore nothing which could be taken as a " sign " of the edge of the glass. With this arrangement the fish gave perfectly satisfactory trials. It was thus shown that the fish had not learned the position of the edge of the glass by association with the white paper.

It is therefore to be concluded that the presence of the slightly protruding strip of paper, ending before the edge of the glass, had *distracted* the fish in some way. No doubt, this was because the fish, relying by habit on its vision, had a tendency to pick up visual clues when there was the least chance of being enabled to do so, and in this case had begun to develop an association with a clue that turned out to be a *false* one. But, however this may be, the point to be brought out is that details in the visual field can exert significant effects on the response.

The above examples illustrate how changes induced in the conditions presented to the fish—changes of kind which do not modify the detour problem, or affect the fish's response movements in any direct way, but which are detected by the fish through its visual receptors, and thus presumably affect the visual pattern to which it reacts—can affect the response in a significant manner. We have considered cases in which there is a *contrast* between two different experiments, and cases in which *changes* are introduced at some point in one series of trials. The same kind of effects are noticed in both.

Where contrasts, or changes, are noted in the response, the cause can only reside in a contrast, or change, in the sensory situation (however we may visualize or define this event) to which the fish reacts. Situation A evokes response a, while situation B evokes response b. We are not now concerned with what causes the particular characteristics of a or b. The point that must be made is that the differences observed in the response of the fish are induced in this way—by a difference in the situation which evokes them.

It may finally be observed that differences in the external conditions have been seen to exert two types of effect. First, there is the more immediate effect on the behaviour shown in the particular trials concerned. Secondly, as in the example of fishes D7 and D8, they may exert a more " long-range " influence, by affecting the selection of that form of behaviour which is eventually established as a learned response.

Detour learning an affector phenomenon.

The observational data just considered have a significant bearing on our problem. In showing that externally induced changes in the affector processes of the fish's reaction have marked effects on the learning process, they virtually demonstrate that *any* change in the affector processes can exert such effects. For those occurring peripherally are farthest removed from those that constitute the final central state of excitation through which the motor centres are activated. If, then, neural changes occur more centrally—such as in the process of neuro-synthesis (see p. 558)—they must be at least as capable of affecting the fish's performance as those induced peripherally.

Though internal changes affecting neuro-synthesis are hidden from direct observation, we have seen that it is necessary to infer their existence in interpreting the results of conditioned response experiments (p. 558). But, furthermore, from evidence considered earlier, it is concluded that they are necessarily involved in the present case. The detour learning observed involves some internal neural change: this change does not involve the motor, or effector, processes of the response (p. 559): therefore an appropriate change in the affector processes remains the only alternative.

Taken together these two main conclusions leave room for only one plausible interpretation of the learning observed. The latter assuredly depends on a change involving the processes of neuro-synthesis. It is an *affector* phenomenon.

For some purposes it is preferable to express this reasoning in a rather different form, lest any shortcomings of the neurological concepts hitherto employed should be supposed to vitiate the deductions.

We may consider the situation (to which the animal's movements are adjusted and modified) as a whole, and call it the *perceptory situation.* This term is employed in its most general sense to express, objectively, the "sensed" situation to which the fish reacts, whatever it may be, whether an aggregate of stimuli, or whether something that has to be distinguished as a "gestalt" or organized pattern. The two main conclusions now may be expressed as follows. (i) The observed learning is not a motor habit; the only apparent alternative is that it involves a significant change in the perceptory situation to which the motor reactions are directed and adjusted. (ii) Changes in the perceptory situation, externally induced, can exert significant effects on the fish's response; therefore any changes in the perceptory situation, including those which may arise internally, have at least comparable effects. The final conception to which we are led is that learning takes place because a new perceptory situation arises which renders possible a more adequate response.

A picture of the process by which the wrasse learnt the detour path may now be sketched in its broad outlines. When first the food is presented behind the obstruction, the fish does not adequately prehend* the relations of the objects external to it, or adequately co-ordinate its sense impressions to enable it to give an effective response. It makes various ineffective movements which tend to become increasingly random, until by chance it gets into a position from which it can reach the food. With repetition of the situation, sooner or later a change occurs in the way in which the fish prehends its surroundings, and a new response is given (to what is essentially a new situation). The change, further, is such that the fish can give a more adequate response, enabling it to circumvent the obstruction, and so evidently involves a prehension of some

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* This term is introduced to express the relation between the animal and the elements of (or relationships in) its surroundings which it proves able to differentiate. It may be defined as equivalent to the term "detect" shorn of its subjective implications. An animal can be said to "prehend" an object or contrast with no commitment as to whether the event involves consciousness on the animal's part.

significant relation, not detected before, between the fish itself, the obstruction, and the food. In the end the main relations are sufficiently well prehended to enable it to make the detour with a maximum efficiency.

It is perhaps not so much the fact that the problem of detour learning appears to be essentially a problem of sense-perception which is important, as the evidence from which this judgment is derived. Investigators who adopt the theories of the Gestalt school have stressed the probable importance of changes taking place in the perceptual field (see, e.g. Wheeler, 1929). As mentioned at the outset (p. 501), E. S. Russell has drawn attention to this aspect of the problem, and has suggested that the interpretation of simple detour learning shown by sticklebacks is rightly to be conceived on these lines. But, perhaps without exception, interpretations of this type have had their origin not so much in logical deduction from experimental results as from the metaphysical viewpoint from which the results have been described. This is not to say that the interpretations are false, but they will be unsatisfactory scientifically until they can be shown to be *required* by the results of experiment. In so far as they have hitherto been thought inappropriate may lie merely in the inadequacy of the necessary experimental data. This remains to be seen. However, since the course of the present discussion is guided by the principle of procedure from fact to hypothesis (and back again), it seems that " organismal " theories of learning (if they may so be called) are most conveniently introduced at a later stage, when the consideration of the data presented above is complete—when, in particular, the nature of the perceptory change involved in the learning has been more closely examined.

It is concluded, then, that the improvement in performance which characterizes the learning we have been studying is the result of a more adequate perception of the conditions presented to the fish. It will be noticed that this does not actually solve the problem of learning, but it does, at least, define where the problem really lies. The crucial point to be established is how the change in the perceptory field comes about, and why the change should be of the particular type found. It will be necessary to turn once again to the experimental data to discover if any light has been thrown on this problem.

I wish to express my gratitude to Dr. E. J. Allen for his encouragement and sympathetic advice given to me on various occasions during the course of this work; to those with whom I have had profitable discussions on problems bearing on animal learning, particularly Dr. E. S. Russell and Dr. C. F. A. Pantin; and to Dr. S. Kemp for reading the manuscript, and offering some helpful suggestions for its final preparation.

SUMMARY.

1. This paper deals with certain experiments on training fish (*Ctenolabrus rupestris* L.) to swim round obstructions to reach food, for the purpose of investigating how their learned response was developed. The whole question as to how learning which involves " problem-solving " is rightly to be interpreted and harmonized with our knowledge of conditioned responses, presents difficulties which have not yet been adequately faced.

2. A description is given of the results of experiments carried out on eleven fish. The fish had to learn a detour route either into a pot or round glass plates. Attention may be drawn to the great diversity in the behaviour of individual fish, both in their reactions to the obstruction at different stages of training, and in the method by which they succeeded in passing it. Some individuals are evidently more capable of profiting by experience than others.

3. As complete a record as possible was made of all performances ; and these data were carefully analysed with a view to exposing the conditions under which efficient responses developed, and to detecting any possible causal influences. The results of this analysis, of which the main features are summarized below, may be partly summed up by saying that learning could progress in spite of considerable and significant irregularities in the fishes' performances. These were such as to preclude all the more straightforward* interpretations of the learning that can be suggested.

4. No general connexion was apparent between the behaviour shown in early trials and that in later trials, when the behaviour, if not perfectly integrated, was at least more uniform. It proved impossible, from examination of behaviour in early trials, to predict whether an efficient learned response would be established, or, if established, what particular movements would be involved. The experiments in which the obstruction was of clear glass, and the detour learned with difficulty, if at all, afford the most critical tests.

5. In particular, the movements which had led to successful solutions in early trials were by no means necessarily " stamped in " or reproduced in an efficient response, if and when this was achieved. Moreover, an efficient response can be established even before the movements by which it is carried out are at all stabilized. The possibility, therefore, that the learning had arisen, in accordance with the " Law of Effect," as a result of the recurrence of those movements which came most frequently to be associated with the solution of the problem, is excluded.

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* i.e., from a physiological point of view.

6. While an efficient response was developing, the integration of the later movements did not proceed in advance of that of the earlier. The data are quite incompatible with the hypothesis that the response developed from independent movements linked by a process of backward association.

7. Since also the "connexionist" hypothesis fails to account for the facts, the possibility that the learning involved nothing more than the development of a motor-habit is now finally eliminated.

8. Only one alternative remains to be explored, namely, that the learning is an *affector* phenomenon. It would thus be associated with the synthesizing, or organizing, processes which must be assumed to occur in the sensory centres of the central nervous system.

9. A certain body of evidence is shown to encourage this view. Details in the external conditions which cannot affect the fish's activity except through the medium of the sense-organs, are found to exert considerable effects on behaviour—both on the performance of individual trials and on the trend of behaviour as a whole through a series of trials. Thus if a meshwork of fine lines is scratched on the glass plate, learning is greatly facilitated, and the movements by which the fish make the detour are significantly different.

10. The conclusion of the evidence considered is that learning is essentially due to the discrimination of some general relation in the external situation which had not previously been prehended (or "detected"). With a clearer appreciation of its surroundings the fish is enabled to give a more effective response. It remains to examine how this critical change takes place, and how its essentially adaptive character is to be explained.

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APPENDIX.

DATA BEARING ON THE POSSIBILITY OF BACKWARD ASSOCIATION.

FISH A.

First series of trials.

The component phases of the learned response were acquired in the following stages.

Trial *8*. Random movements to other parts of the tank mainly eliminated.

Trials *25* to *30*. First permanent reduction in time spent in attempts at swimming straight at food before any leftward movement. Fish now gets into the habit of working steadily down the glass.

Trial *36*. From now on usually moves straight down the glass and passes round the edge first time on 4 occasions out of 5.
Trial *55*. Proficiency in the above virtually established.
Trials *55* to *60*. Further reduction in the duration of the first phase, before first leftward movement, and final proficiency acquired.

There is no indication here of later movements acquiring efficiency earlier.

Second series.

The main step in the re-establishment of the learned response came in trials *B9–11*, and was marked by rather an increase in efficiency of both the first and third phases of the response.

FISH D5.

Phases of the learned response were established in the following order.

1. First phase, over which the fish hardly ever spent any length of time.
2. Second phase: the habit of moving as far as the edge of the glass plate in the first leftward movement.
3. Third phase: the habit of passing round the edge at first attempt.

Note that the integration of the response proceeded from the beginning forwards, and not from the end backwards.

FISH D7.

No one phase can well be said to have acquired proficiency before any other. Progress affected the response as a whole.

FISH D8.

This fish first became proficient at moving leftwards in a half-circle (full left-turn followed, after a longer or shorter forward movement, by a wheeling to the right), simultaneously reducing the time spent in attempts at reaching the food directly.

It was a long time, however, before it became proficient in passing round the edge of the glass on its first leftward movement. A considerable delay in establishing perfect integration was entirely due to errors made in the last phase of the response.

FISH D4.

The first phase never occupied any length of time, and the fish developed a habit of moving leftward efficiently at an early stage.

Until behaviour changed at trial *41*, when a bad lapse set in, the perfection of an efficient response only depended on the ability of the fish to pass round the edge of the glass, once it had moved far enough to the left (third phase). But consistency in this habit was not acquired during this period.

In the eventual learning which set in after trial *42*, the fish at first was taking a considerable time to reach the edge of the glass. But reaching the edge in short time did not wait upon the acquisition of the habit of moving round the edge at the first attempt. Integration of the second and third phases progressed simultaneously.

FISH D6.

The data provided by this fish are particularly instructive, as the long route taken fell into three natural stages, namely (i) withdrawal from L and passage round Q, (ii) passage through K round P, and (iii) passage through J round O.

On page 537 figures are given for the times taken for the respective stages, and it is at once apparent that the last phase was never really efficiently learned. The average times for the passage round O are consistently high.

It is quite evident that the rapid passage from Q to P did not depend on the association with an efficiently integrated passage from P to O. Still less did the habit of turning away from the food at L and rounding Q depend in any way on the complete integration of the rest of the response.

The Air Turbine Ultracentrifuge, together with some Results upon Ultracentrifuging the Eggs of *Fucus serratus.*

By

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With Plate II and 8 Figures in the Text.

INTRODUCTION.

GENERALLY, the force of gravity has little or no effect upon the distribution of the various materials within cells, although they may differ considerably in their relative specific gravity. However, by means of the centrifuge forces can be obtained many times greater than gravity, which otherwise exist only on the very largest planets. Because of this fact, the centrifuge has proved to be a very valuable instrument in the study of many problems of biology. For instance, in experimental cytology and embryology, the subjects with which we are here concerned, it has been used extensively to bring about a redistribution of the various materials within the animal egg, such as the yolk, the pigment, the protoplasm and the fat. From such experiments the role of these various substances as possible organ-forming materials and as affecting cellular differentiation has been studied. Other problems such as fragmentation of the egg, viscosity of the protoplasm, membrane strengths, influence of gravity upon development, differential injury to eggs, molecular weight determinations, polarity, and the cytoplasmic components and inclusions have all been profitably investigated by means of the centrifuge.

The types of devices that have been used to generate centrifugal force in biological experiments are many and varied. For instance, we find a gradual evolution from a simple wagon-like wheel used by Knight in 1815 to study the effect of centrifugal force upon developing plants, to various types of hand centrifuges with high gear ratios, to the fly-wheel of an engine as used by Morgan (1902), to electric and water driven centrifuges, to the Sharples supercentrifuge which develops forces upward to 62,000 times gravity, to the Svedberg oil turbine centrifuge capable of developing forces upward to 400,000 times gravity, and finally to the recently

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* Aided by a grant from the Rockefeller Foundation for work on Cellular Biology.

developed air turbine ultracentrifuge, constructed of air spun rotors without bearings which give rotations of several thousand times a second and develop forces of the order of 400,000 to 7,000,000 times gravity. Forces developed by such centrifuges are limited mainly by the tensile strength of the metal of which the rotors are made. It is this latter type of ultracentrifuge that has been used in the experiments to be described below.

THE ULTRACENTRIFUGE.

Since the air turbine ultracentrifuge has only recently been applied to studies in biological work and since it promises to have a rather wide application in biological experiments, it seemed desirable to give illustrations and a brief description of it here. I shall not attempt to give a detailed explanation of the various parts of the ultracentrifuge, but only to point out its important characteristics so that the reader may have a fair understanding of its construction and operation. Those desiring to construct the apparatus will find complete specifications in the papers by Beams (1930), Beams and Weed (1931), Beams, Weed and Pickels (1933), and Beams and Pickels (1935). The cost of constructing the ultracentrifuge is very low in comparison with that of other types of high speed centrifuges.

The first investigators to use the air turbine for centrifuge work seem to have been Henriot and Huguenard (1927). However, it has been greatly modified and developed into a practical laboratory apparatus by Professor J. W. Beams and his associates of the University of Virginia.

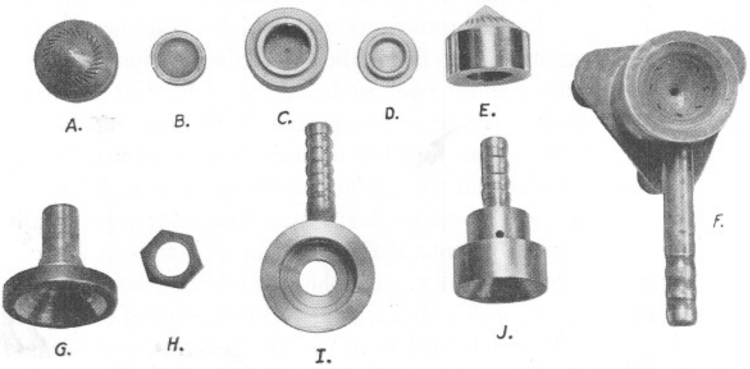

FIG. 1.—The ultracentrifuge. A, bottom of rotor cone showing flutings; B, top of cap which screws into rotor from above; C, top of rotor showing centrifuge cavity; D, bottom of cap as in B; E, side view of rotor; F, assembled stator showing stator cup and eight diagonal holes; G–I, unassembled parts of stator; J, stator with air entering from below instead of from side, as in F.

The ultracentrifuge which I have used is composed of two principal parts: the rotor and the stator (Figs. 1, 2, and 3). The rotor is a small, one and one-eighth inch diameter, all metal (steel, brass, duraluminum, monel metal) structure, shaped like a schoolboy's top, but with a cavity in the centre which holds approximately 4 c.c. of fluid (Fig. 1, A–E). However, rotors may be constructed which hold many times this amount. A small screw cap seals the centrifuge cavity from above (Fig. 1, B and D). The lower portion, or cone-shaped part of the rotor, which is grooved with a series of flutings is mounted in a cup, the stator (Fig. 1, F), also of conical shape, but of a slightly different angle so that the rotor cone touches the stator cup when not running at its top only, which is also its largest diameter (Figs. 2, B; 3, A). To start the ultracentrifuge the rotor is placed in the cup of the stator and air under pressure (2 to 150 lb. per sq. inch) is released and passes through the tube labelled "air pressure" into the stator chamber and then through the eight diagonal holes into the stator cup where it impinges on the flutings of the rotor and starts it rotating (Fig. 3, A). The air that is used to cause rotation then escapes between the surface of the rotor cone and of the stator cup, floating the rotor on a cushion of air just above the stator cup, entirely free of any mechanical contact. At the same time that air under pressure is escaping between the surfaces of the stator and the rotor, air is entering from the atmosphere through a small hole at the vertex of the stator because of the reduced pressure at this point (Fig. 3, A, labelled "stabilising air flow"). This, according to Beams and Pickels (1935), greatly improves

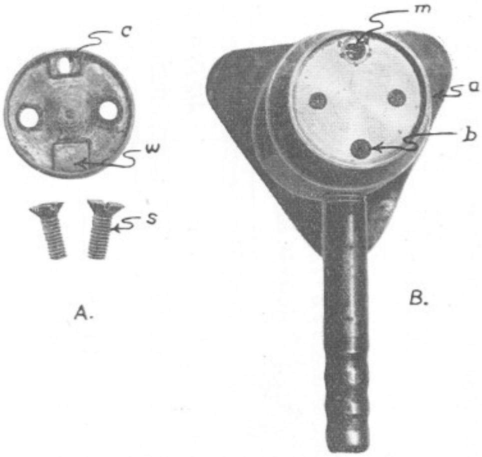

Fig. 2.—The microscope ultracentrifuge. A, detachable top showing centrifuge chamber (*c*) above and balance weight (*w*) below; machine screws (*s*) fasten detachable top into position on rotor in B; B, upper view of rotor (*a*) resting in stator and showing tube leading to mirror (*m*) with counter balance tube (*b*) below.

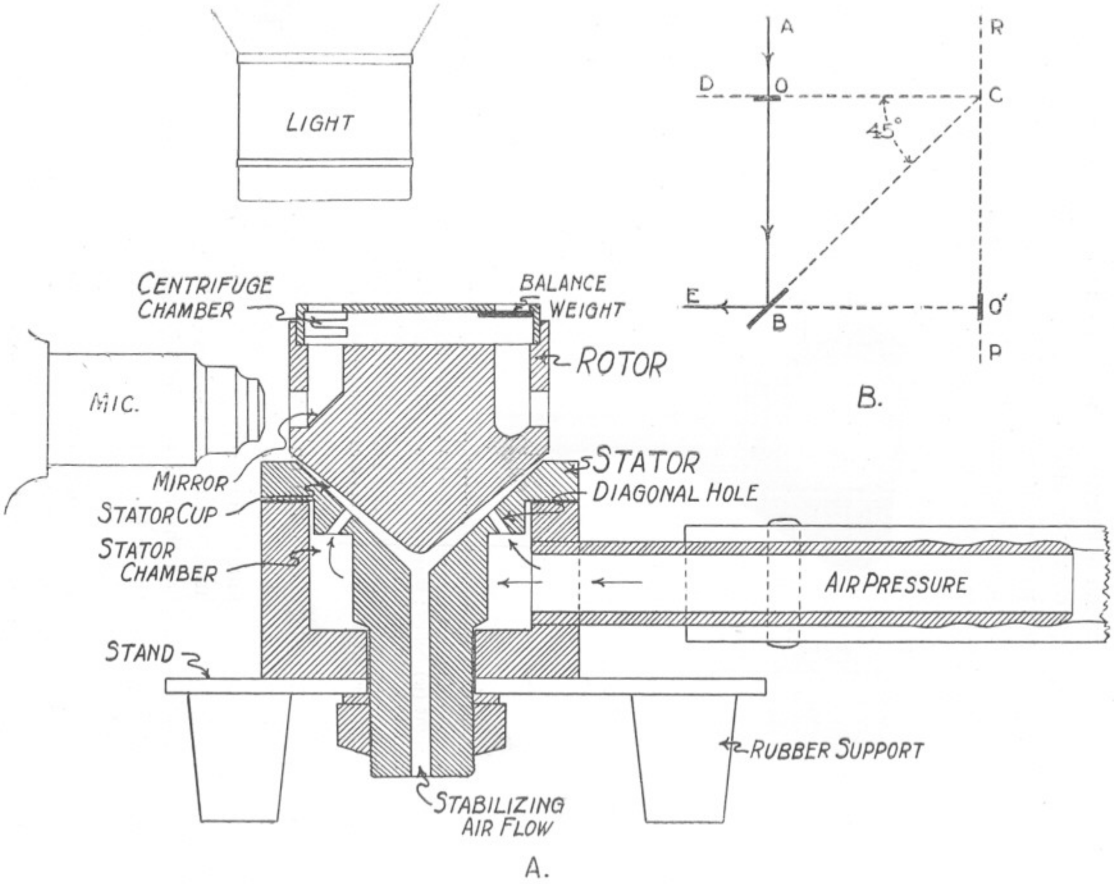

FIG. 3.—A, section through microscope ultracentrifuge. Labels are self-explanatory. B, diagram showing the optical system of the rotor in A (modified from Pickels). The centrifuge chamber has a diameter large in comparison with its thickness. "B, is a small plane mirror mounted on the rotor. Light from a straight filament lamp is focused upon O so that the image of the filament lies along CD and consequently transverse to the direction of the motion of the object thus illuminated. As O then revolves about RP, it becomes visible to the naked eye or in a microscope only as it passes through the indicated position. Consequently, as viewed from E the virtual image O will appear stationary and under apparently continuous illumination when the speed is high enough to prevent flicker" (Pickels, 1936).

stability and helps to adjust automatically the air cushion for different air pressures, speeds, and weights of rotors. This is an important improvement over the first models in which the rotors were supported by a separate column of air from that which was used to cause rotation. The rotor is prevented from being blown out of the stator cup by the principle of Bernouilli. The forces involved in this principle are so great at high

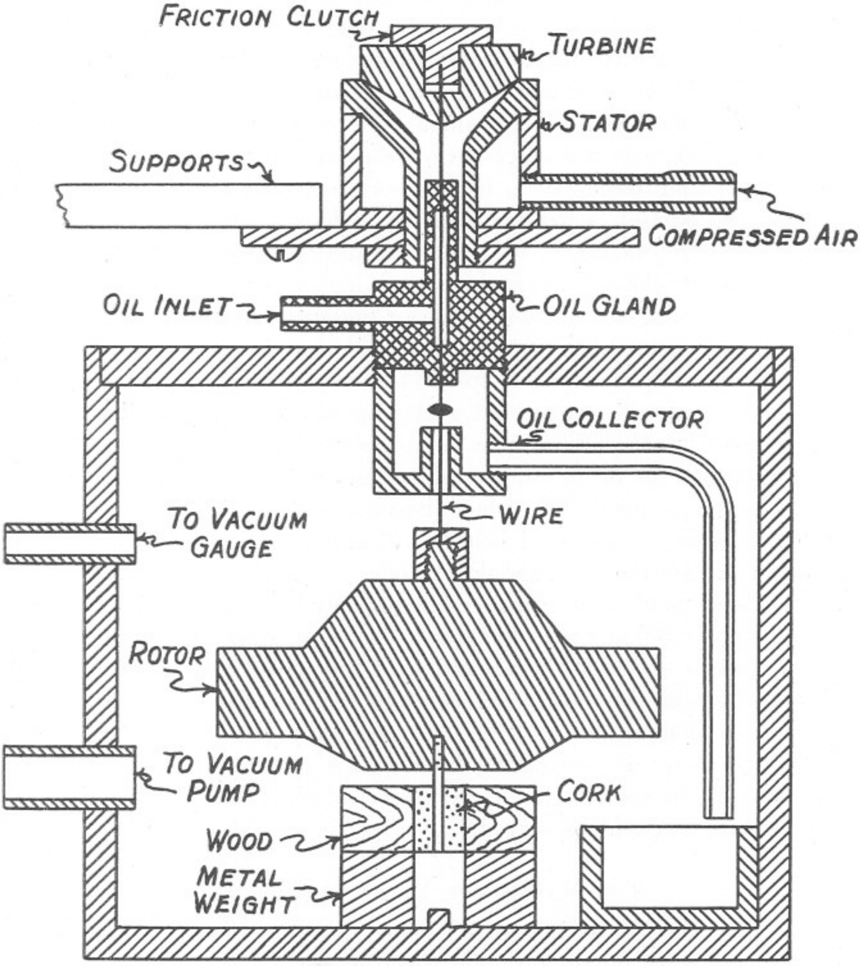

FIG. 4.—Air turbine vacuum ultracentrifuge (redrawn from Beams and Pickels, 1935). In this design the driving mechanism is simply an air turbine rotor as above described (Fig. 1). From the vertex of the driving rotor or turbine a small steel wire extends downward through an oil gland into a vacuum chamber and is attached to a much larger rotor which contains a cavity where the material to be centrifuged is placed. Since the rotor which spins in the vacuum chamber is of much greater diameter than the turbine rotor, enormous centrifugal forces may be obtained.

pressures that the entire ultracentrifuge may be inverted without the rotor falling out of the stator; because of this fact, too, it is not essential that the rotor be exactly balanced. Another important feature of this type of ultracentrifuge, especially in biological work, is that the temperature does not vary in the rotor chamber over a few degrees from that of the atmosphere even though the rotor may be operating at very high speeds.

The speed of the rotor may be accurately and easily determined by the stroboscopic method and the amount of centrifugal force developed calculated. The size and shape of the rotors are subject to wide variation and Beams and Weed (1931) have described rotors in which materials may be introduced, separated, and the lighter and heavier materials collected while rotating. They have also designed rotors to observe the sedimentation velocity of particles at very high speeds. To stop the rotor when it is running at high speeds the air pressure is reduced to 3 to 5 lb., which is sufficient to sustain an air column between the rotor and the stator. When the rotor has reduced its speed (as determined by pitch), the fingers are placed about it and pressed gently against the sides until it stops. The air pressure should never be completely cut off while the centrifuge is operating as the rotor will drop down on to the stator and then jump off. Caution is urged that, when the ultracentrifuge is to be operated at high speeds, it be placed behind a suitable barricade to protect the operator in case the rotor should explode.

Another type of ultracentrifuge has recently been described by Beams and Pickels (1935) and they have very kindly permitted me to reproduce it in Figure 4. In brief, the advantage of this model over the one above described is that the rotor which contains the material to be centrifuged spins in a vacuum and may be kept thermally insulated, which is an important factor in preventing troublesome convection currents from occurring in the centrifuged liquid, especially when the rate of molecular sedimentation is being observed.*

THE MICROSCOPE ULTRACENTRIFUGE.

Recently Harvey and Loomis (1930) have described a unique and ingenious type of microscope centrifuge in which the materials may be continuously observed while centrifuging. Harvey (1934) has adapted this principle to the air turbine ultracentrifuge mentioned above. In such a microscope ultracentrifuge he was able to take clear photographs of eggs being centrifuged at 84,000 times gravity. Figures 2 and 3 show rotors adapted as microscope ultracentrifuges which were constructed for me by Dr. E. G. Pickels in Dr. J. W. Beams' laboratory. The design of the optical system differs considerably from that of Dr. Harvey (Fig. 3, B). The

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* See also Biscoe, J., Pickels, E. G., and Wycoff, W. G., *Jour. Exp. Med.*, 1936, Vol. 64, p. 39.

chamber which holds the material to be centrifuged is made of a specially treated glass (Beams, Weed, and Pickels, 1933), sealed at one end and cemented into position on the detachable top of the rotor (Figs. 2, A; 3, A). The top (Fig. 2, A) is placed over the body of the rotor, as in Figure 3, A, and fastened in position by machine screws so that the chamber containing the material to be centrifuged is directly over the mirror. The mirror is stellite or polished steel and is placed at a 45-degree angle to the chamber (Fig. 3, A, B). The light source is placed directly over the cell containing the material to be observed. When the rotor is turning fast enough to prevent flickering, one obtains through the microscope an almost perfect image of the material being centrifuged (Fig. 3, A).

As pointed out by Harvey, one of the important problems in high speed centrifuging is to prevent crushing of the material that is centrifuged. This may be obviated by supporting this material in an isotonic medium of graded density so that the material comes to lie in a medium of the same density. Isotonic sucrose, neutralised gum arabic or soluble starch solutions may be used for this purpose. Where large pieces of organs, such as the liver, are centrifuged, the cells next to the sides of the ultracentrifuge, i.e. on the centrifugal side of the liver mass, may be somewhat crushed while serving as a buffer for the rest of the cells which are not affected by the crushing action.

MATERIAL AND TECHNIQUE.

Several species of Fucus may be easily collected in abundance upon the rocks a few feet below the high-tide limits along the shores of Plymouth Sound. *Fucus vesiculosus*, *Fucus platycarpus*, *Fucus serratus*, and *Ascophyllum nodosum* were collected during the months of April, May, and June of 1935 at a point just below the Plymouth laboratory. Observations were made upon all the above-named species of Fucus for comparison, but only those upon *Fucus serratus* are recorded here.

The sexes of *Fucus serratus* can easily be distinguished by cutting and examining the conceptacles. The plants were collected a short time after they had been exposed by the ebb-tide and taken into the laboratory, and the males and females placed in separate dishes. After 6 to 10 hours in the laboratory the fruiting tips were observed to extrude the gametes. Those of the female were extruded in capsules of eight forming an olive-green mound-like mass upon the conceptacle. Those of the male were extruded in capsules containing many sperm (antherozoids) and were of an orange colour. A considerable amount of mucilaginous material is secreted, too, if the plants are kept moist. After tips of the fruiting plants were submerged in sea water, the mucilaginous material and the gametes were washed free; they then settle readily to the bottom of the dish.

If the female gametes are examined immediately they will be found in groups of eight surrounded by a gelatinous capsule consisting of a definite membrane or membranes, which dissolve after a few minutes in sea water setting the individual eggs free. If the capsules containing the eggs are extruded under unfavourable conditions, such as rapid drying or at too high a temperature, one frequently finds two or more of the eggs fused together giving rise to a capsule of 1 large egg and 6 of normal size (Fig. 5, A). In extreme cases as many as 6 eggs may fuse, giving rise to 1 giant egg and 2 of normal size within the capsule (Fig. 5, B).

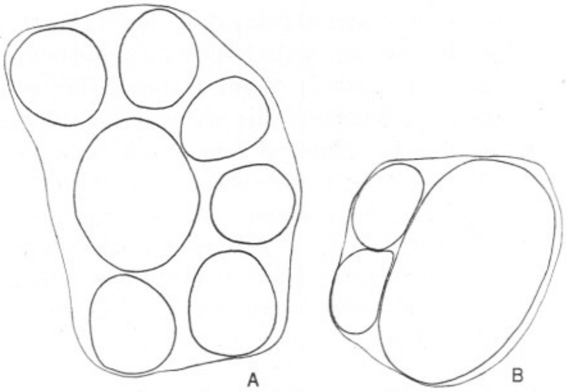

Fig. 5.—Fusion of Fucus eggs inside capsule. A, two eggs fused giving rise to one large egg and six of normal size; B, six eggs fused giving rise to one giant egg and two of normal size.

In addition to observing the eggs alive, they were fixed in Bouin's, Flemming's strong, Flemming's weak, and Champy's solutions. The best results were obtained with Flemming's strong solution made up in sea water. The sections were bleached and stained in Heidenhain's haematoxylin.

The Unfertilized Egg.

Notwithstanding the fact that the centrifuge has proved to be a valuable instrument in the study of many problems of experimental cytology and embryology of animal eggs (see Morgan, 1928, and Wilson, 1925, for reviews of the literature), it has been almost entirely neglected or no results have been obtained in similar types of studies upon plants. Shimamura (1929) centrifuged the egg of *Pinus thunbergii* and reports that " there is no stratification or separation of the contents in the egg cytoplasm." More recently, however, Whitaker (1931) succeeded in stratifying the cytoplasmic materials in the unfertilized eggs of *Fucus vesiculosus*. Various somatic cells of plants have been centrifuged and for a review of the literature on this aspect of the subject the reader is referred to a recent paper by Beams and King (1935).

For a detailed description of the normal cytology of fertilization and of the early cleavages in Fucus the reader is referred to the excellent works of Farmer (1896), Farmer and Williams (1898), Strasburger (1897), Yamanouchi (1909), Oltmann (1922), and Walker (1930).

The normal unfertilized eggs of *Fucus serratus* vary considerably in size (60–90 μ) and possess an alveolar or foam-like type of cytoplasm in which is embedded a well-defined nucleus (Pl. II, Fig. 1). Irregularly distributed throughout the cytoplasm are many chromatophores, fat-bodies and certain other granules of undetermined character. Farmer and Williams have described the chromatophores as located at the surfaces of the foam cavities with their long axes directed away from the nucleus. A cell membrane encloses the cytoplasm and the eggs have been described by some investigators as undergoing amoeboid movement. When the unfertilized egg is centrifuged its components become stratified into three distinct layers from the centrifugal to the centripetal pole as follows (Pl. II, Fig. 2): (1) A layer of very dense alveolar-like clear cytoplasm constituting over two-thirds of the total volume of the egg ; (2) a layer of green chromatophores ; and (3) a layer of fat in the form of globules or vacuoles at the centripetal pole. The nucleus takes up a position between the chromatophores and fatty globules. Sometimes the eggs become greatly elongated in the direction of the centrifugal force and the fatty layer and part

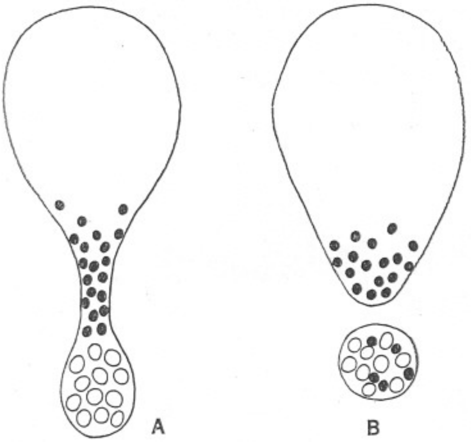

FIG. 6.—Ultracentrifuged unfertilized eggs. A, egg greatly elongated in the direction of the centrifugal force ; fat globules and some of the chromatophores fragmenting from the egg. B, later stage of A.

of the chromatophores may be completely removed from the egg (Figs. 6, A, B; Pl. II, Fig. 3). The eggs are very dense as compared to sea-urchin eggs and it was difficult to find a medium of the same density in which they could be suspended while centrifuging without causing a marked osmotic effect. I employed gum arabic and a sucrose solution made up in sea-water, but even then I was not successful in getting a solution of the same specific gravity as the eggs.

THE FERTILIZED EGG.

In about 10 to 15 minutes after fertilization of the eggs of Fucus a distinct cell wall is formed around them which prevents a marked distortion of the eggs during centrifuging. When a fertilized egg with a cell wall is centrifuged in sea-water at 150,000 times gravity a sharp stratification of its protoplasmic components takes place (Pl. II, Fig. 4). Here, as in the unfertilized egg, three distinct zones are present in the order of their decreasing specific gravity as follows: (1) a layer of dense alveolar

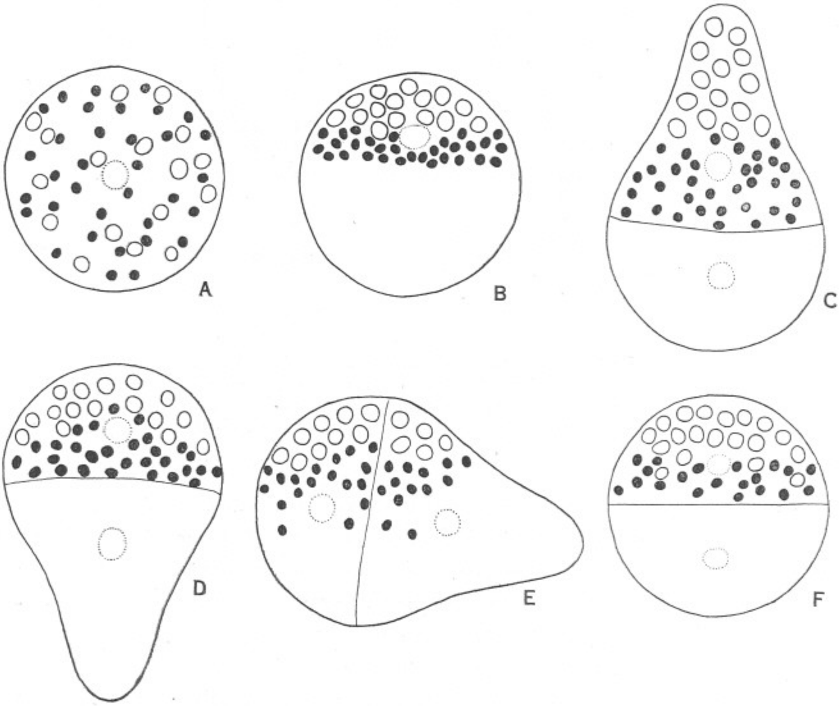

FIG. 7.—A, normal egg; B, stratified egg; C–E, eggs showing appearance of rhizoid protuberances, first cleavage planes and their relations to the planes of the stratified materials. F, egg cleaved without forming rhizoid rudiment.

cytoplasm; (2) a layer of chromatophores and bodies which I have tentatively interpreted as mitochondria; and (3) a layer of fat globules which are readily blackened by osmic acid. The nucleus lies just centripetal to the layer of chromatophores. The egg illustrated in Plate II, Figure 4, was not fixed until one half-hour after it had been centrifuged and shows the initial stages of the migration of the nucleus back to the centre of the egg, its usual position. Conklin (1917) has attributed this phenomenon to the activity of the "spongioplasm." The writer is inclined to believe that the factors involved in the redistribution of the stratified materials are more complex than assumed by Conklin. This point will be further discussed in a forthcoming paper dealing with the effects of centrifuging the eggs of *Ascaris suum*. Small granular bodies are found in the fixed preparations that are readily stratified by ultracentrifuging into a position between the chromatophores and fat globules. I am inclined to interpret them as mitochondria; however, they are obviously in need of further investigation. In Plate II, Figure 5, is depicted a cell fixed 6 hours after centrifuging. It will be observed that the nucleus has returned almost to its usual position within the cell, carrying with it numerous chromatophores and fat globules. However, less frequently, following strong centrifuging cells may be found where only the nucleus migrates to the centre of the egg where cleavage takes place and all or most of the chromatophores and fat globules remain stratified (Fig. 7, C–F;

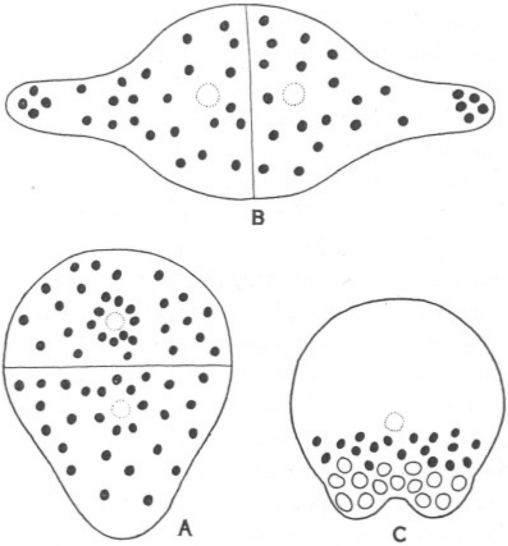

FIG. 8.—A, normal egg; B, bipolar uncentrifuged egg; C, ultracentrifuged egg with two rhizoid protuberances.

Pl. II, Figs. 6–7). In no case was I ever successful in fragmenting the fertilized eggs of Fucus as has been done with the eggs of certain sea-urchins.

As previously pointed out the unfertilized and the fertilized eggs of Fucus for the first 6 to 8 hours after fertilization are unlike many animal eggs, for example, the frog's egg, in that they show no indication of polarity. I have attempted to show diagrammatically (Fig. 7) how the various materials may be stratified in relation to the appearance of the rhizoid protuberance and of the first cleavage plane. Figures 7, A and B, show the typical appearance of the fertilized egg before and after centrifuging, respectively. It will be observed by an examination of Figure 7 that the appearance of the rhizoid protuberance and of the first cleavage plane seems to be irrespective of the plane of the stratified materials. For instance, in Figure 7, C, the rhizoid protuberance appeared at the centripetal pole of the stratified egg and the first cleavage plane occurred parallel to the stratified material separating all of the chromatophores and fat globules into the daughter cell possessing the rhizoid protuberance. However, in Figure 7, D, the rhizoid protuberance has appeared at the centrifugal pole of the egg, and the first cleavage plane, as in the above case, occurred at right angles to the stratified materials dividing the egg so that the daughter cell possessing the rhizoid rudiment is composed chiefly of alveolar cytoplasm and is free of chromatophores and fat globules. In Figure 7, E, the rhizoid protuberance has occurred laterally and the first cleavage plane at right angles to the stratified materials. In still other cases eggs are found which do not give rise to rhizoid rudiments, yet cleavage may take place as indicated (Fig. 7, F).

In some of the control eggs, as well as in the centrifuged material, I have observed certain rather interesting abnormalities. In Figures 8 B and C are shown cells with a dual polarity. Whitaker (1931) has likewise described similar abnormalities in *Fucus vesiculosus*. Although the complete history of these two cells is unknown it seems probable that their dual polarity is due to a fusion of 2 eggs, each of which retained its original polarity. Eggs with as many as 4 nuclei have been found but it is not known whether this is due to a fusion of 4 eggs, polyspermy, or to a division of the nucleus without division of the cytoplasm (Pl. II, Fig. 8).

DISCUSSION.

It has been demonstrated in this paper that the visible inclusions in the eggs of *Fucus serratus* may be shifted and stratified in the order of their relative specific gravity without affecting the normal development or apparently modifying the original polarity, i.e. the original axis of the egg. Neither do the stratified materials seem to play a role as organ-forming substances. In this respect the *Fucus serratus* egg differs from the somatic tissue of another alga, *Griffithsia bornetiana*, recently investigated by Schechter (1934). Schechter found that if tufts of the alga were centrifuged at 150 times gravity for 24 hours or longer, normal shoots appear from the cells at a point where the heavier substances, in this case the chromatophores, have concentrated. In this way reversal of polarity may be produced anywhere along the plant axis. He suggests, however, that the centrifuged substances (inclusions) are not directly determinative of the polarity, but act as stimuli.

The question then follows in what structure or structures of the cells does the polarity reside. This is an old question among students of embryology and one that has never been satisfactorily answered. Lillie (1909), from his work on centrifuged Chaetopterus eggs, concludes that " polarity is a property of the ground substance of the protoplasm " which cannot be disturbed by ordinary centrifuging because it is assumed to be of molecular organization. Conklin (1917, 1924) holds that polarity inheres in the " viscid spongioplasm " which forms a peripheral layer around the egg and a continuous framework throughout the cell that is connected to the nucleus. It is this structure which, he holds, is responsible for the return of the nucleus and other inclusions or components to their usual position within the cell after artificial displacement by centrifuging. The yolk, oil, water, and pigment granules are thought to lie in the meshes of the " spongioplasm." As regards the effect of centrifuging upon the " spongioplasm " Conklin states : " . . . at the same time the strands of the framework may be stretched or bent, but unless the centrifuging is strong enough to kill the egg, this substance is not stratified with the other cell contents."

If one assumes that the " ground substance " of Lillie and the " spongioplasm " of Conklin are molecular, a condition that now applies to protoplasm generally, it might be possible, in view of the recent work of Svedberg (1928), to produce a stratification within the protoplasm of its colloidal components. In this connexion Taylor (1931) has recently raised the question, " But to what extent the living ground substance would endure the rigours of such enormous forces (10,000 to 100,000 times gravity) and remain living is extremely problematical."

It is clear from this work on Fucus that centrifugal force of 150,000 times gravity for 30 minutes does not kill the eggs. But to what extent the " spongioplasm " has been affected by such enormous forces one is unable to state. However, Beams and King (1936) have recently subjected the eggs of *Ascaris suum* to a centrifugal force in excess of 400,000 times gravity for one hour without killing them. This is a force equal to the maximum employed by Svedberg to produce sedimentation of colloids. Ascaris eggs have also been subjected to 150,000 times gravity for 10 days; they not only remain living but undergo cleavage in the ultracentrifuge. It has not yet been determined whether or not a stratification of the colloidal cytoplasmic components has taken place, but if such does take place, it is of particular interest, for then the normal spatial relationship of the separate elements cannot be of vital importance for the maintenance of life. However, if, as we are inclined to believe, little or no separation or stratification of the components has taken place in this material, they must be held together in a firmer way than those in the colloidal systems examined by Svedberg. In other words, the conditions present in this living colloidal system (protoplasm) seem to be different from those in non-living ones.

It would seem that the killing of cells by the present methods of centrifuging is usually due to mechanical distortion or disruption (prevented in the fertilized Fucus egg by a very resistant cell wall and in Ascaris eggs by a shell) rather than to a disturbance of the spatial relationship of their molecular parts.

In Fucus it has been demonstrated by Farmer and Williams (1898), Hurd (1920), Whitaker (1931), and others that light may alter the polarity of the developing spore. They found, and I have also observed, that the rhizoid protuberance always appears on the side of the egg opposite the light (i.e. the shaded side). Hurd further observed that the shorter rays at the blue end of the spectrum were the most effective in determining the polarity. She suggests that this effect may be due to a more rapid oxidation of the egg on the side exposed to the light, setting up a metabolic gradient which is responsible for the polarity. Hurd also found that when eggs were placed in groups very close to one another, each develops a polarity in such a way that its apical point faces toward the group. To this phenomenon, which is even more influential in determining polarity than light, she has given the name of "group orientation effect." Whitaker has shown that even unfertilized eggs of another species may control the polarity in the "group effect." The direct effect, he concludes, cannot be due to any agency depending upon nuclear or cell division.

Lund (1923) has found by passing an electric current through sea water containing eggs of *Fucus inflatus*, that they will all become polarized with the rhizoid protuberance toward the positive pole. This is interesting in view of the findings of McClendon (1910) that the chromatin in the nucleus of the onion root tip moves to the positive pole when exposed to an electric field. However, since Lund did not examine the eggs cytologically it is unknown whether or not the electric current directly affected the mitotic spindle.

It is evident that in many of the eggs like those in Figure 7, all of the chromatophores are segregated into one of the daughter cells at the first cleavage. However, as the spore grows, new chromatophores arise in those cells derived from the chromatophore-free blastomere. Although I do not want to urge the view too strongly, it seems probable that the new chromatophores may arise *de novo* in the cell, perhaps by the activity of certain of the cytoplasmic components.

A few preparations were made by the Kolatchev method in an effort to demonstrate the osmiophilic platelets, but they were unsuccessful. The whole problem of the nature of the mitochondria and the osmiophilic platelets and their relationships to the other cell inclusions of the Fucus egg is badly in need of further investigation.

It has been the author's experience that many of the methods designed to be used on the tissues of fresh-water animals and plants do not always work so successfully upon the tissues of marine animals. It is also a fact of experience that many of the well-known methods fix tissues and cells of marine animals better if they are dissolved in sea water instead of the usual method of using distilled water. In general, a distinct need is felt for a modification of many of our cytological fixatives in order that they will preserve more successfully the cells of marine animals.

Summary.

1. An air turbine ultracentrifuge suitable for biological work and capable of developing a centrifugal force from 10,000 to 500,000 times gravity has been described. Advantages of the ultracentrifuge are : (1) The temperature does not vary in the centrifuge chamber over 2 or 3 degrees from that of the atmosphere ; this is not sufficient to be an important factor in general biological work. (2) The cost of constructing the apparatus is very low in comparison with that of other high speed centrifuges.

2. A modification of the air turbine ultracentrifuge in which the turbine rotor drives a second rotor, in this case the centrifuge rotor which spins in a vacuum, has been described. Here the centrifuge chamber is thermally insulated which is an important item in preventing troublesome convection currents from arising in the centrifuged material where such special problems as the rate of molecular sedimentation are being observed. Forces in excess of one million times gravity can easily be obtained by such an apparatus.

3. A microscope ultracentrifuge in which the biological materials may be observed while centrifuging at high speeds (10,000 to 200,000 times gravity) has been illustrated.

4. The stratification in *Fucus serratus* eggs of the visible inclusions in the order of their relative specific gravity by means of the ultracentrifuge has been described. After centrifuging fertilized *Fucus serratus* eggs at 150,000 times gravity for one half-hour they apparently develop normally.

5. The polarity in centrifuged Fucus eggs as determined by the appearance of the rhizoid protuberance and of the first cleavage plane is unaffected by a stratification of the visible inclusions.

6. The fusion of as many as six unfertilized eggs has been observed.

7. Normal and centrifuged bipolar eggs, i.e. with two rhizoid protuberances, have been found. This condition is probably due to the fusion of two eggs each of which has retained its original polarity.

ACKNOWLEDGEMENT.

The author is greatly indebted to Dr. E. J. Allen, F.R.S., for kindly placing at his disposal during the summer of 1935 all the facilities of the Plymouth Laboratory. To Dr. W. R. G. Atkins, F.R.S., and other members of the staff of the Plymouth Laboratory the author is also indebted for much help and advice regarding the collecting and handling of Fucus. I am also very grateful to Professor J. W. Beams and Dr. E. G. Pickels for constructing the ultracentrifuges for me. Finally, I wish to thank Professors R. L. King and J. Brontë Gatenby for kindly reading the manuscript.

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EXPLANATION OF PLATE II.

All drawings were made from sections at an approximate magnification of 2,000 times. Centrifugal ends of the cells, except Figure 1, are directed toward the bottom of the plate.

FIG. 1.—Normal unfertilized egg.

FIG. 2.—Ultracentrifuged unfertilized egg showing stratification of the visible materials.

FIG. 3.—As in 2, but elongated in the direction of the centrifugal force.

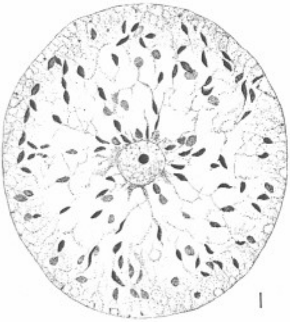
FIG. 4.—Fertilized ultracentrifuged egg showing stratification of materials.

FIG. 5.—As in 4. Nucleus and inclusions shown in the process of returning to their usual position within the egg.

FIG. 6.—Spore derived from egg in which most of the inclusions had been segregated into the daughter cell opposite the one possessing the rhizoid protuberance at the first cleavage.

FIG. 7.—Spore derived from egg in which most of the inclusions had been segregated into the daughter cell possessing the rhizoid protuberance at the first cleavage.

FIG. 8.—Uncleaved ultracentrifuged egg with four nuclei.



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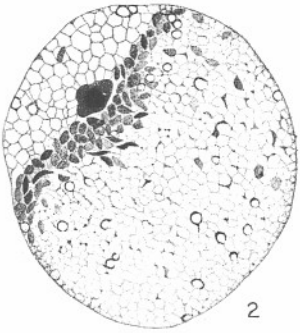

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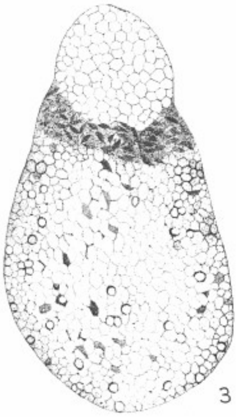

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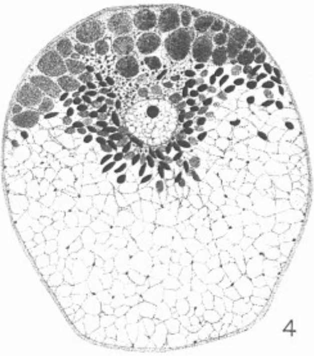

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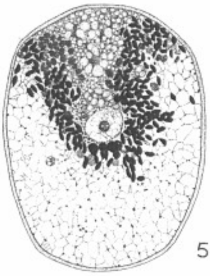

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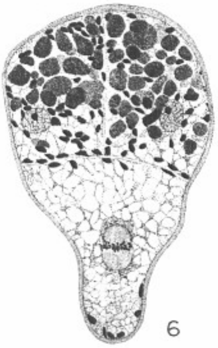

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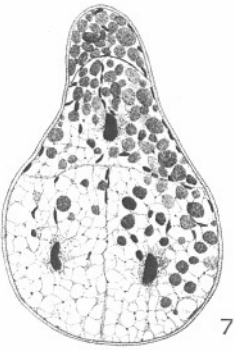

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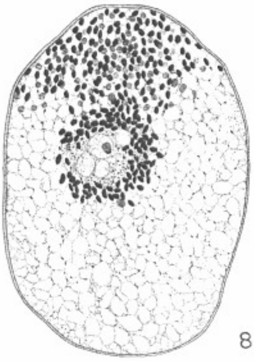

8

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To face page 588.

A Review of the Amphipod Genus *Corophium*, with Notes on the British Species.

By

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Assistant-Keeper at the British Museum (Natural History): late Student Probationer at the Plymouth Laboratory.

With 4 Figures in the Text.

CONTENTS.

INTRODUCTION.

DURING 1934–5 I collected in Plymouth Sound and neighbouring waters seven species of the genus Corophium of which two were undescribed. I also collected one other species, and had sent to me two other species (one new) from other localities in South England. A list of these ten species, with the single other species known from Britain, is given in Appendix II, and their British distribution summarized.

In the course of identifying them I examined 23 of the 32 species of Corophium, and saw all the literature to which I could find references.

The first part of this paper consists of a general account of the morphology and ecology of the genus and a key by which it can be divided into three sections. This part is introductory to the second part, which contains a review of those species which I consider valid. In this review the name of each species is followed by a complete bibliography, only those references being omitted which have already been listed by Stebbing (1906): if a number of references have been made to a species, that which contains the best description or figures is placed in square brackets above the others, and immediately below the name of the species. An account of distribution follows the bibliography, and is followed for many species by notes on ecology and identification.

Description and figures are given of the three new species: and keys have been made to two of the sections (13 spp.). Holotypes and paratypes of new species are in the British Museum (Natural History).

GENERAL ACCOUNT.

HISTORICAL.

The genus *Corophium* was established by Latreille in 1806, to include the single species *C. longicorne* (which had previously been described as *Oniscus volutator* Pallas).

The best general account is that of Stebbing (1906), who defines the genus, and gives a key to 12 species, with descriptions and full bibliography. Bradley (1908) gives a key to 15 species (not 16 as appears, for *C. cylindricum* and *C. acherusicum* are synonymous), and excellent figures and descriptions of *C. salmonis* and *C. spinicorne*. He does not describe the other species, or list bibliography, and his key is inferior to Stebbing's. Both these accounts need revision, since the number of species has since been doubled.

Many fauna lists of separate areas have been published. The following are the most important.

Della Valle (1893), 3 spp., Naples.
Sars (1894), 4 spp., Norway.
Sars (1895), 6 spp., and (1896), 1 sp., Caspian Sea.
Chevreux (1908), 3 spp., Bône, Algeria.
Chevreux and Fage (1925), 6 spp., France.
Stephensen (1929), 5 spp., Nord und Ost-See.
Shoemaker (1934 *a*), 9 spp., E. coast of N. America.
Shoemaker (1934 *b*), 2 spp., W. coast of N. America.

The bionomics of *C. volutator* are described by Hart (1930) ; and those of *C. insidiosum* n.sp. by Ussing (1924) under the name of *C. bonelli*.

ECOLOGY.

As far as is known all species form tubes of mud or muddy sand, either in the substratum or upon ascidians, sponges, etc. These two habitats are each frequented by about half the species of Section A, as defined below, but with the exception of *C. crassicorne* in Section B no species of the other sections is known to burrow. The tubes of *C. volutator* and *C. insidiosum* are described respectively by Hart (1930) and Ussing (1924).

The species of this genus are found in shallow water, and frequently between tidemarks. They are characteristic, especially the species which build tubes on sessile objects, of harbours and estuaries, where there is much silt for the forming of tubes. Many are able to endure slight diminutions of salinity in the surrounding water, and a few species live in fresh, or nearly fresh, water. *C. rioplatense* was described from specimens found in fresh water in the Rio de la Plata, *C. spinicorne* has been found in the San Francisco water supply, and *C. curvispinum* var. *devium* is common in the freshwater reaches of many European rivers.

The feeding of *C. volutator* is described by Hart (1930). This species is principally a selective deposit feeder, and also consumes a small proportion of suspended particles. The form of the limbs chiefly used in feeding—the maxillipedes and the two pairs of gnathopods—is so constant throughout the genus that it is probable that other species differ only in the proportions of the food-supply drawn from these two sources.

In the British species (except for *C. bonelli*) both sexes are usually present in collections, though the female is usually rather commoner than the male: and this appears, from the literature and specimens that I have seen, to be so with most species of the genus. *C. bonelli*, however, is almost certainly parthenogenetic—a condition rarely found elsewhere in the Amphipoda. The evidence on which I base this conclusion is summarized in the account of that species.

Some species, e.g. *C. acutum*, are almost world-wide in distribution. Species which build tubes on sessile objects are clearly likely to be carried by shipping, and *C. acherusicum* has been collected off a ship's bottom at Sheerness.

MORPHOLOGY.

A full definition of the genus is given by Stebbing (1906). The features most characteristic of the genus are the second antennae, the mandibular palp (which is 2-jointed), and both pairs of gnathopods. In the male antenna II, segment 4 is normally stout and terminates with a single or complex tooth: this segment may also bear spines. In many species of Section A this segment is similar in the female to that of the male: in others, and in almost all species of Sections B and C, this segment in the female bears no teeth, but only spines, the arrangement of which is specifically distinctive. These features are well shown in the drawings of Sars (1894), whose general account of the genus on pages 612–3 is also excellent.

The genus may be divided into three sections on the characters of the urosome: no species are known with intermediate characters.

Section A: segments of urosome separate (19 spp.—10 accepted by Stebbing in 1906).

Section B: segments of urosome fused; uropods I and II inserted in notches in the lateral margins of the urosome (8 spp.—2 accepted by Stebbing).

Section C: segments of urosome fused; uropods I and II attached ventrally; lateral margins of urosome without notches (5 spp.—none known to Stebbing).

The fusion of the segments of the urosome has proceeded further in Section C than in Section B, and therefore the species of Section C seem to have developed most, and those of Section A least, from their hypothetical common ancestor. Fusion of the urosome segments is not common in the Amphipoda. The characters of these sections are further considered in the appropriate place in the review of species.

Certain species have frequently been confused with each other, especially *C. crassicorne*, *C. bonelli*, *C. insidiosum*, and *C. acherusicum*, and to a less extent *C. acutum* and *C. lacustre*. This is due to incomplete knowledge of distribution and of literature, and even more to attention wrongly paid to characters which are not specific.

For identification, adult specimens (ovigerous ♀♀ and ♂♂ therewith) of both sexes should be examined, and the following features observed: form of rostrum, eye-lobes, eyes; antenna I, form of basal segment and arrangement on it of outgrowths, spines and setae, ratio of lengths of first three segments, number of segments in flagellum; antenna II, segments 4 and 5, form of segment and arrangement of spines, teeth or processes, and density and length of setae; gnathopod I, form of palm, spines on it, and subsidiary teeth on dactyl; gnathopod II, subsidiary teeth on dactyl; pereiopods 5 and 6, spines on carpus; pereiopod 7, form of basal segment and ratio of its length to that of propod; urosome, segments separate or fused, and shape of lateral margin; uropods I and II, spines on peduncle and rami; uropod III, form of ramus; telson, form.

Of these the characters of the urosome; of antenna I, segment 1; and of antenna II, segments 4 and 5, are the most useful. The gnathopods, though very characteristic of the genus, and not similar in form in every species, are usually very similar in related species. The mouth-parts are very uniform, as far as is known.

The characters of the antennae change with age, and even in adults some variation occurs. Variation in *C. curvispinum* is described by Wundsch (1915), in *C. salmonis* and *C. spinicorne* by Bradley (1908), and in *C. volutator* by Hart (1930). In this paper I have described variation in *C. arenarium*, *C. bonelli*, *C. insidiosum*, *C. acherusicum*, and *C. sextoni*. In these, and in *C. crassicorne*, the antennae of juveniles are shorter in relation to the body; the segments are stouter, and bear more spines in the male and less in the female. The adult male in these five species bears only a few small spines on the antennae. Outgrowths on antenna I, segment 1, and antenna II, segment 5, which are characteristic of the males of some species, are only present in full-grown specimens: the same is true of the very long rostrum of the adult male of *C. aculeatum*, *C. insidiosum*, and *C. uenoi*.

The number of segments on the flagellum of antenna I, of subsidiary teeth on the dactyl of gnathopod II, and of spines on the uropods increases with age.

Measurements of length given in this paper are from rostrum to telson.

REVIEW OF SPECIES.

SECTION A.

This section contains 19 species, of which one is here described as new. I have examined 13 of these, the remaining six being *C. spinulosum* Sars, *C. maeoticum* Sowinsky, *C. salmonis* Stimpson, *C. spinicorne* Stimpson, *C. rotundirostre* Stephensen, and *C. rioplatense* Giambagi.

I have not made a key to the section, since the specific differences do not lend themselves to the necessary terse description, and adequate figures have been published of every species. Stebbing (1906) included a key to 10 species with full synonymy and description. Bradley (1908) gave a key to 13 species, with the synonymy, descriptions and figures of *C. salmonis* and *C. spinicorne* only. His key is not, however, of great use as he relied on characters common to both sexes and these are not well known or distinctive.

In about half the species segment 4 of antenna II in the female differs from that of the male only in being less strongly developed. Several are of large size (8–12 mm.) compared with those of Sections B and C. *C. rioplatense*, *C. curvispinum* var. *devium*, and *C. spinicorne* have been found in fresh water ; and many other species inhabit water of low salinity. The majority of species for which information is available are burrowers. Most are restricted in distribution in comparison with those of Sections B and C.

The type species of the genus is *C. volutator* Pallas, which is recorded from Europe (including the Sea of Azov) and the Eastern coast of North America. It bears much resemblance to *C. arenarium* from England and North France, a species here described as new ; to *C. salmonis* and *C. spinicorne* from California ; to *C. maeoticum* from the Sea of Azov ; and to *C. nobile*, *chelicorne*, *spinulosum*, *robustum*, *mucronatum*, *curvispinum*, and *monodon* from the Caspian Sea and neighbouring waters. In all these species (except *C. arenarium*) antenna II, segment 4, differs little in the two sexes, and in many of the species from the Caspian Sea and Sea of Azov this segment bears a complex armature of terminal teeth. All are at least of moderate size and many are large (4–12 mm.).

C. aculeatum, *C. annulatum*, and *C. runcicorne* from the Mediterranean, with *C. affine* from the North Sea and Arctic seas, form a natural group of rather small burrowing forms (1·5–5 mm.) of slender build, and with uropod III linear in shape. The only known specimens of *C. rotundirostre* (also from the Mediterranean) have antenna II missing ; it is not, therefore, known if this species resembles the other four in having antenna II, segment 4, unlike in the sexes. In other features it is rather similar to *C. annulatum*, though much larger.

C. triaenonyx from Ceylon and *C. rioplatense* from fresh water in the Rio de la Plata are two non-burrowing species of moderate size (3–4 mm.). The form of antenna II, segment 4, in the female distinguishes them from each other and from other groups. Probably a better knowledge of surrounding regions would reveal species related to them.

1. Corophium volutator (Pallas).

[Sars, G. O., 1894, p. 614, pl. 219 as *C. grossipes.*]

1816, *C. v.*, Leach, Encyc. Brit., p. 401. 1821, *C. longicorne*, d'Orbigny, J. Phys. Chim. d'Hist Nat. Arts, 93, pp. 194–200. 1825, "*Corophie à longues cornes*," Desmarest, Consid. Gen. Sur. Classe. Crust., p. 270. 1829, " *La Corophie longues-cornes*," Latreille, in Cuvier's Règne Animal, 4, p. 123. 1840, *C. l.*, Milne-Edwards, H., Hist. Nat. Crust., 3, pp. 66–7. 1857, *C. v.*, White, Pop. Hist. Brit. Crust. 1859, *C. l.*, Bruzelius, Svensk. Ak. Handl., N.S., 3, No. 1, p. 14. 1862, *C. l.* (part—the specimens found with *Jassa falcata* are probably some other sp.), Bate, Cat. Brit. Mus., p. 280, pl. 47, f. 4. 1863, *C. l.*, Bate, Brit. Sess. Eyed Crust., 1, p. 493. 1869, *C. l.*, Brady. Nat. Hist. Trans. Newcastle, 3, p. 120. 1873, *C. l.*, Parfitt, Trans. Devon. Ass. F. Devon, 9, p. 13. 1874, *C. l.*, and ? *C. bonelli*, Bos, Biol. Crust. Hedriopth. Ned., pp. 28, 52. 1879, *C. l.*, Hoek, Tijdschr. Ned. dierk. Ver., 4, p. 115. 1884, *C. l.*, Blanc, Nova Acta. K. Leop. Carol., 47, No. 2, pp. 82–85, f. 102–114. 1885, *C. l.*, Gadeau de Kerville, Estuaire de la Seine, 2, p. 181, Havre. 1886, *C. grossipes*, Herdman, 1st Rep. Liverp. Bay. 1888, *C. v.*, Robertson, Trans. Nat. Hist. Soc. Glasg., 2, p. 61. 1889, *C. g.*, Hoek, Tijdschr. Ned. Dierk. Ver., Ser. 2, 2, p. 230, pl. 8, f. 4–8. 1898, *C. v.*, Sowinski, Bull. Acad. Sci. St. Pétersb., Ser. 5, 8, p. 361. 1901, *C. g.*, Elliott, F. Fl. and Geol. Clyde Area, p. 342. 1901, 1903, *C. g.*, Allen and Todd, J. Mar. Biol. Assoc., 6, pp. 151, 295. 1906, *C. g.*, Scott, Proc. R. Phys. Soc. Edinb., 16, pp. 172, 379. 1906, *C. l.*, Sinel, Trans. Soc. Nat. Sci. Guernsey, p. 212. ? 1906, *C. l.*, Sinel, Outline Nat. Hist. our Shores, p. 119. 1906, *C. v.*, Norman and Scott, Crust. Devon and Cornwall, p. 95. 1906, *C. v.*, Stebbing, Das Tierreich, 21 (1), p. 686. 1907, *C. g.*, Colgan, Irish. Nat., 16, p. 181. 1907, *C. g.* (part), Gurney, Trans. Norfolk. Norw. Nat. Soc., pp. 414, 417, 421, 427 (part), 435 (part), table II (part) (see also *C. lacustre*). 1907, *C. v.* Norman, Ann. Mag. Nat. Hist., Ser. 7, 20. 1907, *C. l.*, Patterson, Wild Life on a Norfolk Estuary, p. 223. 1908, *C. v.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1911, *C. v.*, Chevreux, Mem. Soc. Zool. Fr., p. 270. 1914, *C. v.*, Stubbs, Zoologist (4), 18, p. 54. 1918, *C. g.*, Hellen, Medd. Soc. Fauna Fl. Fennica, 45, p. 136. 1920, *C. v.*, Mercier, C. R. Acad. Sci., 170, p. 410. 1922, *C. l.*, Flattely and Walton, Biology of the Seashore (London), p. 167. 1922, *C. g.*, Tesch, Fl. and Fauna Zuiderzee, p. 335, f. 7. 1923, *C. v.*, Schlienz, Arch. Hydrobiol. Plankt., 14, p. 429. 1925, *C. v.*, Chevreux and Fage, F. de France, 9, p. 364, f. 372. 1926, *C. v.*, Legueux, Bull. Soc. Linn. Normandie, Ser. 7, 8, pp. 93–4. 1926, *C. v.*, Poisson and Legueux, Bull. Soc. Zool. Fr., p. 322. 1926, *C. v.*, Ranson, C. R. Socs. Sav. Paris and Dep., p. 413, f. 1. 1927, *C. v.*, Stephensen, Vidensk. Medd. Naturh. Foren., 84, p. 139. 1929, *C. g.*, Gurney, Trans. Norfolk. Norw. Nat. Soc., 12, p. 550. 1929, *C. g.*, Percival, J. Mar. Biol. Assoc., 16, p. 81. 1929, *C. v.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1929, *C. v.*, Stephensen, Die Tierwelt der Nord- und Ostsee, 14, x. f., p. 168–9, f. 40. 1930, *C. v.*, Hart, Trans. Norfolk. Norw. Nat. Soc., 13, p. 32–3. 1930, *C. v.*, Hart, J. Mar. Biol. Assoc., 16, p. 761, f. 1–4. 1930, *Corophium*, Lambert, Proc. Zool. Soc. Lond., p. 801. 1930, *C. v.*, Trusheim, Senckenbergiana, 12, p. 254, f. 1–3. 1931, *C. v.*, Elmhirst, Proc. Roy. Soc. Edinb., 51, No. 21, p. 171. 1931, *C. v.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, p. 168. 1932, *C. v.*, Elmhirst, Glasg. Nat., x, No. 2, pp. 56–62. 1933, *C. v.*, Nicol, Dove. Mar. Lab. Rep., Ser. 3, No. 1, p. 51. 1934, *C. v.*, Serventy, Norf. Norw. Nat. Soc., Scolt Head Island, pp. 204–5. 1934, *C. v.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 23–4. 1935, *C. v.*, Nicol, J. Mar. Biol. Assoc., 20, p. 203.

DISTRIBUTION. Europe: Ireland, Scotland, England, Wales; W. Norway, the Baltic; European coasts to the Adriatic; Sea of Azov. America: Maine (in stomach of a duck); Bay of Fundy.

C. volutator is the type species of the genus, and is by far the most familiar and frequently collected. Its ecology is treated by Hart (1930).

It is frequently very abundant, forming tubes intertidally in the mud of estuarine mud-flats, salt-marsh pools, and brackish ditches. In some of the streams running into the Tamar it lives in almost fresh water associated with a number of insect larvae, e.g. *Calopteryx splendens* (Dragonfly). In many of its localities, however, the water is nearly of full salinity.

1a. COROPHIUM VOLUTATOR form ORIENTALIS Schellenberg.

1928, *C. v.* f. *o.*, Schellenberg, A., Trans. Zool. Soc. Lond., 22, p. 673.

DISTRIBUTION. Suez Canal. ? Coast of Cirenaica.

Schellenberg's specimens are in the British Museum (1928.9.5, 321–325). I am unable to distinguish from them some specimens from Cirenaica, collected by Chaworth Musters (1926.10.28, 15–21).

There are two ovigerous females in Schellenberg's material, and these differ only from *C. arenarium* n.sp., described below, in bearing no spines on antenna II, segment 5; these spines are not always present in *C. arenarium*. These females bear two spines on antenna II, segment 4, not a "spine-like tooth." Further collecting will probably show that *C. arenarium* is the same as *C. volutator* form *orientalis*.

A number of the features remarked on by Schellenberg as if they were characteristic of his specimens are also present in *C. volutator*, and in *C. arenarium* from Leigh-on-Sea and Roscoff. These are: the form of the gland-cone, the proportions of gnathopod II, the presence of toothed ridges on the telson (omitted from Sars' figures of *C. volutator*, 1894), and the form of the peduncle of urosome III. Stebbing's small-scale drawing of this segment, to which Schellenberg refers, is misleading and much inferior to that of Sars. The only one of Schellenberg's distinctions

EXPLANATION OF FIGURE 1.

Corophium arenarium n.sp. × 52.

A–C.—♂ paratype.
  A.—Antenna II.
B, C.—Antenna I, segment 1 from above and from side.
D–I.—♀ holotype.
  D.—Antenna II.
  E.—Antenna I, segment 1 from above.
  F.—Antenna I, peduncle from side.
  G.—Uropod I.
  H.—Uropod II.
  I.—Uropod III.

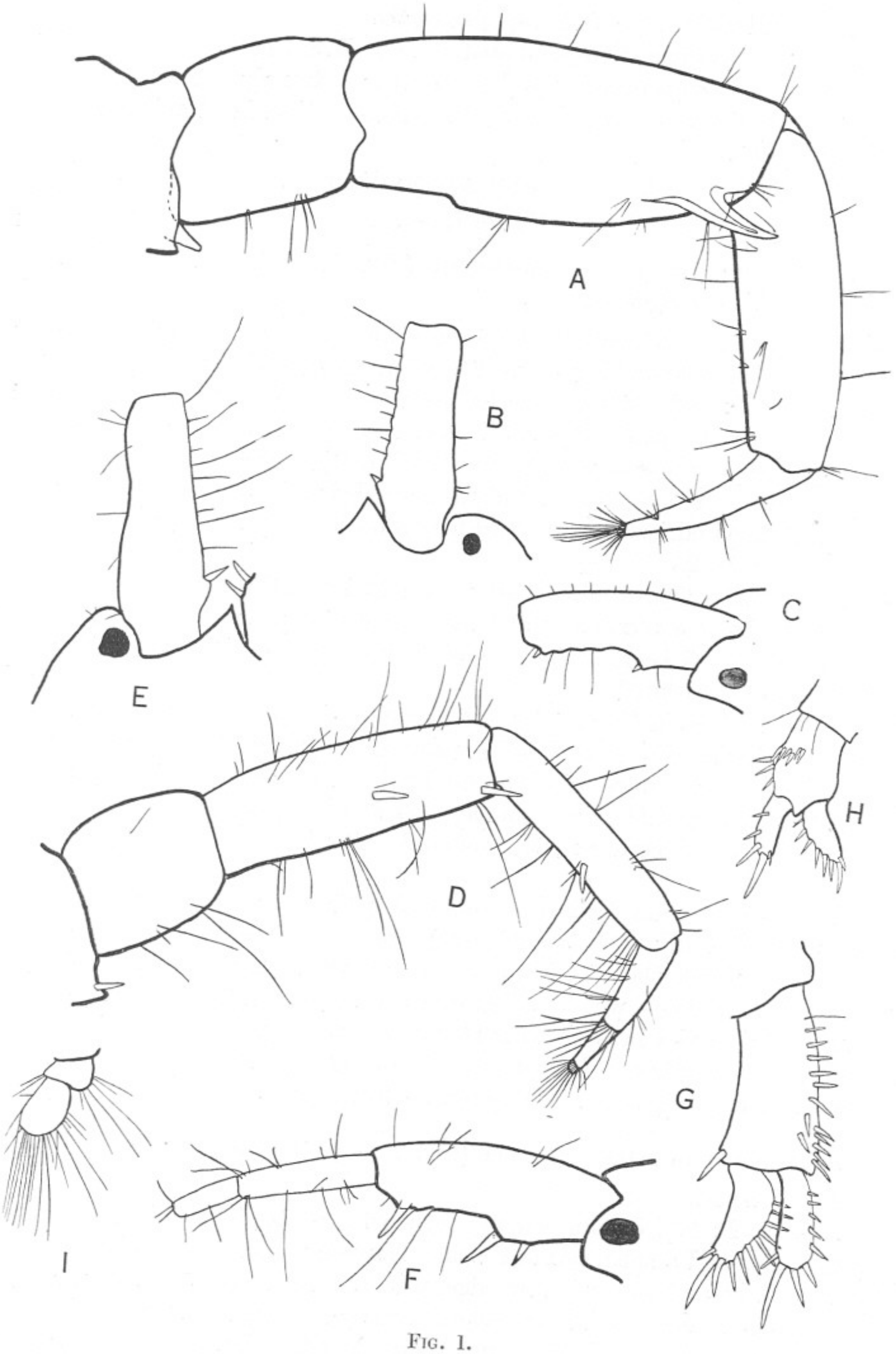

Fig. 1.

which I find valid is that in his specimens the merus of pereiopod 6 bears only simple, as distinct from ciliated, setae. I also note that in both sexes the lower edge of antenna I, segment 1 is strongly convex, so that this segment appears in side view much stouter than in *C. volutator* or *C. arenarium.*

2. COROPHIUM ARENARIUM n.sp.

Figure 1, A–I.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 1, D–I). Leigh-on-Sea, Essex, 3.viii.30, ovigerous.

Length 6 mm. *Rostrum* in the form of an equilateral triangle. *Eye-lobes* rounded, not reaching to tip of rostrum. *Eyes* rather small.

Antenna I : 30% of total length ; segment 1 $>2+3$, lower edge with 2 spines near the base—the edge between these and the terminal spine concave, bearing 3 setae ; inner edge with 1 (left) or 2 (right) spines near base, and several long setae distally ; outer edge with a few short setae : segment 2, cylindrical, with several long setae ; flagellum, 11-segmented $<$segments $1+2$.

Antenna II : 35% of total length ; segment 4, cylindrical, with 2 spines on lower edge, one terminally, and one at about $\frac{2}{3}$ of the way to the distal end ; segment 5 bears a single spine at the centre of its lower edge ; flagellum, 3-segmented.

Mouth-parts as in *C. volutator* ; all the appendages are very similar to those of that species. *Gnathopod I*, palm nearly straight, making rather less than a right angle with the hind margin of the propod ; dactyl simple. *Gnathopod II*, dactyl simple. *Pereiopods* 5–6, merus very setose, with front distal corner much produced. *Pereiopod* 7, basal segment oval.

Urosome segments distinct. *Uropod I*, peduncle with 13 spines on outer edge (distally set in a double row), 1 on inner edge ; rami with 9–10 spines, of which the distal spines are $>\frac{1}{2}$ the length of the ramus. *Uropod II*, peduncle with 3 spines on the outer edge, and 6 spines continuing this series in a slanting row across the upper surface ; inner ramus with 5 spines, outer with 8. *Uropod III*, ramus elongate-ovate, with numerous long setae. *Telson* terminally rounded.

DESCRIPTION OF MALE PARATYPE (Fig. 1, A–C). Leigh-on-Sea, 3.viii.30.

Length 4 mm.

Antenna I : 40% of total length ; segment 1 $>2+3$, lower edge with a small basal and a small terminal spine, between which the edge is crenulate and bears 3 setae ; inner edge, with a small basal spine, beyond which it is crenulate and bears several setae (in other males, presumably younger, these crenulations are not present), outer edge with scattered short setae; flagellum, 9-segmented at least, but mutilated distally (10- or 11-segmented in males from Roscoff).

Antenna II: 70% of total length; segment 4 with a single long terminal tooth; segment 5, simple, cylindrical; flagellum obscurely 3-segmented.

Other features as in female.

This specimen is plainly not fully grown. A male from Leigh-on-Sea, collected on June 28th, 1936, measured 5 mm. Antenna I was slightly over 50% of this length, and had 15 segments in the flagellum; antenna II was slightly over 100% of the body-length. The spines on the basal segment of antenna I had disappeared.

IDENTIFICATION AND RELATIONSHIPS. This species is certainly very closely related to *C. volutator*, from which all male and some female specimens can scarcely be distinguished except by their smaller size and different habitat. The notes on variation below suggest that it is only a variety of this species. Until, however, further work has been done on the varieties and growth-changes of *C. volutator* the most satisfactory course is to regard *C. arenarium* as a distinct species. M. Chevais of Paris tells me he hopes shortly to publish a paper on these two species.*

VARIATION. The material originally examined consisted of a few males and ovigerous females from Leigh-on-Sea, Essex, collected by Mr. F. J. Lambert in 1930. In the early spring of 1936 M. Chevais of Paris sent me large collections from Roscoff. Though the females were as large as the type only six were ovigerous (probably it was too early in the year). On June 28th, 1936, Mr. Lambert kindly conducted me to the type locality, where I was able to study the habits of this form and collect numerous specimens, including 28 ovigerous females of 4–6 mm. length.

The majority of these females closely resembled the type; in others antenna II resembled that of *C. volutator* female, bearing a terminal tooth on segment 4, and no spines on segments 4 and 5. The number of specimens belonging to these extreme forms, and intermediates is shown in Table I. The number of segments in the flagellum of antenna I is given as an index of age: it appears that these differences are not due to growth, but are present in specimens of uniform maturity.

In *C. volutator* a terminal spine is often present on antenna II, segment 4, in immature females, but never, in my experience, in ovigerous females. Nor, even in immature specimens, have I seen the other spines on segments 4 and 5 which are frequent in *C. arenarium*.

ECOLOGY. On June 28th, 1936, *C. arenarium* was found burrowing in firm but slightly muddy sand between Ray Gut and the channel running past Leigh Station. Its range extended from about half-tide mark to low water of neap tides. The water which covers these flats

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* In "Travaux de la Station biologique de Roscoff."

at high tide is practically of full North Sea salinity. I understand from M. Chevais that the conditions at the Plage de Madeira, Roscoff, are similar.

TABLE I.

VARIATION OF SPINES ON ANTENNA II OF *C. arenarium*.

	Number of specimens.	Average and extreme number of segments in Ant. I, flag., as an index of age.
Antenna II as in type	17	11·6 (10–13)
Antenna II, 2 spines on segment 4, 0 on segment 5.	4	11·2 (10–12)
Antenna II, Segment 4 with median spine and terminal tooth, no spine on segment 5.	2	12·0 (12)
Antenna II, segment 4 with terminal tooth, no spines on segments 4 or 5 (resembled *C. volutator* ♀).	5	12·6 (11–13)

At Leigh the number of burrows per sq. m. was in the order of 10 to 100. Above each of these was a slight pile of sand, around which radiated furrows of about $\frac{1}{4}''$ in length, made presumably by the second antennae. Internally the burrows were smooth, and coated with a shining brownish secretion. Many were in the form of a U, with vertical arms of 2″–4″ in length, the other opening being about $\frac{1}{2}''$ from the sand-pile, and not discernible from outside. The animal was generally found about $\frac{1}{2}''$ to $\frac{3}{4}''$ below the opening with the sand-pile. Some burrows appeared to be straight and to have no second opening.

Several burrows contained two specimens, always, as far as could be told on the spot, a male and a female. Two pairs which I collected separately each consisted of a large male (5 mm.) and a smaller female (4 mm.) with brood pouch lamellae well developed, but not fringed with hairs. I did not record whether large males were ever found alone. During the day's collecting adult females were 3 or 4 times as common as males of comparable size.

In other burrows I found females (never with males) with newly hatched young of about 1 mm. long. These young specimens formed burrows of a few millimetres in length, communicating with that of the parent by minute holes in the smooth lining, usually about $\frac{3}{4}''$ below the sand-pile. The only female found with young which I later examined under a microscope had brood lamellae fringed with long hairs, but was not bearing eggs.

These few observations can give no more than indications of the habits of the animal. It seems likely that in the burrows containing couples the males were waiting for the females to moult in order to impregnate them then, since these females had no hairs on the brood lamellae, and so could not carry eggs without first moulting. It appears also from the behaviour of the newly hatched young that the burrows are of some permanence. Presumably the young must become independent of the female at latest by the time of her next moult.

Thamdrup (1935) gives a more detailed description of this type of tube, made in sand between tidemarks on the Danish coast (pp. 40, 41, 47, Figs. 12–16), and compares it with the ordinary tube of *C. volutator* (p. 47, Fig. 20), which he also found, but not in the same areas. His observations on the presence of pairs of adults, and of young, in these tubes agree with mine but are more complete. He does not remark on any morphological differences between the inhabitants of these two types of tubes. I have not been able to examine his specimens, but I think that he must have found both species.

3. COROPHIUM NOBILE G. O. Sars.

[Sars, G. O., 1895, p. 292, pl. 20, 21.]

1906, *C. n.*, Stebbing, Das Tierreich, 21 (1), p. 687. 1908, *C. n.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924–5, *C. n.*, Behning, Int. Rev. Hydrobiol., 12, p. 228; 13, p. 46. 1924, *C. n.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500. 1928, *C. n.*, Behning, Binnengewasser, 5, Leben des Wolgas, p. 122.

DISTRIBUTION. Caspian Sea, Black Sea, R. Volga for 232 km. from the mouth.

4. COROPHIUM CHELICORNE G. O. Sars.

[Sars, G. O., 1895, p. 299, pl. 22.]

1906, *C. c.*, Stebbing, Das Tierreich, 21 (1), p. 687. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1924, *C. c.*, Martynov, Russk. Gidrobiol. Zh., p. 210. 1924, *C. c.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500. 1925, *C. c.*, Behning, Int. Rev. Hydrobiol., 12, p. 228, 13, p. 46. 1928, *C. c.*, Behning, Binnengewasser, 5, Leben das Wolgas, p. 122. 1929, *C. c.*, Buchalowa, Zool. Anz., 85, p. 254.

DISTRIBUTION. Caspian Sea, Black Sea, R. Volga for 232 km. from the mouth.

4a. COROPHIUM CHELICORNE G. O. Sars, praenatio FLUVIATILE Martynov.

1924, *C. c.*, prn. *f.* Martynov, Annu. Mus. Zool. Acad. St. Petersb.

DISTRIBUTION. R. Don.

5. COROPHIUM SPINULOSUM G. O. Sars.

[Sars, G. O., 1896, p. 481, pl. 12, f. 18–25.]

1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 688. 1908, *C. s.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1924, *C. s.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea.

6. COROPHIUM ROBUSTUM G. O. Sars.

[Sars, G. O., 1895, p. 304 (as *C. robustum*); pl. 23, f. 10–16 (as *C. bidentatum*)].

1896, *C. r.*, Sowinski, Mem. Soc. Nat. Kiew., 15, p. 376. 1906, *C. r.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. r.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. r.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea, Black Sea.

7. COROPHIUM MUCRONATUM G. O. Sars.

[Sars, G. O., 1895, p. 307, pl. 24, f. 1–7.]

1896, *C. m.*, Sowinsky, Mem. Soc. Kiew., 15, p. 375. 1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. m.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. m.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea.

8. COROPHIUM CURVISPINUM G. O. Sars.
8a. C. C. var. DEVIUM Wundsch.
8b. C. C. subsp. SOWINSKYI Martynov.
8c. C. C. prænatio FLUVIATILIS Martynov.

[Sars, G. O., 1895, p. 302, pl. 23, f. 1–9, and Wundsch, H. H., 1915, p. 56, pl. 1–7, f. 1–9.]

1895, *C. c.*, Sars, Bull. Acad. Sci. St. Petersb., Ser. 5, 3, p. 302, pl. 23. 1906, *C. c.*, Stebbing, Das Tierreich, 21 (1), p. 690. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1911, *C. c.*, Beling, Arb. Biol. Dnjeper. Sta. Kiev., 1, p. 114. 1912, *C. c.* v. *d.*, Dershavin, Arb. Ichth. Kasp.-Wolg. Fisch. in Astrachan, 2, Pt. 5. 1912, *C. d.*, Wundsch, Zool. Anz., 39, p. 729, f. 1–16. 1913, *C. d.*, Wundsch, Z. Fisch., 14, p. 136, f. 1. 1914, *C. c.* and *C. c.* f. *d.*, Behning, Zool. Jb., 37, p. 385, f. A–N. 1914, *Cyrtophium spongicola*, Welitchkovsky, F. d. dist. Walonyki. Gouv. Woronege. Charkof, 12. 1915, *C. c.* and *C. c.* f. *d.*, Wundsch, S. B. Ges. Naturf. Fr. Berl., No. 3, pp. 56–81, Pl. 4, 5, Text-f. 1–9. 1919, *C. c.*. Wundsch, Arch. Hydrobiol. Plankt., 12, p. 693. 1923, *C. c.* f. *d.*, Kulmatycki, Arch, Rybact. Polsk., 4. 1923, *C. c.* f. *d.*, Schlienz, Arch. Hydrobiol., 14, p. 429. 1924, *C. c.*, Behning, Int. Rev. Hydrobiol., 12, p. 228. 1924 (a), *C. c.* prn. *f.*, Martynov, Russk. Gidrobiol. Zh., 3, p. 213. 1924 (b), *C. c.* subsp. *s.* and *C. c.* subsp. *s.* prn. *d.*, Martynov, Annu. Mus. Zool. Acad. Sci. Leningrad, 25, p. 49. 1925, *C. c.* f. *d.*, Kulmatycki, Arch. Rybact. Polsk. 1925, *C. c.*, Medwedewa, Arb. Biol. Wolga. Sta., 8, pp. 105–115. 1927, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 142. 1928, *C. c.*, Behning, Russk. Gidrobiol. Zh., 7, p. 263. 1928, *C. c.*, Behning, Binnengewasser, 5, Leben des Wolgas. 1929, *C. c.*, Stephensen, Die Tierwelt der Nord und Ostsee, 14, x, f., pp. 168–70, f. 40. 1930, *C. c.* f. *d.*, Kulmatycki, Frag. Faun. Mus. Zool. Polon., 1, No. 5. 1930, *C. c.*, Wolski, Frag. Faun. Mus. Zool. Polon., 1, p. 152. 1931, *C. c.* f. *d.*, Kulmatycki, Frag. Faun. Mus. Zool. Polon., 1, No. 11. 1931, *C. c.* f. *d.*, Kulmatycki, Verh. Int. Vereinig. Limnol. Stuttgart., 14, p. 429. 1935, *C. c.* f. *d.*, Crawford, Nature, 136, p. 685.

This variable, adaptable, and widely distributed species is found in salt, brackish, and fresh water, and several varieties have been described. Martynov (1924, *b*) restricts the use of the name *curvispinum* to specimens from the Caspian Sea, and employs a new name, subsp. *sowinskyi*, for specimens from the Black Sea. The name *devium* of Wundsch he applies to specimens from the R. Don, and rivers to the west of it, and considers these to form a " praenatio " of subsp. *sowinskyi*. He did not examine specimens from the Volga. The praenatio *fluviatilis* from the R. Oskol is described by Martynov (1924, *a*) from the figures of Welitchkovsky (1914), who named his specimens *Cyrtophium spongicola* n. sp.

This complicated scheme has not been adopted by any other writer. Wundsch regards *C. curvispinum* as an inhabitant of the Caspian Sea and Black Sea, and uses the name *C. curvispinum* forma *devium* for examples from fresh water; other authors follow this plan, or use the name *C. curvispinum* for all specimens.

Good accounts of the local races of this species are given by A. Behning (1914) (Caspian, Volga delta, Volga at Saratow, Black Sea, Dnieper at Kiev) and H. H. Wundsch (1919) (Caspian, Dnieper at Kiev, Muggelsee, near Berlin).

DISTRIBUTION. Caspian Sea (type locality) and the Volga to 2,772 km. from the mouth; Black Sea and lowland courses of Danube, Dnieper and Don; rivers emptying into the Baltic and North Sea (Niemen to Elbe): also two lakes in the Caucasus. England: River Avon at Tewkesbury; Crawford (1935).

Wolski (1930) gives the most up-to-date list of localities. Wundsch (1915) states that *C. c.* var. *devium* was at that time spreading rapidly in Germany, moving through canals and rivers from East to West, usually downstream. The English specimens (13 in number, both sexes) were identified by Prof. Wundsch as *C. curvispinum* var. *devium*.

ECOLOGY. Forming tubes on weeds in sluggish waters. *C. c.* var. *devium* is restricted to the freshwater lowland courses of rivers.

9. COROPHIUM MONODON G. O. Sars.

[Sars, G. O., 1895, p. 309, pl. 24, f. 8–16.]

1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 690. 1908, *C. m.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. m.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500.

DISTRIBUTION. Caspian Sea.

10. COROPHIUM MAEOTICUM Sowinski.

[Sowinski, W., 1898, Bull. Acad. Sci. St. Petersb., v. 8, p. 362, pl. 1, f. 1–5.]

1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 740. 1924 (*a*), *C. m.*, Martynov, Russk. Gidrobiol. Zh., 3, p. 210. 1924 (*b*), *C. m.*, Martynov, Annu. Mus. Zool. de L'Acad. Sci. Rus., 25, p. 44.

DISTRIBUTION. Sea of Azov. Penetrates some way into the R. Don, and builds tubes on *Cordylophora lacustris* and *Plumatella repens*, presumably in fresh water (Martynov, 1924, *b*).

11. COROPHIUM SALMONIS Stimpson.

[Bradley, J. C., 1908, p. 235, f. 20–35, 38, 39.]

1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 692.

DISTRIBUTION. California: Puget Sound. Alaska: Karluk beach and estuary (from stomachs of sockeyes and cohos—*Oncorhynchus nerka* and *O. kisutch*).

12. Corophium spinicorne Stimpson.

[Bradley, J. C., 1908, p. 287, f. 1–19, 36, 37.]

1888, *C. s.*, Stebbing, Rep. Voy. Challenger, 29, p. 303. 1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 692. 1925, *C. s.*, Essig, Pan. Pacif. Entom., 1, p. 189.

DISTRIBUTION. San Francisco Bay (salt-marshes): San Francisco water supply—one specimen, from fresh water, recorded by Essig and identified by C. R. Shoemaker of the Washington Museum.

13. Corophium affine Bruzelius.

[Sars, G. O., 1894, p. 618, pl. 221, f. 2.]

1862, *C. a.*, Bate, Cat. Brit. Mus., p. 283. 1901, *C. a.*, Elliott, Laurie and Murdoch, F. Fl. and Geol. Clyde Area, Glasgow, p. 343. 1905, *C. a.*, Scott, Proc. Roy. Phys. Soc. Edinb., 16, pp. 172–3. 1906, *C. a.*, Stebbing, Das Tierreich, 21 (1), p. 688. 1908, *C. a.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1927, *C. a.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 139. 1929, *C. a.*, Stephensen, Die Tierwelt der Nord und Ostsee, 14, x. f., pp. 168–9, f. 40. 1929, *C. a.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1933, *C. a.*, Stephensen, Fauna Arctica, 6, p. 372.

DISTRIBUTION. Europe: Lofoten Is. to N. Friesian Is.; Skagerrak, and N. Kattegat; Scotland (Firth of Forth, Firth of Clyde, Shetland Is.); Faroe Islands. A record by Sowinsky (1898) from the Bosphorus, in Mém. Soc. Kiev, v. 15, p. 457, is based on a single specimen which was not figured, and was lost. It probably did not belong to this species.

ECOLOGY. *C. affine* burrows in the sea-bottom in depths of from 8–60 m. (Stephensen, 1929).

14. Corophium aculeatum Chevreux.

[Chevreux, E., 1908, pp. 70–72, f. 1–3.]

1911, *C. a.*, Chevreux, Mem. Soc. Zool. Fr., 23, pp. 270–1.

DISTRIBUTION. Bône (Algeria) dredged from soft grey mud in about 8 m. of water.

IDENTIFICATION. The male is distinguished by the great length of its rostrum from all other males in this section.

15. Corophium annulatum Chevreux.

[Chevreux, E., 1908, pp. 73–74, f. 4, 5.]

1911, *C. a.*, Chevreux, Mem. Soc. Zool. Fr., 23, p. 271.

DISTRIBUTION. As for *C. aculeatum*.

I have seen specimens identified by M. Chevreux. The broadly truncate rostrum and the outgrowth near the base of the inner edge of antenna I, segment 1, distinguish the adult male of this species from all others in this section.

16. Corophium runcicorne Della Valle.

[Della Valle, A., 1893, p. 13, pl. 4, f. 7 ; pl. 8, f. 1–16, 19.]

1906, *C. r.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. r.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1908, *C. r.*, Chevreux, Bull. Soc. Zool. Fr., 33, p. 69. 1911, *C. r.*, Chevreux, Mem. Soc. Zool. Fr., 23, p. 270. 1925, *C. r.*, Chevreux, Bull. Soc. Zool. Fr., 50, p. 392. 1925, *C. r.*, Chevreux and Fage, F. de France, 9, p. 365, f. 373. 1925, *C. r.*, Schellenberg, Meeresf. W. Afrikas, 3, p. 191.

DISTRIBUTION. Mediterranean Coasts: Naples, Bonifacio, Algiers, Bosphorus.

ECOLOGY. Burrows in sand in 15–80 m.

IDENTIFICATION. The male is uniquely characterized by a curved, forwardly-pointing outgrowth from the base of the outer edge of antenna I, segment 1.

17. Corophium rotundirostre Stephensen.

1915, *C. r.*, Stephensen, Rep. Danish Oceanogr. Exped. Medit., 2, D. 1, p. 52, fig. 33.

DISTRIBUTION. Mediterranean, off the coast of Sicily (37°29′ N., 12°34′ E.).

ECOLOGY. Burrowing in clay in 112 m.

IDENTIFICATION. Only two specimens were found (1 male, 1 female) and these both lacked antenna II. In other features they rather resembled *C. annulatum*, but were far bigger (4–5·5 mm., compared with 1·5–2 mm. in length).

18. Corophium triaenonyx Stebbing.

[Stebbing, T. R. R., 1904, Spol. Zeyl., v. 2, p. 25, pl. 6 A.]

1906, *C. t.*, Stebbing, Das Tierreich, 21 (1), p. 740. 1908, *C. t.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1922, *C. t.*, Chilton, Trans. Proc. N.Z. Inst., 53, pp. 232–3.

DISTRIBUTION. Ceylon: L. Negombo.

ECOLOGY. Forming tubes under bark of coconut piles, in brackish water.

IDENTIFICATION. The male is not distinctive, but the female is characterized by the spines on antenna II, segment 4, which lie in a row of six or so along the lower edge, and a row of two on the inner surface.

19. Corophium rioplatense Giambagi.

[Giambagi, D., 1926, An. Mus. Nac. Buen. Aires, v. 34, p. 137, f. 1–3.]

1934, *C. r.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 23.

DISTRIBUTION. Rio de la Plata.

ECOLOGY. Forming tubes on bivalve shells in fresh water.

IDENTIFICATION. The male is not distinctive, but the female is characterized by a laminar expansion running the length of antenna II, segment 4, and bearing four or five spines. This expansion is particularly pronounced distally.

SECTION B.

Urosome segments fused. Uropods I and II inserted in notches in the lateral margins of the urosome.

This section contains eight species, two of which (*C. sextoni* and *C. insidiosum*) are here described as new species. I have examined all except *C. californianum*. All are of small or moderate size, from 2 to 6 mm. in length. The male of *C. bonelli* and the female of *C. californianum* are unknown : in the other six species the 4th peduncular segment of antenna II is unlike in the two sexes. *C. crassicorne* burrows in muddy sand, the remainder build tubes on hydroids, etc. *C. bonelli*, *C. acherusicum*, and *C. insidiosum* are widely distributed. The section is confined to water of nearly full salinity, except for *C. insidiosum* which has frequently been found in salinities of about 15°/$_{\circ\circ}$.

KEY TO SPECIES.

1. Antenna II, segment 4 with a complex terminal tooth reaching nearly to end of segment 5 . . . *C. californianum* ♂
   Antenna II, terminal tooth on segment 4 absent, or not reaching middle of joint 5 . . . 2
2. Eye-lobes acute, eyes poorly developed ; animal burrowing in muddy sand 3
   Eye-lobes rounded or truncate, eyes well developed ; animal building tubes upon sessile objects . . . 4
3. Antenna II, segment 4 with a large and a small terminal tooth *C. crassicorne* ♂
   Antenna II, segment 4 armed with a row of 6–8 large spines . *C. crassicorne* ♀
4. Antenna II, segment 4 with a large terminal tooth and a smaller one above (♂) 5
   Antenna II, segment 4 armed only with spines (♀) . . . 9
5. Rostrum lanceolate, about $\frac{1}{3}$ as long as basal segment of antenna I . . 6
   Rostrum triangular, short . . . 7
6. Antenna I, segment 1 with blunt outgrowth on inner surface about opposite middle of rostrum . . . *C. insidiosum* ♂
   Antenna I, basal segment with no such outgrowth . . . *C. uenoi* ♂
7. Antenna II, segment 4 very setose . . . *C. tuberculatum* ♂
   Antenna II, segment 4 with few, short setæ . . . 8
8. Antenna I, flagellum 5-segmented, <2nd segment ; antenna II, segment 4 with 2–3 spines, segment 5 without processes . . . *C. sextoni* ♂
   Antenna I, flagellum 7–10-segmented, >2nd segment ; antenna II, segment 4 without spines, segment 5 with 2 processes . . *C. acherusicum* ♂
9. Antenna II, segment 5 without spines . . . *C. tuberculatum* ♀
   Antenna II, segment 5 with 1 or 2 spines . . . 10
10. Antenna II, segment 4 with spines set in a single row . . . 11
    Antenna II, segment 4 with all spines, except the terminal, set in pairs . 12
11. Antenna II, segment 4 with 4–6 spines set on a flange . . . *C. sextoni* ♀
    Antenna II, segment 4 cylindrical, with 3 spines . . . *C. uenoi* ♀
12. Antenna II, segment 4 with 3 pairs of spines, and a single terminal spine . *C. acherusicum* ♀
    Antenna II, segment 4 with 2 pairs of spines, and a single terminal spine . 13
13. Antenna I, segment 1 with the basal spines on inner and lower edges sharply recurved . . . *C. bonelli* ♀
    Antenna I, with these spines straight . . . *C. insidiosum* ♀

This key can only be satisfactorily used for adult specimens.

20. COROPHIUM CRASSICORNE Bruzelius.

Figure 4, A–F.

[Sars, G. O., 1894, p. 615, pl. 220.]

1862, *C. spinicorne* (♀) and *C. c.* (♂), Bate, Cat. Amph. Brit. Mus., pp. 281–2, pl. 47, f. 5, 6. 1888, *C. c.*, Robertson, Trans. Nat. Hist. Soc. Glasg., 2, p. 66. 1898, *C. c.*, Sowinski, Bull. Acad. Sci. St. Petersb., Ser. 5, 8, pp. 361–2. 1901, *C. crassicornis*, Elliott, F. Fl. and Geol. Clyde Area, p. 342. 1905, *C. c.*, Scott, Proc. R. Phys. Soc. Edinb., 16, p. 172. 1906, *C. c.* (part), Stebbing, Das Tierreich, 21 (1), p. 690 ("found in Norfolk in almost fresh water," refers to *C. lacustre*). ? 1907, *C. c.*, Norman, Ann. Mag. Nat. Hist., Ser. 7, 20, p. 369. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1914, *C. c.*, Walker, Spp. of Amph. and Isop. taken by Runa July–Aug., 1913. 1923, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 78, p. 73. 1925, *C. c.*, Chevreux and Fage, F. de France, 9, p. 367, f. 375. 1927, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 139. 1929, *C. c.*, Stephensen, Die Tierwelt der Nord-und Ost-See, 14, x. f., pp. 168–9, f. 40. 1929, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Amphipoda Crustacea, pp. 1–40. 1931, *C. c.*, Elmhirst, Proc. Roy. Soc. Edinb., 51, No. 21, p. 171. 1931, *C. c.* (part) Plymouth Marine Fauna, 2nd Ed. 1931, *C. c.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, No. 2, p. 168. 1932, *C. c.*, Elmhirst, Glasg. Nat., X, No. 2, pp. 56–62. 1933, *C. c.*, Stephensen, Fauna Arctica, 6, p. 372. 1934, *C. c.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 24.

Papers by Hoek (1879, 89) placed by Stebbing (1906) in the synonymy of this species refer rightly to *C. acherusicum*.

DISTRIBUTION. Europe: "from Jan Mayen (not Greenland and Iceland) along the European coasts to Bosporus"—Stephensen (1929). America: Bay of Fundy to Gardiner's Bay, Long Island; Chichagof Harbour, Athi, Alaska—Shoemaker (1934).

ECOLOGY. *C. crassicorne* burrows in muddy sand, and is usually obtained by dredging in shallow water. At Fairlie Sands, Millport, in the Clyde, it is found between tidemarks, and I have seen a collection of 1,017 specimens taken from an area of 0·25 sq. metres from this locality.

I have dredged *C. crassicorne* at Plymouth in small numbers from Cawsand Bay, from White Patch, from near the Melampus buoy, and in the mouth of the Yealm. These grounds are all in shallow water (about 5 fm.) and the first three lie in Plymouth Sound. All four grounds are chiefly composed of fine sand and silt. Soil from Cawsand Bay contains 78% of fine sand and 19% silt, according to a determination made by the method of Allen (1899—Journ. Mar. Biol. Assoc., N.S., V, pp. 378–380). For soil from Melampus these figures are 37% and 6%, the remainder being chiefly formed by large stones between which this muddy sand is packed. Flourishing beds of *Zostera marina* (a plant also associated with *C. crassicorne* in the Clyde—Robertson, 1888) once existed at Cawsand, White Patch, and the mouth of the Yealm; in 1934–5 these had become much reduced.

Most of the records in Plymouth Marine Fauna (1931) probably refer to *C. bonelli*, as the localities given are suitable for this species and not *C. crassicorne*. Further I have found in the Laboratory at Plymouth jars of *C. bonelli* labelled *C. crassicorne*. The records of Percival (1929) must refer to *C. acherusicum* (p. 617), which I found abundant on the Neille Point buoys.

BREEDING AND SEX-RATIO. Ovigerous females were present in the collections made in April and July, but not in those made in October (26 specimens), November (9), or December (4). Of 67 specimens whose sex was determined 19·5% were males. Of 200 specimens examined from collections sent me from Millport, and collected in August, 1931, 49% were males.

IDENTIFICATION. The small eyes and sharp eyelobes are features not found in other species of this section. In the female the form of antenna II, segment 4, is distinctive at all ages ; it is almost crescent-shaped in section, with the concavity facing inwards and upwards.

GROWTH-CHANGES. Juvenile females have fewer spines on the antennae than adults. In juvenile males the rostrum is less pronounced, and the spines on antenna I, which are short and blunt in the adult, are long and sharp : antenna II, segment 4, is relatively stouter than in the adult, and bears a few small spines on the ventral surface basally, which later disappear ; there are no outgrowths on antenna II, segment 5. These changes are illustrated in Fig. 4, A–F. The larger specimen was 2·9 mm. long from rostrum to telson, and antennæ I and II were 53% and 70% of this length. For the other specimen these figures were 2·6 mm., 39% and 45%.

21. COROPHIUM BONELLI G. O. Sars.

Figure 2, H–O.

HISTORICAL. In 1830 Milne-Edwards gave the name *C. bonelli* to an Amphipod from an unknown locality, but his description is not precise enough for assured identification, and none of his specimens survive. In 1894 G. O. Sars described and figured female specimens of a Corophium collected in south-west Norway, which he called by Milne-Edwards' name. Neither of these authors makes mention of a male.

Though females continued to be found in great numbers, the first male to be assigned to this species was one collected in Alaska with three females, and described, but not figured, by Shoemaker (1920). In 1924 Stephensen figured one of a number of males from the east coast of Denmark, making mention in his description of the small differences between these males and the specimen examined by Shoemaker.

C. pseudacherusicum was named by Schellenberg (1931) from a few females from Tierra del Fuego. He noted a few slight differences between his specimens and the figures of Sars.

EXAMINATION OF SPECIMENS. Thanks to the kindness of Dr. Huus of Oslo, Dr. Stephensen of Denmark, Prof. Schellenberg of Berlin, Dr. Panning of Hamburg, Prof. Fage of Paris, Prof. Brian of Genoa, Prof.

Dohrn of Naples, and Dr. Shoemaker of Washington, I have been able to examine specimens from many parts of the world, as noted in Appendix I (a) and (b).

I found that :—

(1) The females could be separated into two forms, never both present in the same collection. The small but constant differences between them are tabulated in Table II.

(2) Of these forms none was ever found with males in the same collection, even when present in thousands (except occasionally with males of *C. sextoni*, *C. acherusicum*, or *C. acutum*). A list of specimens of this form is given in Appendix I (a).

(3) To this form belonged all the females identified with *C. bonelli* by G. O. Sars. They are 164 in number, from four localities in south-west Norway, and are now at the Oslo Museum.

Sars did not set apart a type, and therefore I have considered all these specimens as co-types of the species. They resemble his figures and description so closely that I have no doubt, in view of the evidence of locality, that figures, description and specimens belong all to a single species, which I shall call *C. bonelli* G. O. Sars, to avoid confusion with Stephensen's use of the name *C. bonelli* (M.-Edw. ?) G. O. Sars. There are, however, some slight differences, in features important for diagnosis, between Sars' figures and his specimens, and I have therefore redescribed *C. bonelli* on page 613.

(4) To this form also belong the 15 specimens from Tierra del Fuego, on which was based Schellenberg's description of *C. pseudacherusicum*. Schellenberg used Sars' figures and description for comparison with his specimens. From these he drew up the list of differences between his species and *C. bonelli*, with the exception of the difference in shape of the basal joint of the mandibular palp, for the observation of which he compared his specimens with some from the Kieler Bucht, Germany. These I have seen, and found to belong to the other form, which I have described on page 615 as *C. insidiosum* n.sp.

The specimens from Tierra del Fuego are indistinguishable from those of Sars. I therefore regard *C. pseudacherusicum* as a synonym of *C. bonelli* G. O. Sars.

(5) The other form of female was almost always found with males, which usually made up 20–40% of the whole number in a collection (see Appendix I (b)). Adult males were not distinguishable from that figured by Stephensen (1924) as *C. bonelli* (M.-Edw. ?) G. O. Sars, and all certainly belonged to one species, as the whole range of variation was sometimes represented in single large collections.

TABLE II.

	C. bonelli G. O. Sars (ovigerous ♀♀). Norway (G. O. Sars det.), England, France, Denmark, East Coast of N. America.	*C. insidiosum* n. sp. (ovigerous ♀♀). Plymouth, Venice, Denmark, Germany.
Antenna I, joint 1, spines on lower edge	4, rarely 5, never 3; distal 3 straight, basal 1 or 2 sharply recurved.	3 or 4, rarely 5; all straight.
Antenna I, joint 1, spines on inner edge	1–3; basal 1 sharply recurved.	1–3; basal 1 not, or slightly, recurved.
Antenna II, joint 5, spines on lower edge	2, less frequently 1.	1; in 2 out of 400 specimens, 2.
Mandibular palp, basal joint	Distinctly prolonged.	Not distinctly prolonged.
*Gnathopod I, palm	Very oblique; spines stout, those near the hinder edge far the longest.	Nearly straight: spines slender, of uniform size.
Gnathopod II, accessory teeth on dactyl	2, rarely 1.	3, rarely 2 or 4.
*Uropod I, spines on inner edge of peduncle	3 or 4, well spaced.	1, terminal.

* These distinctions are based on an investigation of *C. bonelli* from Norway and Plymouth and *C. insidiosum* from Plymouth and the Lake of Venice only.

The specimens described by Shoemaker (1920) do not fit into this scheme. I have not seen them, but Dr. Shoemaker has sent me excellent tracings of the most important features. Both sexes differ from *C. insidiosum* in having the basal joint of the mandibular palp much prolonged, and the dactyl of gnathopod II with only one accessory tooth. The other features of the male considered by Shoemaker (1934a) to be

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EXPLANATION OF FIGURE 2.

A–E.—*Corophium insidiosum* n.sp.,♀ holotype × 52.
  A.—Antenna I, segment 1 from side.
  B.—Antenna I, segment 1 from above.
  C.—Antenna II.
  D.—Gnathopod I, propod.
  E.—Gnathopod II, dactyl.
F.—♀ paratype, Plymouth, mandibular palp × 250.
G.—♂, L. of Venice, mandibular palp × 250.
H–O.—*C. bonelli* G. O. Sars.
H–J.—Ovigerous ♀, Millbay, Plymouth, 22.vii.07.
  H.—Mandibular palp × 250.
  I.—Antenna II × 38.
  J.—Antenna I, segment 1 and 2, from above, × 38.
K–M.—Ovigerous ♀, Tierra del Fuego, 30.x.1892, Hamburg Museum 10752 (co-type of *C. pseudacherusicum*), × 38.
  K.—Antenna II.
  L.—Antenna I, peduncle, from side.
  M.—Antenna I, from above.
N, O.—Ovigerous ♀, Norway (determined by Sars as *C. bonelli*), × 38.
  N.—Antenna I, from side.
  O.—Antenna II.
P.—*C. acherusicum* da Costa, ♀, Neille Pt., Plymouth, 29.1.35, antenna II (setae omitted) with an exceptionally large number of spines, × 38.

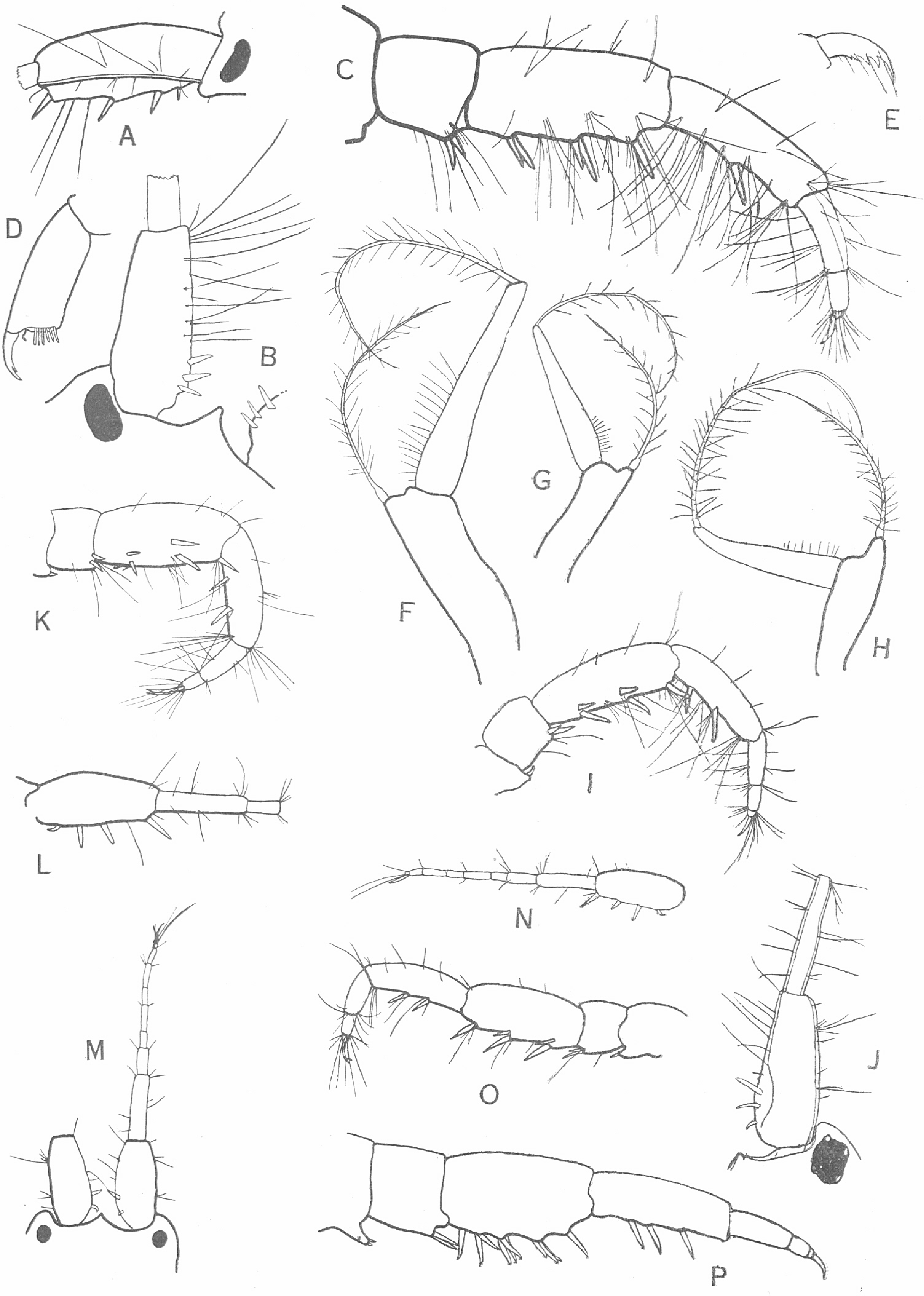

FIG. 2.

distinctive are also found in juvenile males of *C. insidiosum*, and the antennae of the female resemble those of *C. insidiosum* in the number and arrangement of spines. Until more material is obtained the precise status of these specimens must be uncertain. They certainly closely resemble *C. insidiosum* in both sexes, but appear to be distinct.

REFERENCES. Owing to the confusion between *C. bonelli* and *C. insidiosum* it is frequently impossible to tell to which of these species a paper refers.

References presumably applicable to C. bonelli only.

? 1830, *C. b.*, Milne Edwards, Ann. Sci. Nat., 20, p. 385. ? 1840, *C. b.*, Milne Edwards, Hist. Nat. Crust., 3, p. 67. ? 1862, *C. b.*, Bate, Cat. Amph. Brit. Mus., p. 282. ? 1873, *C. b.*, Parfitt, Trans. Dev. Ass. Sci. and Lit., 6, p. 249. 1879, *C. crassicorne* var., Hoek, Tijdschr. Ned. Dierk. Ver. IV, p. 118, Pl. 8, f. 9, 10. 1882, *C. b.*, Sars, Vid. Selsk. Forh. Christ., No. 18, p. 112. 1889, *C. c.*, Walker, 3rd Rep. Higher Crust., L. M. B. C. distr. Liverpool, p. 211. ? 1893, *C. b.*, Chevreux and Bouvier, Ann. Sci. Nat., Ser. 7, 15, p. 140. 1893, *C. b.*, Della Valle, F. Fl. Neapel, 20, p. 368. 1894, *C. b.*, Sars, Crust. Norway, 1, p. 616, pl. 221, f. 1. ? 1897, *C. b.*, Sowinski, Mém. Soc. Kiew, 15, p. 456. ? 1900, *C. b.*, Chevreux, E., Rés. Comp. Sci. Monaco, 16, p. 109. ? 1901, *C. b.*, Elliott, Laurie and Murdoch, F. Fl. Geol. Clyde Area, Glasgow, p. 343. 1905, *C. b.*, Scott, Proc. R. Phys. Soc. Edinb., 16, p. 172. 1906, *C. b.*, Norman and Scott, Crust. Devon and Cornwall, p. 95. 1906, *C. b.*, Stebbing, Das Tierreich, 21 (1), p. 691. ? 1907, *C. b.*, Norman, Ann. Mag. Nat. Hist., Ser. 7, 20, p. 369. 1910, *C. b.*, Chevreux, Mém. Soc. Zool. Fr., 23, p. 271. 1914, *C. b.*, Walker, Ann. Mag. Nat. Hist., Ser. 8, 13, p. 558. 1929, *C. b.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1930, *C. b.*, Barnard, Brit. Ant. Terra Nova Exp., Nat. Hist. Crust., XI, p. 393. 1931, *C. b.*, and *C. crassicorne* (part), Plymouth Marine Fauna, p. 197. 1931, *C. pseudacherusicum*, Schellenberg, Furth. Zool. Res. Swed. Antarct. Exp. 1901–3, No. 6, p. 258, f. 1932, *C. cylindricum*, Barnard, Disc. Rep. V, p. 244. 1933, *C. b.*, Stephensen, Fauna Arctica, 6, p. 372.

References to C. bonelli and C. insidiosum, with confusion between the species.

1924, *C. b.*, Stephensen, Vidensk. Medd. Naturh. Forening, Copenhagen, 78, pp. 73–78, f. 3. 1924, *C. b.*, Ussing, Tom. cit., pp. 69–72. 1925, *C. b.*, Chevreux and Fage, F. France, 9, Amph., p. 369, f. 377. 1927, Stephensen, Tierwelt Nord und Ostsee, 14, x. f., pp. 168–9. 1931, *C. b.* and *C. pseudacherusicum*, Schellenberg, Furth. Zool. Res. Swed. Antarct. Exp., 6, p. 258. 1931, *C. b.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, pp. 168–70. 1932, *C. b.*, Brian, Boll. Mus. Zool. Anat. Comp. Genova, 12, No. 52. 1934, *C. pseudacherusicum*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 26.

Table III shows my interpretation of the meaning given to the names *C. bonelli* and *C. pseudacherusicum* in certain recent papers.

TABLE III.

Paper.	*C. bonelli* refers to :—	*C. pseudacherusicum* refers to :—
Shoemaker (1920) .	Sars' (1894) figures of *C. b.*, ♀ ; 1♂, 3♀♀ from Alaska (sp. indet.).	—
Stephensen (1924) .	Sars' figures of *C. b.*, ♀ ; ♂♂ and ♀♀ of *C. i.* from Denmark.	—
Schellenberg (1931) .	Sars' figures of *C. b.*, ♀ ; ♀♀ of *C. i.* from Germany.	*C. b.* from Tierra del Fuego.
Brian (1932) . .	♂♂ and ♀♀ of *C. i.* from L. of Venice ; Sars' observations on sex-ratio of *C. b.*	—
Shoemaker (1934). .	As Shoemaker (1920)	♂♂ of *C. i.* from Denmark ; ♀♀ of *C. b.* from Tierra del Fuego and N. America.

Brian's statement that *C. bonelli* is an example of "geographic parthenogenesis" is due to a confusion of this species with *C. insidiosum*. So is the observation by Shoemaker (1934a) that the form of the mandibular palp is different in the two sexes of *C. pseudacherusicum*.

REDESCRIPTION OF FEMALE OF *C. bonelli* G. O. SARS (Fig. 2, H–O), from specimens from Norway named by G. O. Sars.

Length about 4 mm. in ovigerous females. *Rostrum* short, triangular. *Eyes* black, well-developed. *Eyelobes* rounded.

Antenna I: segment $1 < 2+3$, lower edge with three large, straight, equally spaced spines distally and one or two shorter, sharply recurved spines proximally; inner edge with one to three spines, proximal one short and sharply recurved; flagellum, 8-segmented in fully grown specimens.

Antenna II: segment 4 with a basal and a median pair of spines and a terminal single spine, on the lower edge; segment 5 frequently with two spines of which the proximal is sometimes as large as the distal, sometimes smaller or absent even in the largest specimens—the distal spine is always present.

Mandibular palp, basal segment much prolonged beyond base of second segment. *Gnathopod I*, palm very oblique, with a row of stout spines of which those near the hinder edge of propod are far the largest; dactyl with one small accessory tooth. *Gnathopod II*, dactyl with two, or more rarely one, accessory tooth.

Urosome segments fused; sides of urosome hollowed out at the insertion of uropods 1 and 2.

The male is unknown. Since the female has been collected, often in thousands, from many parts of the world, it is very probable that reproduction in this species is normally parthenogenetic. This has never, however, been tested by rearing experiments. Parthenogenesis is known in *Talitrus alluaudi* Chevreux, and there is some evidence for it in *Haustorius arenarius* (Slabber), but it is certainly unusual in the Amphipoda. There is no reason to suppose that it occurs in any other known species of Corophium.

DISTRIBUTION. See Appendix I (a).

OCCURRENCE AT PLYMOUTH. In the Laboratory at Plymouth are several collections made between 1889 and 1911, chiefly from Millbay Channel, but also from Asia Shoal, West Channel, and between Drake's Island and Mount Edgecumbe. Each of these contains several hundreds of specimens.

In 1934 from several dredgings on these grounds I obtained only five specimens, four from New Grounds and one from near Drake's Island. The place of *C. bonelli* was taken by *C. sextoni* n.sp., a species not present in the earlier dredgings.

C. bonelli builds tubes of mud on hydroids, etc., in water usually of full salinity. Breeding females are present in collections made at Plymouth in April, July, August, and October.

IDENTIFICATION. This species has often been confused with *C. crassicorne* and *C. acherusicum*. *C. crassicorne* is easily distinguished by its burrowing habits, the pointed eyelobe and by antenna II, segment 4, which in the female is expanded along its lower edge into a broad flange on which about eight spines are set in a row. Many of the distinctions between *C. acherusicum* and *C. bonelli* tabulated by Chevreux (1911) and Stephensen (1924) do not hold good for specimens of *C. bonelli* as redescribed here. The species are, however, distinct, and ovigerous females may be identified from Table IV. Younger specimens of either species have fewer spines.

TABLE IV.

	C. bonelli ♀.	*C. acherusicum* ♀.
Antenna I	>antenna II, peduncle.	<antenna II, peduncle.
Antenna I, segment 1	<2+3.	>2+3.
Antenna I, segment 1, inner and lower edges	Basal spines sharply recurved.	All spines straight.
Antenna II, segment 4	5 spines, arranged 2, 2, 1.	7 spines, arranged 2, 2, 2, 1.
Pereiopod 7	Basal joint<propod.	Basal joint>propod.

VARIATION AND GROWTH CHANGES. As indicated in the redescription of this species on page 613 the number of spines on the antennal segments is not constant even in adults : in juveniles several spines are usually absent, especially the proximal spines of antenna I, and antenna II, segment 4. In very small specimens (*ca.* 1·5 mm.) the proximal spine of antenna II, segment 5, is missing, and it frequently does not develop at all. Adult specimens are common in which the proximal spine is smaller than the distal, or in which it is absent from one antenna and present on its fellow. The percentage of ovigerous females in which it was found varied in collections from different localities, but not in correlation with latitude. The highest figure was 77 (from Plymouth), and the lowest 20 (from Trondhjem Fjord, Norway) ; however, figures greater than 70 were obtained from some Norwegian collections. Occasional specimens bear an additional spine beside the median pair on antenna II, segment 5, but the number is far less variable than in *C. acherusicum*. The number of accessory teeth on the dactyl of gnathopod II is usually two in ovigerous females and one in small specimens.

22. COROPHIUM INSIDIOSUM n.sp.

Figure 2, A–G.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 2, A–E). West Wharf, Millbay, Plymouth, 8.v.35, ovigerous.

Length 4·5 mm. *Rostrum* pointed, short. *Eyelobes* rounded, elongate. *Eyes* black, well developed.

Antenna I: about 30% of total length; segment 1 $<2+3$; lower edge with four straight spines, proximal one small, and a few long setae; inner edge with three straight spines near base, several long setae distally; outer edge with scattered short setae; segment 2 cylindrical, with several tufts of long setae; flagellum 7-segmented.

Antenna II: scarcely longer than antenna I; segment 4 with 5 spines on lower edge—a basal and a median pair and a single terminal spine—besides many long setae; segment 5 with one median spine, and many long setae; flagellum 3-segmented.

Mouth-parts and limbs in general like those of *C. bonelli*. *Mandible*, palp with basal segment not prolonged. *Gnathopod I*, palm almost square, with six slender spines of uniform size on each face; dactyl with a minute accessory tooth. *Gnathopod II*, right dactyl (figured) with four accessory teeth; left dactyl with the more usual number, three. *Pereiopod* 7, basal segment oval=propod in length.

Urosome as in *C. bonelli*. *Uropod I*, peduncle with one terminal spine on inner edge. *Telson* trapezoidal, with a wide terminal furrow, bordered with hooked spines.

DESCRIPTION OF MALE PARATYPE. West Wharf, Millbay, Plymouth, 8.v.35.

Length 3·5 mm. *Rostrum* spear-shaped, reaching nearly half-way along antenna I, segment 1; depressed at tip.

Antenna I: about 50% total length; segment 1, lower edge with a keel bearing one small terminal spine, and a few long setae; inner edge with only a few short setae—between these edges on the inner face a symmetrical blunt process opposite a point between the middle and tip of rostrum; outer edge with scattered short setae: segment 2=segment 1, narrowed at base, with a keel below bearing 16 long setae, rounded above with scattered setae of medium length: segment 3 $<\frac{1}{2}$ segment 2; flagellum 10-segmented, $<$segments $1+2$.

Antenna II: about 60% total length; segment 4, very stout, with a single large terminal ventral tooth, above which is a smaller single tooth; with only a few setae: segment 5, cylindrical, lower edge with a uniform series of eight tufts of long setae: flagellum, 3-segmented, basal segment with a row of five tufts of long setae.

Other features as in female.

I have not figured the male, since all characters of importance are excellently drawn by Stephensen (1924).

DISTRIBUTION. See Appendix I (b).

ECOLOGY. *C. insidiosum* like *C. bonelli* builds tubes of mud on weeds or hydroids; it appears, however, to frequent as a rule water that is less saline. The most nearly marine conditions under which I have found it at Plymouth are at Tinside, and at Millbay Pontoon and West Wharf. These are subject to a considerable diminution in salinity when the Tamar is running full. Millbay Inner Basin is an enclosed brackish pool. The buoys at Bull Point and Neille Point lie some miles up the Tamar Estuary. Chelson Meadow is reclaimed land: the ditches are brackish, filled by land drainage and occasionally by salt water coming over the sea-wall. Here *Corophium insidiosum* was found in numbers, building tubes on *Ruppia maritima* in the most saline ditches, that is to say those nearest the sluice which opens into the Plym Estuary. In the same collections *Sphaeroma hookeri* (Isopoda) was abundant, and a few *Melita palmata* and *Leptocheirus pilosus* (Amphipoda) were present. A hundred yards from the sluice the numbers of Corophium were much reduced, and it was associated with large numbers of *Sphaeroma hookeri* and *Gammarus chevreuxi*.

Ussing (1924) observes that the optimum salinity for *C. bonelli* in the Mariagerfjord is 13–18°/₀₀. I have seen his specimens, and found them to be *C. insidiosum*. The Italian and German localities also appear to be estuarine rather than marine.

IDENTIFICATION. The very long rostrum of the male is not found elsewhere in this section except in *C. uenoi*, and in Shoemaker's undetermined specimens from Alaska. The outgrowth on the inner surface of antenna I, segment 1, is absolutely distinctive.

The arrangement of spines on the antennae of ovigerous females is sufficient for identification.

23. COROPHIUM UENOI Stephensen.

1932, *C. u.*, Stephensen, Annot. Zool. Jap., 13, p. 494–8, f. 3, 4.

DISTRIBUTION. Japan, in a tidal pool, presumably a tube-builder.

IDENTIFICATION. This species is very close to *C. bonelli* and *C. insidiosum*, from both of which it is distinguished by the female having only three spines, set in a longitudinal row, on antenna II, segment 4. In the type specimen brood-lamellae were developed, and presumably this arrangement of spines is typical of adult females. I have seen the male and cannot distinguish it from juvenile males of *C. insidiosum*; from adult males it is distinguished by the absence of an outgrowth on the inner surface of antenna I, segment 1.

24. COROPHIUM ACHERUSICUM Costa.

Figure 2, P.

[Della Valle, A., 1893, p. 364, pl. 1, f. 11 and pl. 8, f. 17, 18, 20–41.]

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NOTES ON LITERATURE. Barnard (1916) records *C. acherusicum* from S. Africa. He describes antenna II, segment 5, in the male as bearing "in small specimens up to 2·5 mm., a well-marked tooth on lower margin about ⅓ from base or sometimes nearly in the middle, in other and larger specimens without a tooth and much more sparsely setose." The smaller specimens are *C. acutum*, the larger *C. acherusicum*, and both these species are represented in collections from Durban sent by Barnard to the British Museum.

The figure given by Paulmier (1905) must be referred to *C. tuberculatum* Shoemaker, though the urosome segments have been drawn separate in error. Through the kindness of Dr. Stoner of the New York Museum I have been able to examine some of Paulmier's specimens; both *C. acherusicum* and *C. tuberculatum* were present in tubes labelled *C. cylindricum* by Paulmier.

DISTRIBUTION. Europe: S. England (Plymouth, Thames Estuary*); Coasts of France and Holland; Mediterranean. Africa: N. Coast from Suez Canal to Senegal, Durban Bay,* Dar-es-Salaam. America: Baffin's Bay to Brazil, ? Falkland Is., Cuba,* Alaska.* Asia: Hong Kong.* New Zealand: Lyttelton Harbour.*

ECOLOGY. *C. acherusicum* forms tubes on weed and hydroids in shallow water, usually in harbours, and especially on floating objects such as buoys,

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* Specimens examined in British Museum.

rafts, and pontoons. The Sheerness specimens are from fouling on a ship's bottom.

OCCURRENCE AT PLYMOUTH. Buoys and rafts: Tinside bathing raft; buoys at Neille Point, Saltash, Barn Pool; Millbay Pontoon. Intertidally in small numbers at Neille Point Mussel Bed. It was most abundant on the Neille Point buoy where thousands were obtained from a breffit of weed, and least common on Millbay Pontoon where it was outnumbered by *C. acutum*, *C. sextoni*, and *C. insidiosum*.

IDENTIFICATION. Normal ovigerous females bear seven spines on antenna II, segment 4, arranged 2, 2, 2, 1. Occasional specimens bear up to four additional spines on this segment either alongside an original pair of spines, or between two pairs. I have seen such specimens from Plymouth, Sheerness, the Lake of Venice, and Alaska. In some, antenna II, segment 5, bore three spines in a row. (See Fig. 2, P.)

Adult males may be known by the following combination of characters: rostrum short; antennae scarcely setose; antenna II, segment 5 with a small process near the base and a large blunt process terminally.

GROWTH-CHANGES. In the female the number of antennal spines, and of accessory teeth on the dactyl of gnathopod II, increase with age.

In the male there is a progressive deterioration of spines in number and size, and an appearance of processes on antenna II, segment 5, as shown in Table V.

TABLE V. (*C. acherusicum*, male).

	Juvenile 2–2·5 mm.	Adult 3–4 mm.
Antenna I, segment 1, spines on lower edge	3–4	1–4
Antenna II, segment 4, spines near base	1–2	0
Antenna II, segment 5, spines	0–2	0
Antenna II, segment 5, processes	0	small basal and large terminal.
Gnathopod II, dactyl, accessory teeth	1–2	2–3
Pereiopod 7, carpus inner edge	nearly straight	strongly convex

BREEDING AND SEX-RATIO. Most of the females found in August (1935) and September (1934) were ovigerous; in January (1935) adult

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EXPLANATION OF FIGURE 3.

Corophium sextoni n.sp.

A–F.—♀ holotype.
A.—Antenna II, ×50.
B.—Antenna I, segment 1 from inner side, ×50 (setae not drawn on inner or outer edge).
C.—Head from above, ×50.
D.—Mandibular palp, ×100.
E.—Gnathopod II, dactyl, ×50.
F.—Urosome, ×50.
G. H.—♂ paratype, ×50.
G.—Antenna II.
H.—Uropods I and II.

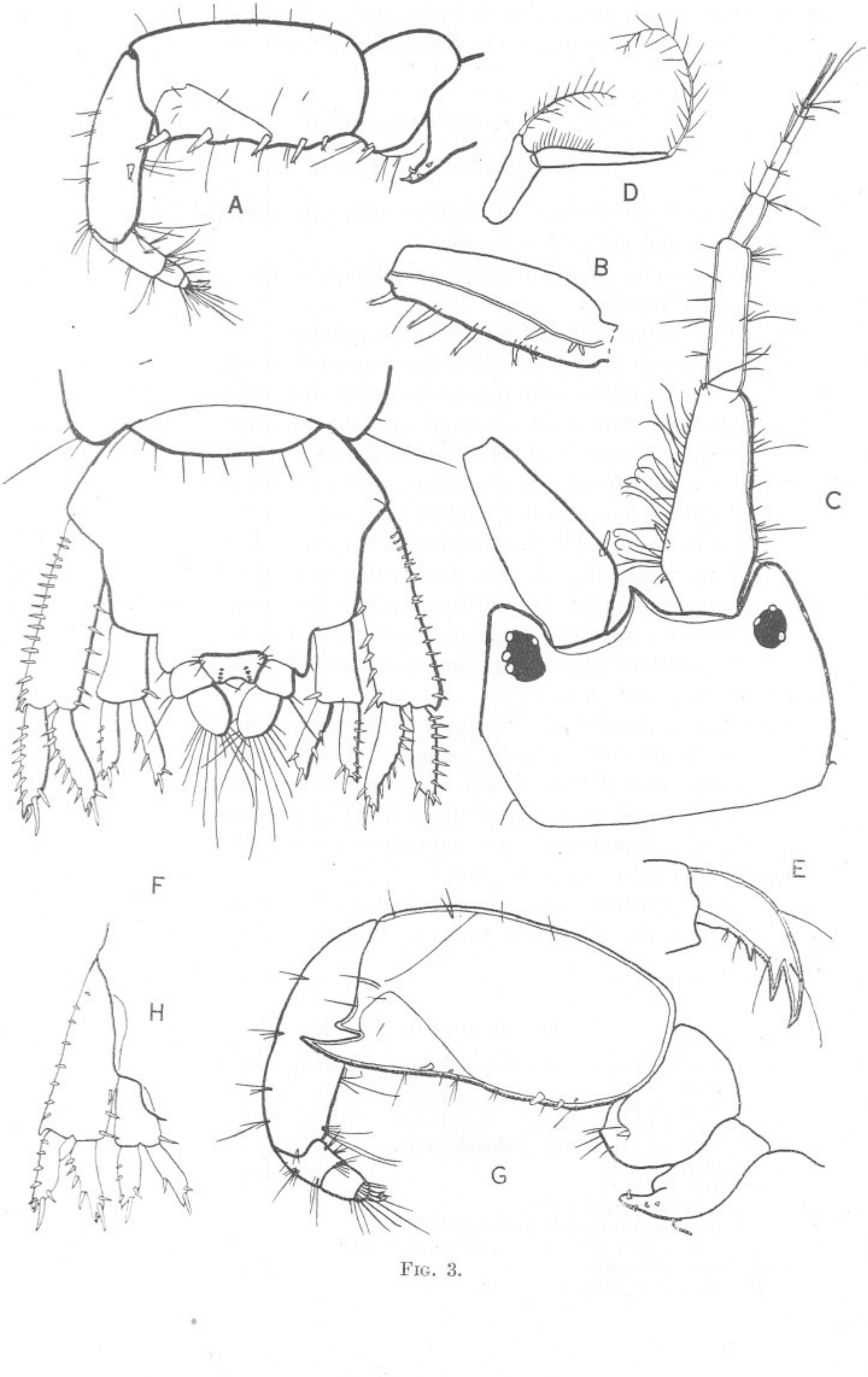

FIG. 3.

females were much outnumbered by juveniles. Both sexes were present in all collections I examined, the female being rather the commoner.

25. Corophium sextoni n.sp.

Figures 3, A–H; 4, G–H.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 3, A–F). Winter Shoal, Plymouth Sound, 18.x.34, ovigerous.

Length 4·5 mm. *Rostrum* short, triangular, acute. *Eye* large black. *Eyelobes* long, rounded.

Antenna I: about 30% of total length; segment $1 > 2+3$; lower edge convex, with five spines of which the proximal one is very short and recurved, the distal ones progressively longer and straighter, two setae; inner edge with two short recurved spines near base, beyond these a straight longer spine and 20–30 rather long setae; outer edge with several short setae, and tufts of longer ones at $\frac{2}{5}$ and $\frac{3}{4}$; segment 2 with scattered setae; flagellum 5-segmented, shorter than segment 2.

Antenna II: about 35% of total length; segment 4 about twice as long as broad, pear-shaped in cross section with the lower edge produced into a flange running lengthwise and bearing five straight spines, increasing in length distally; segment 5 rather stout, with a short straight median spine on the lower edge; flagellum 3-segmented; antenna as a whole with few setae, and those short.

Mouth-parts, *gnathopods*, and *pereiopods* resembling in general those of *C. bonelli*. *Mandibular palp*, segment 1 slightly produced terminally. *Gnathopod I*, dactyl with small accessory tooth; propod with palm convex, oblique, set with several spines of which the posterior are largest, *Gnathopod II*, dactyl, with two subsidiary teeth. *Pereiopods* 5 *and* 6. spines on carpus short, in two rows.

Urosome segments fused, lateral border emarginate at insertion of uropods I and II. *Uropod I*, peduncle with five to six spines on inner

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EXPLANATION OF FIGURE 4.

A–F.—*Corophium crassicorne* Bruzelius from Fairlee Sands, Millport, ×50.
A–C.—Adult ♂.
  A.—Antenna II.
  B.—Antenna I from above.
  C.—Antenna I from side (peduncle only).
D–F.—Juvenile ♂.
  D.—Antenna II.
  E.—Antenna I from above.
  F.—Antenna I from side (peduncle only).
G, H.—*Corophium sextoni* n.sp., ♂ paratype, ×50.
  G.—Head from side.
  H.—Head from above.

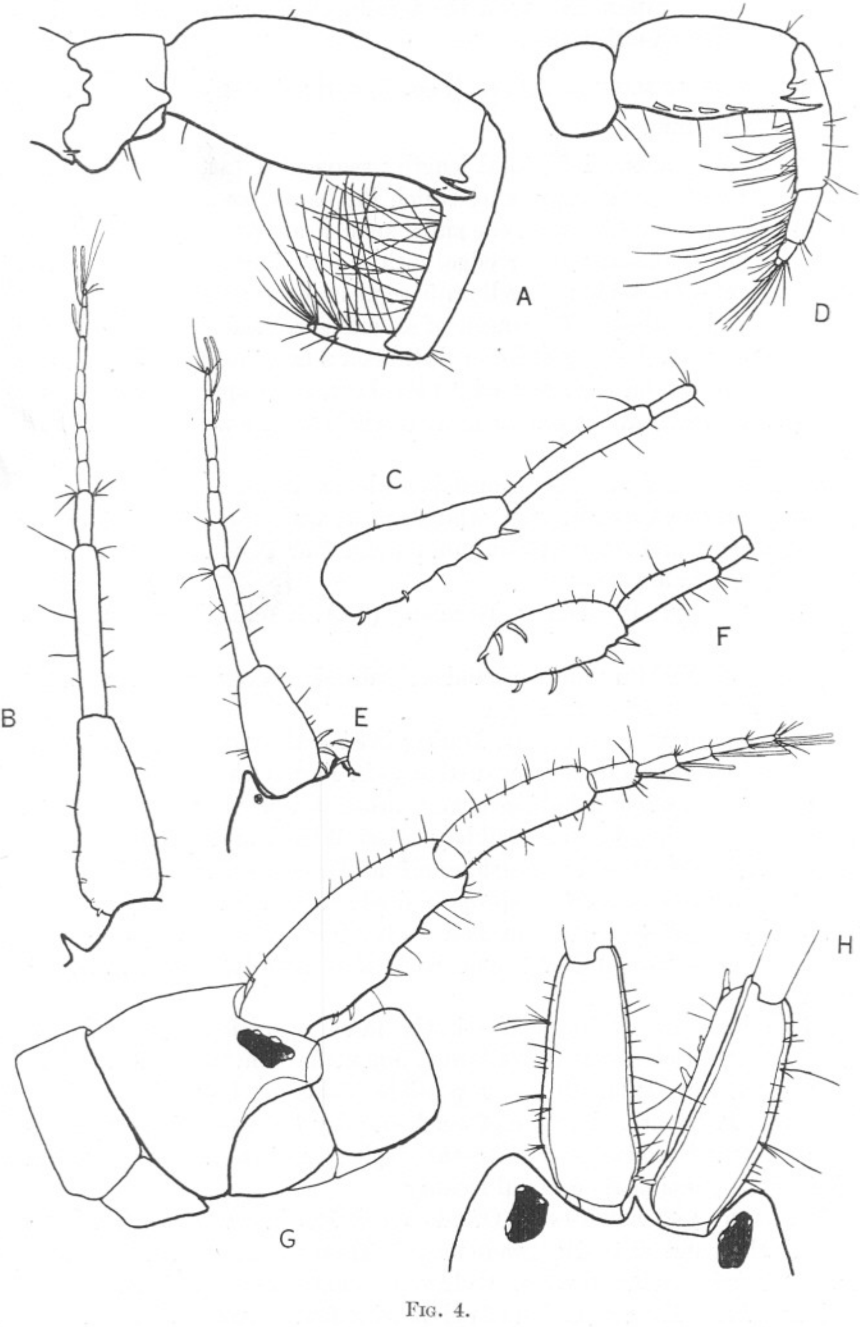

FIG. 4.

edge. *Telson* trapezoidal, with the terminal emargination bordered by four denticles on either side.

DESCRIPTION OF MALE PARATYPE (Figs. 3, G–H; 4, G–H).

Length 4·0 mm.

Antenna I: about 40% total length; segment 1 $>2+3$; lower edge convex with five small spines, of which the basal two are recurved, and a few setae; inner edge with one small spine near base, and several setae beyond, mostly short; outer edge with a few short setae; segment 2 with a few short setae; flagellum 5-segmented=segment 2.

Antenna II: about 55% length of animal; segment 4 less than twice as long as broad, bearing at lower distal end a large tooth with a smaller tooth above it; on the lower edge two short, stout spines or processes; flagellum 3-segmented; antennae as a whole with few setae, and those short.

Urosome as in female, but appendages less spinose.

Colour of paratypes in life: whitish grey, with two slaty bars across each segment, and slaty marking on antennae and head; sexes similar. Eggs, bright pale yellow.

DISTRIBUTION. Plymouth; Wembury (J. A. Kitching); off mouth of Tagus.*

ECOLOGY. Building tubes of mud on hydroids, sponges, weed from just above low-water mark to 25 fm.

OCCURRENCE AT PLYMOUTH. During 1934–5 this was the commonest species of the genus in shallow dredgings in Plymouth Sound, especially if stones or Laminaria holdfasts were brought up. It was also found intertidally at Tinside and Millbay West Wharf, and on the floating pontoon at Millbay, and the bathing raft at Tinside. An unusual habitat was the carapace of a *Maia squinado*, dredged in 25 fm. off Rame Head, on which about 40 specimens had built their tubes. *C. acutum* and *C. insidiosum* were often found with this species, but in smaller numbers.

The abundance of this species is the more surprising since it is not present in the rich collections of Corophium made from the same dredging grounds in 1895–1911. It seems possible, therefore, that it is not indigenous at Plymouth. In spite of much enquiry I am unable to find any record from elsewhere, except for the single female from Portugal; and so I cannot guess at its original locality.

SEX-RATIO AND BREEDING. Of 240 specimens in one collection from Plymouth Sound 99, or 41%, were males. There was no evidence of much seasonal variation in this ratio. Ovigerous females were found in February to December. The proportion of egg-bearing females was high from May

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* 1 ♀ in Copenhagen Museum; Dana Station 4155, 12.6.1930.

to October, but fell off in November and December and was very small in February and March.

VARIATION. The females begin to breed at a length of 3·5 to 4 mm., and attain a length of 5·5 to 6·0 mm. The number of spines on the antennae is more variable than in *C. bonelli* or *C. insidiosum*. The following figures were obtained from 15 ovigerous females :

Antenna I, segment 1, inner edge. 1–3 spines ; mean 2·5.
,, ,, lower edge. 4–7 ,, ,, 5·3.
Antenna II, segment 4, ,, ,, 4–6 ,, ,, 4·6.

GROWTH CHANGES. In the female the number of spines on the antennae increases with age. In the male the spines on all antennal segments decrease in size, but not apparently in number ; and the degradation is never so complete as in *C. acherusicum* or *C. crassicorne*. Antenna II, segment 4, always remains stout and does not become elongated in the adult males as in these two species.

IDENTIFICATION. The female may be identified from antenna II, segment 4, which cannot be confused except with that of *C. crassicorne*. The large eye and rounded eyelobe will distinguish it from this species.

In the male the shortness and sparseness of the setae on the antennae is characteristic of *C. sextoni* and *C. acherusicum*. In adult males of *C. acherusicum*, however, antenna I has 7–10 segments in the flagellum, and in antenna II, segment 4, is elongate and bears no spines.

26. COROPHIUM TUBERCULATUM Shoemaker.

[Shoemaker, C. R., 1934a, pp. 29–30.]

1905, *C. cylindricum*, Paulmier, Bull. N.Y. State Mus., 91, Zool., 12, p. 167, f. 37 (see above : *C. acherusicum*—Notes on Literature).

DISTRIBUTION. America : Nantucket to S. Carolina.

ECOLOGY. This species is found in oyster-washings, etc., from the mouth of rivers and in harbours.

27. COROPHIUM CALIFORNIANUM Shoemaker.

1934, *C. c.*, Shoemaker, J. Wash. Ac. Sci., 24, No. 8, pp. 359–60, f. 2.

One male specimen only is known, collected from the holdfast of water-logged kelp dredged in 48 fm. in Montery Bay, California.

SECTION C.

Urosome segments fused. Uropods I and II inserted below urosome, not in notches in its lateral margins.

This section contains five species of small or moderate size (2–6 mm.), none of which was known to Stebbing (1906). I have seen all except *C. louisianum* and *C. baconi*. The female of *C. louisianum* is not known, and in *C. simile* antenna II, segment 4, is similar in the sexes. In the remaining three species it is dissimilar. *C. acutum*, *C. lacustre*, and *C. simile* build tubes on hydroids, etc.; the habits of the other two species are unknown. All are marine except for *C. lacustre* which lives in water of a salinity from practically $0{\cdot}0^{\circ}/_{\circ\circ}$ to about $15^{\circ}/_{\circ\circ}$. *C. acutum* and *C. lacustre* are widely distributed.

KEY TO SPECIES.

1.	Margin of urosome consisting of a single convex curve	2
	Margin of urosome consisting of two convex curves, separated by a distinct nick	8
2.	Antenna II, segment 4 with one large curved terminal tooth, and a smaller tooth or lobe above it	3
	Antenna II, segment 4 not so armed	7
3.	Antenna II, segment 5 with no processes on lower margin	4
	Antenna II, segment 5 with distinct processes on lower margin	5
4.	Antenna I, segment 1 with a prominent, forward-pointing angular protuberance near base of inner surface	*C. louisianum* ♂
	Antenna I, not so armed	*C. simile* ♀
5.	Antenna II, segment 5, process long, pointed, near middle of joint	*C. acutum* ♂
	Antenna II, segment 5, process short, blunt, near base of joint	6
6.	Antenna I, segment 1 with 2 spines on lower edge	*C. simile* ♂
	Antenna I, segment 1 with no spines on lower edge	*C. lacustre* ♂
7.	Antenna I, segment 1 with 1 spine: Antenna II, segment 4 with 2 spines; segment 5 with none	*C. lacustre* ♀
	Antenna I, segment 1 with 3 spines: Antenna II, segment 4 with 3 spines; segment 5 with one	*C. acutum* ♀
8.	Antenna II, segment 4 with 3 spines and no teeth	*C. baconi* ♀
	Antenna II, segment 4 with no spines and two terminal teeth, segment 5 with a long hooked terminal tooth on inner margin	*C. baconi* ♂

28. COROPHIUM ACUTUM Chevreux.

[Chevreux, E., 1908, p. 75, f. 6.]

1911, *C. a.*, Chevreux, Mém. Soc. Zool. Fr., 23, p. 271. 1916, *C. acherusicum* (part), Barnard, Ann. S. Afr. Mus., 15, p. 272 (see also *C. acherusicum*). 1925, *C. a.*, Chevreux and Fage, Faune de France, 9, p. 366, f. 359, 374. 1928, *C. a.*, Schellenberg, Trans. Zool. Soc. Lond., XXII, p. 633. 1934, *C. a.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 26, 27.

DISTRIBUTION. Europe: France (R. Lannion, Concarneau), Monaco; England (Plymouth and Studland). Africa: Suez Canal*; Durban.* America: Long Island Sound, Woods Hole, Cape May, Rio de Janeiro. New Zealand: Auckland.*

OCCURRENCE IN ENGLAND. Plymouth, and Studland, Dorset (Dr. J. A. Kitching, coll.). At Plymouth in 1934–5 this species was the commonest Corophium among sponges, coralline Algae and roots of Laminaria near low-water mark on the shores of Plymouth Sound. In these situations it outnumbered *C. sextoni*, *C. bonelli*, and *C. insidiosum*, but in

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* Specimens examined in British Museum.

shallow water dredgings (5–20 fm.) it was far less common than *C. sextoni*. In May, 1935, all these species except *C. bonelli* were abundant on the wharfs and pontoon of the Millbay Docks.

ECOLOGY. This species is a tube-builder, intertidally or in shallow water. It haunts harbours and the most saline reaches of estuaries.

SEX-RATIO AND BREEDING. Three collections, of over 100 specimens each, contained 42% and 45% (Plymouth) and 34% (Suez Canal) of males. As in *C. acherusicum*, *C. insidiosum*, and *C. sextoni* males appear to be slightly less common than females.

Egg-bearing females were found in February, March, May, and from July to November. The proportion of females with eggs to those without eggs was higher in the summer than in the winter, though some are probably to be found all the winter through.

29. COROPHIUM LACUSTRE Vanhöffen.

[Vanhöffen, E., 1911, S. B. Ges. Naturf. Fr. Berl., p. 400, f. 1–4, and Sexton, E. W., 1912, Proc. Zool. Soc. Lond., p. 664, pl. 74, f. 13–17.]

1896, *C. crassicorne*, Scherren, Nature, 54, No. 1399, p. 367. 1906, *C. crassicorne* (part), Stebbing, Das Tierreich, 21, p. 691 ("found in Norfolk in almost fresh water"). 1907, *C. grossipes* (part), Gurney, Trans. Norfolk Norw. Nat. Soc., 8, pp. 423, 427 (part), 435 (part), Table II (part). 1917, *C. l.*, Vanhöffen, S. B. Ges. Naturf. Fr. Berl., p. 113, f. 2. 1918, *C. l.*, Hellén, Medd. Soc. Fauna Fl. Fennica, 45, p. 136. 1922, *C. crassicorne*, Tesch, Fl. F. der Zuiderzee, pp. 333–4, f. 6. 1923, *C. l.*, Schlienz, Arch. Hydrobiol. Plankt., 14, p. 429. 1924, *C. l.*, Spandl, S. B. Akad. Wiss. Wien., 133, p. 475. 1926, *C. acutum* var. *chevreuxi*, Poisson and Legueux, Bull. Soc. Zool. Fr., 51, pp. 320–5, f. 5, 6. 1927, *C. l.*, Stephensen, Die Tierwelt der Nord-und Ost-See, 14, X, f., pp. 168–9, f. 40. 1931, *C. l.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, pp. 168–70. 1934, *C. l.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 27.

DISTRIBUTION. Europe: Germany (Frisches Haff, Bremerhaven, Elbe); Finland (Borga); Holland (Zuiderzee); France (Canal de Caen); England (R. Thurne and Heigham Sound, Norfolk). America: Chesapeake Bay to Winyah Bay.

I have compared specimens from Germany (Vanhöffen), France (Le Roux), and America (Shoemaker), with those from Norfolk, and find them indistinguishable.

OCCURRENCE IN ENGLAND. 8.ix.35, River Thurne near Potter Heigham, Norfolk (two collections) and Heigham Sound, found by Mr. G. A. Steven abundantly among *Cordylophora lacustris* and on stems of *Phragmites communis*. The only other Crustacean present was *Gammarus zaddachi*, two specimens of which were present in one collection.

The specimens referred to by Scherren (1896) as *C. crassicorne*, and Gurney (1907) as *C. grossipes* (part), were found in the same localities. Their habits were the same as those of Steven's specimens, and very different from those of *C. crassicorne* or of *C. volutator*, of which *C. grossipes* is a synonym. None of these specimens remain. When they were collected *C. lacustre* was still undescribed, and this is the reason for the misidentification of specimens undoubtedly belonging to this species.

ECOLOGY. *C. lacustre* builds muddy tubes upon submerged plants or animals, especially *Cordylophora lacustris*. It inhabits water of low salinity. Schlienz (1923) states that the species extends in the Elbe from areas where the range of salinity is 0·17 to 0·87 parts of NaCl per thousand, to areas where this range is 0·17 to 20·61. In Norfolk it is known so far only from waters in which there is no tidal effect, but which are kept brackish by a subterranean salt-water table. Gurney (1907) records salinities up to 78 gm. per gallon (1·1 parts NaCl per 1000) in the River Thurne above the tidal reaches.

30. COROPHIUM SIMILE Shoemaker.

1934, *C. s.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 28–9.

DISTRIBUTION. America: Atlantic Coast, S. Carolina to Vineyard Sound, Mass. Found in sponges, or by washing oysters, or scraping piles in sheltered, but not estuarine, water.

31. COROPHIUM LOUISIANUM Shoemaker.

1934, *C. l.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 30–1.

DISTRIBUTION. America: Atlantic Coast, Louisiana, and Missouri (only two specimens known: both ♂♂).

32. COROPHIUM BACONI Shoemaker.

1934, *C. b.*, Shoemaker, Journ. Wash. Sc. Sci., 24, No. 8, pp. 356–9, f. 1.

DISTRIBUTION. America: Pacific Coast, off Peru and Southern California, and in the Behring Sea.

ACKNOWLEDGEMENTS.

Throughout the course of this work I have benefited by the advice of Mrs. E. W. Sexton and of Dr. K. Stephensen, who have also kindly looked over this manuscript before it went to the printers. I wish to express my thanks to them, and to all those others who have helped me in ways recorded more precisely above.

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Corophium quadriceps, Dana, 1852, P. Amer. Ac., 2, p. 219; Dana, 1853, 1855, U.S. Expl. Exp., 13 (2), p. 836, pl. 55, f. 8; Bate, 1862, Cat. Brit. Mus., p. 283, pl. 48, f. 7 (copied from Dana 1853–5); Stebbing, 1888, Rep. Voy. Challenger, 29, p. 255; Della Valle, 1893, F. Fl. Neapel, 20, p. 376.

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C. contractum, Stimpson, 1855, P. Ac. Philad., 7, p. 383; Bate, 1862, Cat. Brit. Mus., p. 282; Thomson, 1881*, Trans. Proc. N.Z. Inst., 13, p. 220, pl. 8, f. 9; Thomson and Chilton, 1886*, Trans. Proc. N.Z. Inst., 18, p. 142; Della Valle, 1893, F. Fl. Neapel, 20, p. 374; Hutton, 1904, Index Faun. N.Z. London; Stebbing, 1906, Das Tierreich, 21 (1), p. 692.

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* From internal evidence it seems likely that Chilton (1922), and so also Thomson (1881), and Thomson and Chilton (1886) were referring to *C. acherusicum*. Chilton was unable to distinguish his specimens from Dutch ones of this species lent by Hoek (as *C. crassicorne*); and specimens of *C. acherusicum* from Lyttelton Harbour are in the British Museum.

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APPENDIX I.

List of Specimens Examined of C. bonelli and C. insidiosum.

(a) *C. bonelli*.

Locality and date.		Source of specimens.	Number of ♀♀.
England, Plymouth	1889	British Museum	100
	1908	,, ,,	14
	1895	Marine Biological Association, Plymouth	100
	1905	,, ,,	100
	1907	,, ,,	100
	1911	,, ,,	100
	1934	G. I. Crawford	5
Wales, Tenby	1880	British Museum	1
Colwyn Bay	1898	,, ,,	7
Scotland, Tobermory	1913	,, ,,	6
Loch Swen	1933	Dr. J. A. Kitching	133

Locality and date.		Source of specimens.	Number of ♀♀.
Ireland, Valentia	1896	British Museum	3
Roundstone	1874	,, ,,	50–100
Guernsey	1906	,, ,,	9
France, Portrieux, Grandcamp, St. Vaast		Paris Museum	6
Italy, Naples		Naples Museum	several
Denmark, Lodshusene	1878	Copenhagen Museum	20
,, No locality		,, ,,	50–60
Norway, Oslofjord*		Oslo Museum	68
Haugesund*		,, ,,	17
Bergenfjord*		,, ,,	28
Risør*		,, ,,	29
Bergensfjord		British Museum	1
Trondhjhemfjord	1893	,, ,,	32
Solsvig	1908	,, ,,	10
North America, East Coast†		Washington Museum	6
South America, Uschaia‡	1892	Hamburg Museum	11
Picton Is.‡	1892	,, ,,	1
Punta Arenas‡	1892	,, ,,	3
500 miles E.N.E. from Rio de Janeiro	1913	British Museum	1
Falkland Islands	1926	,, ,,	5

In all these collections no ♂♂ were present.

(b) *C. insidiosum.*

Locality and date.		Source of specimens.	Number of ♀♀.	Number of ♂♂.
England, Plymouth :				
Millbay Pontoon	3.viii.34	G. I. Crawford	15	0
,, ,,	3.ix.34	,,	25	7
,, ,,	7.ix.35	,,	9	0
,, W. wharf	8.v.35	,,	94	15
,, inner basin	8.v.35	,,	27	19
Tinside	5.ii.35	,,	2	0
Bull Point buoy	31.v.35	,,	0	1
Neille Point buoy	2.viii.35	,,	2	1
Chelson Meadow	9.viii.35	,,	246	199
Denmark :				
Mariagerfjord, Aamolle	Oct. '22	Copenhagen Museum	8	3
,,	27.v.23	,, ,,	many	5
Frederikshavn	5.viii.23	,, ,,	9	2
,, ,,	13.xii.34	,, ,,	3	2
Östersóen (near Graasten)	Sept. '29	,, ,,	1	1
Germany, Kieler Bucht		Berlin Museum	5	2
Italy, Lake of Venice	Oct. '29§	Prof. A. Brian	100	100
	29.x.35‖		40	40
America :				
Oakland, San Francisco	2.ix.31	Copenhagen Museum	4	3

* Labelled by Sars as *C. bonelli* M. Edw.
† *C. pseudacherusicum*—Shoemaker (1934a).
‡ *C. pseudacherusicum*—Schellenberg (1931).
§ 4,097 ♀♀, 1,244 ♂♂—Brian (1932).
‖ 1,492 ♀♀, 398 ♂♂—Brian in a letter, 1935.

APPENDIX II.

THE BRITISH SPECIES OF COROPHIUM.

Species.	British localities, and habits.
C. volutator (Pallas)	Coasts of Great Britain and Ireland ; burrowing in intertidal mud flats, often in estuaries.
C. arenarium n.sp.	Leigh-on-Sea, Essex ; burrowing in sand between tide-marks.
C. curvispinum G. O. Sars var. *devium* Wundsch	R. Avon at Tewkesbury ; building tubes of mud on weed and stones in fresh water.
C. affine Bruzelius	From Forth and Clyde northwards ; burrowing, below low-water mark.
C. crassicorne Bruzelius	Coasts of Great Britain ; burrowing in muddy sand from just above low-water mark downwards.
C. bonelli G. O. Sars	Coasts of Great Britain and Ireland ; building tubes on weed, etc., from low-water mark downwards.
C. insidiosum n.sp.	Plymouth ; building tubes on weed usually in brackish water.
C. acherusicum da Costa	Plymouth, Sheerness, New England Creek (Essex) (formerly, the creek is now shut in and brackish) ; building tubes on weed, etc., especially on rafts and buoys.
C. sextoni n.sp.	Plymouth ; habits as in *C. bonelli*.
C. acutum Chevreux	Plymouth, Studland (Dorset) ; habits as in *C. bonelli*.
C. lacustre Vanhöffen	R. Thurne and Heigham Sound, Norfolk ; building tubes, usually in clumps of *Cordylophora lacustris* in brackish (nearly fresh) water.

Notes on the Distribution of Burrowing Isopoda and Amphipoda in Various Soils on the Sea Bottom near Plymouth.

By

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With 1 Figure in the Text.

CONTENTS.

INTRODUCTION.

Preliminary Remarks.

THE earliest detailed account of the nature of the sea bottom near Plymouth is that of Allen (1899), wherein analyses of the soils on the 30 fm. line are coupled with lists of the animals collected by trawl and dredge. Ford (1923) described a number of soils in shallower water, and gave a quantitative list of the bottom fauna, collected with a grab which covered an area of 0·1 sq. m. Smith (1932) described in great detail the soils of the area of shell-gravel which surrounds the Eddystone Lighthouse. By none of these workers, however, was special attention paid to the smaller burrowing Crustacea, which are often overlooked unless they are made the special object of collecting. Some species, e.g. of Bathyporeia and Ampelisca, may be very common, and certainly play an important part in the ecology of the sea-bottom. See Steven (1930) and Hunt (1925).

The object of the present paper is to summarize the results of my collecting of Isopoda and Amphipoda in 1934 and 1935, and to record the nature of the soil in which each species was found. From their small size and the habit of many species of burrowing by ejecting sand grains in a swimming current it seems to me probable that the burrowing Amphipoda, Isopoda, and Cumacea are much influenced in their distribution by the nature of soil. I did not, unfortunately, make precise observations on the Cumacea, or on the Tanaidacea, collected.

Reibisch (1905 and 1906) recorded 87 species of Amphipoda dredged in the North Sea. Many of these were burrowing species, and he recorded the type of bottom from which a number of species were obtained. Zirwas (1911) treated the Isopoda similarly. The distribution of Isopoda and Amphipoda between tidemarks is discussed in a number of papers, among which that of Elmhirst (1931) is outstanding.

The methods of burrowing of *Haustorius arenarius* are described by Dennell (1933), and those of *Talitrus saltator*, *Bathyporeia robertsoni*, *Microprotopus maculatus*, and *Corophium volutator* by Schellenberg (1929).

Collecting Methods.

The collections in Cawsand Bay were made from M.B. *Gammarus*, chiefly with the fine-meshed dredge (Naturalist's pattern) and the D-net. The contents of the dredge (usually about 10 litres) were emptied into a bucket and repeatedly stirred up, the fauna being skimmed off with a flat hand-net of bolting silk, until no more appeared. The contents of the D-net were similarly treated, after the finer particles of sand had been washed out through the mesh. One collection was made with a tow-net towed clear of the bottom behind the shrimp-trawl frame: a sort of ground-rope of loose chain was so fixed as to stir up the fauna of the bottom. As a collecting instrument this was as effective as the D-net, but less convenient to use.

The other collections were made from the S.S. *Salpa* with the fine-meshed dredge (Salpa-pattern). Sometimes a canvas bag was fastened inside the net to avoid washing out of particles of soil of the finer grades: but since the soil was observed to pack very firm in the dredge, and to be washed out very slowly even in rough weather, I think it probable that samples taken from the centre of the mass brought up were in their original condition, and that the loss of soil was not considerable, even when the canvas bag was not used.

The soil brought up was emptied into baths of measured capacity, and an estimate made of its volume. A sample was set aside in a breffit for analysis in the laboratory, and the remainder was sieved through the four "Challenger" sieves. The soil which passed the finest sieve was stirred in water and the smallest specimens collected with a hand-net. In fine weather the resulting collections were probably complete except for very small specimens, or rare species : in rough weather small species must have been frequently missed.

The number of specimens of any species obtained in this way is not a measure of the density of population. The area over which the dredge was worked is not known nor the depth to which it dug, and, owing to the shape of the digging edge, the surface layers of the bottom were collected over a larger area than the deepest layers sampled. It is possible, but I think unlikely, that some species of Amphipoda and Isopoda, as of worms, lie too deep for the dredge to secure them.

For quantitative work a grab would have been necessary, and would have to have been used for repeated observations on the same station over a long period, since the density of animals on the sea-floor is subject to large seasonal and annual fluctuations (Blegvad, 1928). It was not possible to take such an extended set of observations, and considering the further disadvantages of the grab enumerated below, I decided that the fine-meshed dredge was the most suitable instrument for a preliminary survey of the distribution of Amphipoda and Isopoda on various soils. The grab is only effective in calm weather and is not equally effective on all grounds ; for comparing the numbers of animals on diverse grounds it is probably inferior to the dredge. The soils at Plymouth are less suited to the grab than the rather uniform muddy soils chiefly worked by Blegvad (1928) and other Danish workers. Moreover, the instrument available at Plymouth covers only 0·1 sq. m., whereas a 50-litre dredge haul covers 1 sq. m., assuming the mean depth of the digging edge to be 5 cm.

Method of Analysing Soils.

At least 400 c.c. of soil from each station (in stony grounds up to 1000 c.c.) were graded in the sieves standardized by Allen (1899), following precisely the procedure detailed by him on pp. 378–380. By this method eight grades are distinguished.

I. Stones. All inorganic material which will not pass through a 15 mm. sieve.
II. Coarse Gravel. Material left on a 5 mm. sieve.
III. Medium Gravel. Material left on a 2·5 mm. sieve.
IV. Fine Gravel. Material left on a 1·5 mm. sieve.
V. Coarse Sand. Material left on a 1·0 mm. sieve.
VI. Medium Sand. Material left on a 0·5 mm. sieve.
VII. Fine Sand. Material which passes through a 0·5 mm. sieve and, when stirred up with sea-water, settles in 1 minute.
VIII. Silt. Remains in suspension at the end of 1 minute.

The dry-weight of soil of each grade is expressed as a percentage of the total dry-weight of the sample, and these 8 percentages form a record of the nature of the soil, which is comparable with all records similarly obtained. This analysis, particularly for very silty soils, is not so precise as analysis by elutriation methods. It distinguishes, however, between soils which cannot easily be distinguished by inspection.

It should be noted that in soils containing high percentages of fine sand (VII) the mean size of the particles of this grade is much larger in clean grounds (i.e. those with little silt) than in silty grounds. It would, therefore, be misleading to express the nature of such soils by " numerical representations " such as Smith (1932) was able to apply to the Eddystone gravels. Further, in grades I to VI, and perhaps also in grade VII, some of the particles are thin laminae of shell and slate, and others are rounded pebbles. The pebbles in any grade are heavier than the laminar particles, and a pebbly gravel is less suited for small burrowing Crustacea than a shelly gravel, the larger particles of which afford good shelter to Gammarids

Theoretically the eight percentages expressing the nature of the soil are free to assume any values which add up to 100. In practice I found that only certain types of values were assumed, and it is likely that everywhere on the sea-bottom the currents will restrict the freedom of these percentages to assume any value. For example, it is improbable that the percentages of grades I and III will be high, and those of II and IV low. The soils examined by Allen (1899) and by myself can be simply classified as below.

I have arbitrarily defined a simple soil as one having a maximum in one grade, and either no secondary maximum or one of less than 5% : and a mixed soil as one having a secondary (rarely also a tertiary) maximum of over 5% of the whole. A mixed soil may be regarded as formed by the mixture of two (or three) simple soils in proportions only roughly ascertainable from the percentages of the 8 grades. Unless the coarser of these components is present in much greater bulk, the lighter gives character to the soil. For example, a mixture of fine sand and coarse gravel will support a certain number of species usually found in fine sand alone, but not those from coarse gravel alone. The fine sand between the particles of gravel maintains its own character, but by filling in the interstices entirely alters that of the gravel. Most of the mixed soils which I have examined consist of a medium or fine sand with a small mixture of coarse or medium gravel.

The simple soils may be arbitrarily classified as follows :

" mud "—maximum in VIII.
" fine sand with mud "—maximum in VII : VIII $>10\%$.
" fine sand "—maximum in VII : VIII from 2 to 10%.
" fine clean sand "—maximum in VII : VIII $<2\%$.
" medium sand " up to " stone "—maximum in VI up to I.

I have found no soil with a maximum in I, and such a ground would probably be barren. The coarser the soil, the less well defined the maximum.

By this classification the Rame mud grounds are included under "fine sand with mud," but they have a much higher percentage of silt than the soils analysed from Cawsand Bay, and the mean size of fine sand particles is smaller. It is in comparing soils with high percentages of silt that the method adopted here is least satisfactory.

A list of stations and of soil-analyses is given in Appendices I and II. The localities best worked were Cawsand Bay, Whitsand Bay and Bigbury Bay.

Burrowing Isopoda and Amphipoda.

A list of hauls and of catches of Isopoda and Amphipoda is given in Appendix III (p. 644), with separate lists of burrowing and non-burrowing species. Intertidal collections are not included in these lists but are summarized below.

Between Tidemarks.

Only 11 species of burrowing Isopods and Amphipods were collected from intertidal areas, and in only a few localities (marked with an asterisk) were precise measurements taken of the size of soil particles. In other places an estimate was made of the type of soil.

Isopoda.

Eurydice pulchra Leach. Drake's Island*, Mothecombe*, Treyarnon (N. Cornwall), Saunton (N. Devon); in fine to coarse sand from about half-tide mark downwards.

Amphipoda.

Ampelisca brevicornis (A. Costa). Drake's Island in muddy sand; Salstone in very muddy sand, both at L.W.M.

Bathyporeia pelagica Bate. Trevarrian (N. Cornwall)*, Kynance Cove, Mothecombe*, Wembury*, fine to medium sand, from half-tide mark downwards.

Haustorius arenarius (Slabber). Mothecombe, sand, L.W.M.

Urothoë brevicornis Bate. Drake's Island, sand, L.W.M.

U. grimaldii var. *poseidonis* Reibisch. Salcombe Millbay, fine clean sand*, L.W.M.

Perioculodes longimanus (Bate and Westw.). St. Michael's Mount, Salcombe Millbay, muddy to fine sand, L.W.M.

Pontocrates arenarius (Bate). Wembury*, Dawlish, fine to medium sand from half-tide mark downwards.

P. norvegicus Boeck. Trevarrian (N. Cornwall), Kynance Cove, Mothecombe*, Wembury*, fine to medium sand from half-tide mark downwards.

Guernea coalita (Norman). Drake's Island, shell gravel at L.W.M.

Photis longicaudata (Bate and Westw.). Salstone, muddy soil, at L.W.M.

With the exception of *Eurydice pulchra* and *Urothoë grimaldii* var. *poseidonis* (both of which have been caught below tidemarks by other collectors) these species are all contained in the list of burrowing species collected below low-water mark, and considered in the next section.

Below Low-Water Mark.

The three areas on which my information is most complete are Cawsand Bay, Whitsand Bay, and Bigbury Bay. The soil in Cawsand Bay (St. 2) is fine sand with mud. That in Whitsand Bay (St. 34–39) and Bigbury Bay (St. 43–47, 53, 54) is fine clean sand. I also collected in Bigbury Bay from gravel (St. 50, 51), and fine sand with mud (St. 52), see Fig. 1.

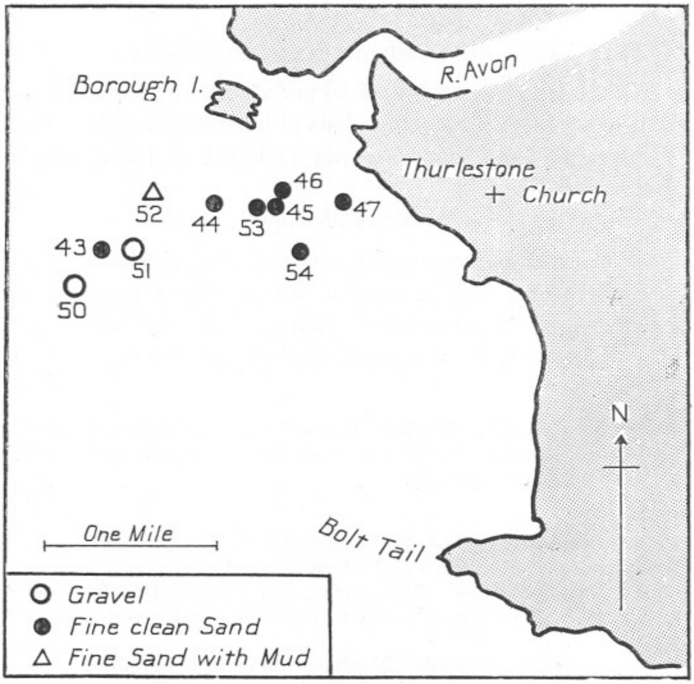

FIG. 1.—Map showing positions of stations in Bigbury Bay, and nature of soil.

A dredge haul from the latter contained *Amphiura filiformis* and *Syndosmya alba*, abundant; *Echinocardium cordatum*, 20 specimens about 1½ inches long; *Cardium echinatum*, 6 large specimens; and a quantity of fragments of oak and hawthorn leaves. The precise numbers of specimens of Isopods and Amphipods caught at these and other stations are noted in Appendix III (p. 644); the following lists simply classify the burrowing species as "abundant," meaning more than 100 in at least one of the hauls, and "few," meaning not more than 10 in any haul. Intermediate frequencies are denoted by "common."

Cawsand Bay (Fine Sand with Mud).

AMPHIPODA.

Ampelisca brevicornis, common.
Bathyporeia pelagica,* few.
Urothoë elegans, few.
Argissa stebbingi, 2 in 7 hauls.
Harpinia antennaria, common.
Perioculodes longimanus, common.
Synchelidium haplocheles, few.
Monoculodes carinatus, 1 in 7 hauls.
Megaluropus agilis, few.
Guernea coalita, 1 in 7 hauls.
Microprotopus maculatus, common.
Siphonoecetes colletti, 1 in 7 hauls.
Corophium crassicorne, common.

The burrowing faunas of the fine clean sand in Whitsand Bay and Bigbury Bay afford an interesting comparison. The soil is very similar, except that that of Bigbury is reddish, while that of Whitsand is greyish-white and composed largely of shell and slate. Some of the hauls in Whitsand contained loose weed, with a fauna of its own, but the presence of weed did not appear to affect the burrowing fauna.

	Whitsand Bay.	*Bigbury Bay.* (Fine clean sand)
ISOPODA.		
Eurydice spinigera,	few.	2 in 7 hauls.
AMPHIPODA.		
Hippomedon denticulatus,	2 in 6 hauls.	4 in 7 hauls.
Ampelisca brevicornis,	—	3 in 7 hauls.
Bathyporeia guilliamsoniana,	few.	few.
B. pelagica,	common.	abundant.
Haustorius arenarius,	1 in 6 hauls.	—
Urothoë brevicornis,	few.	—
Leucothoë sp. indet,	—	2 in 7 hauls.
Perioculodes longimanus,	—	few.
Pontocrates arenarius,	few.	—
P. norvegicus,	—	few.
Synchelidium sp. indet.,	—	few.
Megaluropus agilis,	—	few.
Siphonoecetes dellavallei,	—	few.
Corophium crassicorne,	—	1 in 7 hauls.

The remaining stations are too scattered to form the basis of similar comparisons.

A systematic consideration follows of all burrowing species of Isopoda and Amphipoda collected below low-water mark.

Isopoda.

Eurydice spinigera was present in small numbers in Bigbury Bay and Whitsand Bay in fine clean sand. Two specimens of *E. truncata* were obtained from coarse sand near the Eddystone.

I only found *E. pulchra* between tidemarks. It swam freely in pools on the sands, and in the sea as the tide rose. From this fact, and from the frequency with which species of Eurydice are captured in tow-nets, it

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* See p. 639

appears that they are not so intimately dependent on the soil as are the burrowing Amphipoda. *E. pulchra* burrows with great ease, principally by means of a swimming current.

Amphipoda.

Hippomedon denticulatus was never common. It was present in fine clean sand in Whitsand Bay and Bigbury Bay: also in Bigbury at St. 51 in coarse stony gravel (with a little fine sand): and in Eddystone coarse sand.

Ampelisca spp. were very common except in fine clean sand. None were found in Whitsand Bay and only a few *A. brevicornis* in Bigbury Bay. *A. brevicornis* was common in Cawsand Bay, and intertidally at Drake's Island, in fine sand with mud; and in much muddier soil on the Salstone just above low-water mark. It was not found in coarse grounds. The remaining four species were all frequent in mixed soils. *A. spinipes* and *A. typica* were moreover found in gravels, the former more commonly. *A. tenuicornis* was found in mixed soils, and in the very muddy fine sand of the Rame mud, often in large numbers. *A. diadema* was present less commonly in mixed soils.

The burrowing of Ampelisca is not dependent on a flow of water set up by the pleopods, but is performed by the scraping and hauling of the gnathopods, aided by the urosome as soon as it gets a purchase. The fifth and sixth pereiopods are spread out and prevent sand rolling into the hole. In captivity *A. tenuicornis* made a case of sand-grains (not pebbles) loosely aggregated, and indistinguishable from the substratum.

The local Haustoriidae burrow almost entirely by ejecting sand-grains in a powerful swimming current. They do not form tubes. They are pre-eminently inhabitants of sand, and soils containing much clogging silt or many heavy particles are not suitable for them. It is noticeable that the coarseness of the soils inhabited by species of the genus Urothoë is in proportion to the size of adult specimens.

The burrowing of Haustorius is described by Dennell (1933). That of *Urothoë brevicornis* and *U. grimaldii* var. *poseidonis* appeared to me very similar. Burrowing movements were made with the antennae and gnathopods; the third and fourth pereiopods swept off encroaching particles to one side; while the fifth to seventh pereiopods formed a funnel, widest at the hind end, along which the pleopods swept sand-grains in a powerful and diverging current. In their native soil these species burrowed out of sight within five seconds. *Bathyporeia pelagica* from Bigbury Bay could disappear within one second; and some Bathyporeia (sp. indet.) observed in sandy pools near Saunton, N. Devon, entered the sand without any apparent check to their rate of swimming.

Haustorius arenarius was found in fine clean sand in Whitsand Bay, but not in Bigbury Bay. In one unlocalized haul from Whitsand Bay four specimens were obtained. *Bathyporeia pelagica* was abundant and *B. guilliamsoniana* was present in fine clean sand in both Whitsand Bay and Bigbury Bay. *Bathyporeia elegans* Sars is a name applied to a slender form of *B. pelagica* with less well-developed eyes. The specimens of this genus from the finer sand of Cawsand Bay were of this form, but it is doubtful if it is a distinct species.

Of the species of Urothoë obtained the smallest is *U. elegans*, which was found in Cawsand Bay and in silty mixed soils on the Rame–Eddystone Grounds and Melampus, Plymouth Sound. *U. marina*, the largest species, was collected in coarse sand and fine gravel—see also Smith (1932). The two species of intermediate size, *U. grimaldii* var. *poseidonis* and *U. brevicornis*, were both found in fine clean sand, but only very locally, the former at Millbay, Salcombe (intertidally), and the latter on Drake's Island and in Whitsand Bay.

Argissa stebbingi was found in one haul from Cawsand Bay, and in D-net hauls from Middle Sound and Melampus, in rather silty soil (not analysed).

Metaphoxus fultoni was characteristic of gravels, and was even found in the stony gravel of Bigbury Bay (St. 50, where over 95% of Grade I by weight was non-calcareous). The animal is so small that I presume it lives interstitially in the manner described by Nicholls (1935) for certain copepods. *Harpinia antennaria* was only found in grounds that were wholly or predominantly fine sand with mud, and was most common in Cawsand Bay.

A number of specimens of Leucothoë were found in hauls in which all the other species were certainly burrowers. It seems, therefore, that some members of this genus burrow, while others (e.g. *L. spinicarpa*) habitually live among sponges, ascidians, etc. The specimens from Rame mud were *L. lilljeborgi*, the rest could not be named.

The Oedicerosidae do not build tubes, and live principally in sand. They are, however, less restricted in their choice of soils than the Haustoriidae, at least near Plymouth. *Pontocrates arenarius* and *P. norvegicus* were both found in fine clean sand in shallow water or between tidemarks, but never together. *Perioculodes longimanus* was characteristic of the finer Cawsand Bay soil, and was present in Bigbury but not in Whitsand Bay. *Synchelidium haplocheles* was found in Cawsand Bay, and Synchelidium sp. (perhaps *maculatum*) was present in small numbers in Bigbury Bay. *Westwoodilla caecula* was infrequent in mixed soils. Appendix III contains only one record of *Monoculodes carinatus*, and that is from Cawsand Bay; but it appears (Ford, 1923) that gravel is its usual substratum. A specimen that I dredged from shell-gravel on New Grounds was observed, with its scorched brownish colouring, to harmonize closely with that ground. *Eusirus longipes* was only collected from Rame mud.

Of the Gammaridae, *Megaluropus agilis* was common in Cawsand Bay and Bigbury Bay, and is probably a genuine burrower. *Maera othonis* was observed in the laboratory to make a refuge under large shell fragments by pushing out the finer soil with its second gnathopods, creeping on its side, like a Gammarus, when disturbed, and concealing itself under the first suitable fragment found. Since *Cheirocratus sundevalli* and *Ceradocus semiserratus* were found on the same gravelly or mixed grounds, I suppose that their habits are similar.

Guernea coalita is another very small species living in coarse grounds, probably interstitially.

The Photidae and Corophiidae are tube-builders, and a number are burrowers. Of the Photidae only two species were found in numbers, *Microprotopus maculatus* and *Photis longicaudata*, from mixed and simple soils with much fine sand and silt. Of the Corophiidae, *Siphonoecetes dellavallei* was a member of the characteristic fauna of Bigbury Bay, and *Corophium crassicorne* of Cawsand Bay. *S. dellavallei* was also dredged commonly off the bar of the River Yealm in a soil noted as " shelly-slaty fine-gravel," and in small numbers inside Drake's Island. *C. crassicorne* was also obtained off the bar of the Yealm and at White Patches (Zostera bed), and Melampus, Plymouth Sound.

ACKNOWLEDGMENTS.

The success of my collecting trips is practically entirely due to the help and advice of Captain Lord of the S.S. *Salpa*, and to the co-operation of all the crew (especially Mr. J. Martin who did much of the sieving with me). I wish to express my warmest thanks and appreciation to them all.

My best thanks are due to Dr. K. Stephensen, of the Copenhagen University Museum, who gave me his opinion on all those specimens about which I was in doubt.

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APPENDIX I: LIST OF STATIONS.

No. of Station.	Date.	Area.	Marks or Bearings.	Depth (fm.).	Nature of Soil.
2	6.vii.34 (repeated later)	Cawsand Bay .	Breakwater light on Bovisand fort: clock tower on highest near bushy-topped tree (2*a* was a sample taken nearby; 2*b* was taken off Pier Cellars).	3–5	Fine sand with mud.
6	18.vii.34	Off Penlee Point .	Mewstone on Wembury Church: white house (sea level) on Penlee on 3 tall trees to W. of large wood on Maker Heights.	23	Mixed.
23	14.viii.34	Rame mud .	Mewstone open from Yealm Head, on trees on skyline: Penlee Point overlapping Blackball: Rame Chapel on flagstaff.	20	Fine sand with much mud.
24	14.viii.34	Rame mud .	Mewstone on head to W. of Yealm: Penlee Point just overlapping Blackball: Rame Chapel on flagstaff. About 300 yd. S.S.E. from last; "Turritella ground."	20–25	As last, but less silty and grittier.
C	14.viii.34	Rame–Eddystone	In a direct line from Rame Head to Eddystone.	28	Mixed soil, chiefly medium sand.
26	4.ix.34	Eddystone . .	Eddystone bearing S.E. about ¼ mile.	ca. 30	Red fine gravel.
27	4.ix.34	Eddystone . .	Eddystone bearing S.E. by S. about ¼ mile.	*ca.* 30	Pale sandy gravel.
28	4.ix.34	Eddystone . .	Eddystone bearing S.S.E. about ¼ mile.	*ca.* 30	Pale medium gravel.
32	3.x.34	Rame–Eddystone	Rame Chapel on flagstaff.	27	Mixed soil, chiefly fine sand.
33	3.x.34	Rame–Eddystone	Rame Chapel on flagstaff.	25	Fine sand, rather muddy and gravelly.
34	16.xi.34	Whitsand Bay .	N.N.E. of Queener Rocks: church just in view at end of haul (going W.).	3–5	Fine clean sand.
35	,,	,,	Opposite wreck of *Chancellor*: Rame Church inside Polhawn house.	3–4	,, ,,
36	,,	,,	¼ mile W. from 35.	3–4	,, ,, (weedy).
37	,,	,,	E. of Shadows Rocks.	3–4	,, ,,
38				3–5	,, ,,
39	,,	,,	Just E. of 34.		,, ,, (weedy).
41	4.xii.34	Plymouth Sound	About 50 yd. N.E. to N. of Melampus buoy: buoy started on Picklecombe Pt., ended on middle of Drake's Is.		Mixed soil (fine sand and coarse gravel).
43	22.i.35	Bigbury Bay .	Burgh Is., N.E.: Bolt Tail, S.E.	17	Fine clean sand.
44	,,	,,	Burgh Is., N.: Thurlestone Church, just S. of E.	11	,, ,, (rather red).
45	,,	,,	Burgh Is., N. by W.½W.: Thurlestone Church, E.	7½	,, ,, (red).
46	,,	,,	Burgh Is., N.W. by N.½N.: Thurlestone Church, E. by ½S.	5	,, ,,
47	,,	,,	Burgh Is., N.W.: Thurlestone Church, E.	4¼	,, ,, (red).
50	10.v.35	,,	Burgh Is., N.E.: Bolt Tail, S.E.½E.	19–20	Medium stony gravel.
51	,,	,,	Burgh Is., N.E.½N.: Bolt Tail, S.E.¼S.	18	Coarse stony gravel.
52	,,	,,	Burgh Is., N.E.: Bolt Tail, S.E. by S.	16	Fine sand with mud (leaves of oak, etc.) (= Ford, 1923, Station 13).
53	,,	,,	Burgh Is., N. by W.: Thurlestone Church, E.	9½	Fine clean sand.
54	,,	,,	Burgh Is., N.N.W.: Thurlestone Church, E. by N.	4–5	,, ,,

APPENDIX II: ANALYSES OF SOILS.

Stations in same order as in Appendix III; the maxima are shown in heavy type.

	Fine Sand with Mud.					Fine Sand.									Coarse Sand.	Fine Gravel.	Medium Gravel.		Coarse Gravel.	Mixed Soils.				
Stations.	23	24	2	2*a*	52	34	35	37	39	44	45	47	53	54	27	26	28	50	51	6	C	32	33	41
Grades.																								
I	0·8	1·9	0·1	—	2·3	—	6·4	2·0	1·9	0·3	0·2	—	0·8	1·5	0·4	0·3	1·9	4·6	14·2	4·9	—	1·4	0·6	4·2
II	0·7	3·5	0·2	—		0·1						—			7·2	6·1	13·3	30·9	**28·8**	**7·1**	8·9	**11·8**	7·0	**17·2**
III	1·0	2·3	0·2	0·1		0·2						—			22·5	20·9	**36·5**	**32·6**	15·7	3·8	**10·6**	10·1	**7·2**	6·4
IV	1·8	2·4	0·3	0·1		0·3						—			24·4	**33·1**	28·0	18·8	12·3	3·1	5·8	8·8	5·0	7·1
V	3·7	4·8	0·6	0·4		0·5						—			**27·7**	29·2	13·0	7·0	9·6	6·4	5·8	8·3	4·0	10·2
VI	5·3	6·2	1·0	0·8		4·0	18·6	3·2	4·1		0·5	1·4			12·6	5·5	4·4	2·5	4·4	11·8	**43·9**	19·2	8·7	11·2
VII	**48·8**	**55·3**	**78·4**	**82·7**	80·8	**94·7**	**74·6**	**94·2**	**93·8**	**98·5**	**98·4**	**98·2**	**97·4**	**97·7**	4·2	3·9	2·6	2·8	9·6	**52·1**	24·1	**34·7**	**55·5**	**37·4**
VIII	38·0	23·6	19·3	15·7	16·9	0·3	0·3	0·5	0·4	1·3	0·8	0·4	1·8	0·8	1·1	1·7	0·4	0·7	3·2	10·7	1·0	5·8	12·0	6·4

APPENDIX III: FAUNA LISTS.

Type of Ground.	Fine Sand with Mud.											Fine Sand.													Coarse Sand.	Fine Gravel	Medium Gravel.		Coarse Gravel	Mixed Grounds.				
Station No.	23	24	2	2	2	2	2	2	2a	2b	52	34	35	36	37	38	39	43	44	45	46§	47	53	54	27	26	28	50	51	6	C	32	33	41
Instrument‡	F.M.D.†	F.M.D.	F.M.D.	D-net.	D-net.	Tow-net.*	D-net.	D-net.	F.M.D.	D-net.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.*	F.M.D.†	F.M.D.†	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.†	F.M.D.	F.M.D.
Approx. Volume in Litres	100	150	–	–	–	–	–	–	–	–	–	70	50	30	30	40	80	30	30	30	40	40	–	–	–	50	–	–	–	–	3	40	30	–
ISOPODA.																																		
(a) *burrowing.*																																		
Cirolanidæ.																																		
Cirolana borealis Lilljeborg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Conilera cylindracea (Montagu)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Eurydice spinigera Hansen	–	–	–	–	–	–	–	–	–	–	–	1	4	1	3	6	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
E. truncata (Norman)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
(b) *in weed.*																																		
Idoteidæ.																																		
Idotea baltica (Pallas)	–	–	–	–	–	–	–	–	–	–	–	c.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I. emarginata (Fabr.)	–	–	–	–	–	–	–	–	–	–	–	c.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I. linearis (L.)	–	–	–	–	–	–	–	–	–	–	–	c.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Zenobiana prismatica (Risso)	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AMPHIPODA.																																		
(a) *burrowing.*																																		
Lysianassidæ.																																		
Hippomedon denticulatus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	1	–	–	2	1	1	–	–	–	1	–	–	–	–	–
Ampeliscidæ.																																		
Ampelisca brevicornis (A. Costa)	–	–	23	–	5	2	1	2	2	–	4	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
A. spinipes Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	6	–	–	1	2	–	3	1	–
A. diadema (A. Costa)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	–	15	20	–
A. tenuicornis Lilljeborg	2	108	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	–	18	24	1
A. typica (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	2	1	4
Ampelisca sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	1	3	3	–	22	–	–	22	83	3
Haustoriidæ.																																		
Bathyporeia guilliamsoniana (Bate)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	3	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
B. pelagica Bate	–	–	7	1	4	6	–	4	1	–	9	1	–	–	2	1	24	386	306	72	7	8	373	517	–	–	–	–	4	–	–	–	–	–
Haustorius arenarius (Slabber)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Urothoë marina (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	1	–	–	–	–	–	–	–	–
U. brevicornis Bate	–	–	–	–	–	–	–	–	–	–	–	4	7	–	3	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
U. elegans Bate	–	–	7	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	19
Argissidæ.																																		
Argissa stebbingi J. Bonnier	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Phoxocephalidæ.																																		
M. fultoni (T. Scott)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3	4	2	1	–	–	–	1	–	–
Harpinia autennaria Meinert	2	3	47	–	2	1	–	4	10	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3
Harpinia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoidæ.																																		
Leucothoë lilljeborgi Boeck	1	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoë sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2	1	–	1	–	–	–	1	1	4
Lilljeborgiidæ.																																		
Lilljeborgia brevicornis Lilljeborg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Oedicerosidæ.																																		
Perioculodes longimanus (Bate & Westwood)	–	2	37	12	70	37	3	72	8	25	2	–	–	–	–	–	–	5	–	2	–	–	1	2	–	–	–	–	–	–	–	–	–	2
Pontocrates arenarius (Bate)	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. norvegicus Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	3	–	1	–	9	–	–	–	–	–	–	–	–	–	–
Synchelidium haplocheles Grube	–	–	–	1	3	–	–	1	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Synchelidium sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	7	1	–	–	–	–	–	–	–	–	–	–
Monoculodes carinatus (Bate)	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Westwoodilla caecula (Bate)	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	3	–
Eusiridæ.																																		
Eusirus longipes Boeck	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammaridæ.																																		
Cheirocratus sundevalli (Rathke)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	5	–	15
Cheirocratus sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–
Megaluropus agilis Hoek	–	–	–	1	2	2	–	1	–	6	–	–	–	–	–	–	–	–	1	–	–	–	5	9	–	–	–	–	–	–	–	–	–	–
Ceradocus semiserratus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	17	–	–	–	–	2	1	–
Maera othonis (M.-Edwards)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	6	3	?1	–	4	–	4	24	2
Dexaminidæ.																																		
Guernea coalita (Norman)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	1	–	–	–	–	–	–	–
Photidæ.																																		
Microprotopus maculatus Norman	–	–	2	16	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata (Bate and Westwood)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	2	3	6
Leptocheirus hirsutimanus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
L. pectinatus Norman	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–
Podoceropsis sophiæ Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	2	–	1	–	–
Megamphopus sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	3
Corophiidæ.																																		
Siphonoecetes colletti Boeck	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. dellavallei Stebbing	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	8	–	–	4	c	–	–	–	–	–	–	–	–	–	–
Corophium crassicorne Bruzelius	–	–	9	6	7	8	–	26	9	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	4
(b) *in weed.*																																		
Lyssianassidæ.																																		
Lepidepecreum longicorne (Bate and Westwood)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Socarnes erythrophthalmus D. Robertson	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	?	–
Orchomenella nana (Kröyer)	–	–	–	4	–	7	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoidæ.																																		
Leucothoë spinicarpa (Abilgaard)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1

* Tow-net dragged about 1 ft. from bottom behind a chain designed to dig up the bottom.

‡ F.M.D. = fine meshed dredge, with (†) or without canvas bag inside, as noted.

c = common.

§ Many specimens lost by tube cracking.

f = few.

APPENDIX III: FAUNA LISTS—*contd.*

	Mud.	Fine Sand with Mud.										Fine Sand.																		Mixed Grounds.				
	23	24	2	2	2	2	2	2	2a	2b	52	34	35	36	37	38	39	43	44	45	46	47	53	54	27	26	28	50	51	6	c	32	33	41
Stenothoidæ.																																		
Stenothoë monoculoides (Montagu)	–	–	1	8	11	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. marina (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Metopidæ.																																		
Parametopa kervillei Chevreux	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthonotozomidæ.																																		
Panoploea minuta	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Calliopiidæ.																																		
Apherusa bispinosa (Bate)	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. ovalipes Norman and Scott	–	–	–	11	26	10	8	16	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Atylidæ.																																		
Nototropis swammerdami (H. Milne-Edwards)	–	–	–	–	–	–	3	1	–	–	–	49	–	1	1	6	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. vedlomensis (Bate)	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
N. falcatus (Metzger)	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nototropis sp.	–	–	–	–	–	–	5	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammaridæ.																																		
Melita palmata (Montagu)	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. obtusata Montagu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Maera grossimana (Montagu)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Gammarus locusta (L)	–	–	–	4	1	18	3	4	2	2	–	100	7	10	5	3	57	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Dexaminidæ.																																		
Dexamine spinosa (Montagu)	–	–	–	35	43	9	–	5	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aoridæ.																																		
Aora typica Kröyer	–	–	–	38	9	5	–	8	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coremapus versiculatus Norman	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Photidæ.																																		
Eurystheus maculatus (Johnston)	–	–	–	–	1	6	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphithoidæ.																																		
Amphithoë vaillanti Lucas	–	–	–	36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Amphithoë sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleonexes gammaroides Bate	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jassidæ.																																		
Jassa falcata (Montagu)	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jassa sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corophiidæ.																																		
Erichthonius brasiliensis (Dana)	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
Corophium sextoni Crawford	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
C. bonelli G. O. Sars	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Caprellidæ.																																		
Phthisica marina Slabber	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Pariambus typicus (Kröyer)	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

The Fauna of Certain Estuaries in West England and South Wales, with Special Reference to the *Tanaidacea, Isopoda* and *Amphipoda.*

By

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With 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

DURING the summer of 1935 Captain Nicholson of Saltash kindly put his motor-boat at my disposal and took me for seven full-day collecting trips on the estuaries of the Tamar and its confluents, the Tavy and Lynher. I also made some collections from land in the estuaries of the Plym and Exe (S. Devon), Taw (N. Devon), Camel (N. Cornwall), and Towy (S. Wales).

All collecting was done intertidally or in shallow water and was practically confined to the brackish-water reaches. No gear was used except a hand-net of stramin, and a zinc sieve of 1-mm. mesh. More attention was paid to the Crustacean orders Tanaidacea, Isopoda, and Amphipoda than to the rest of the fauna, observations on which were only occasionally made.

No salinity measurements were taken, since Percival (1929) had already recorded enough to give a general impression of salinity-range at various parts of the Tamar estuary, and I had not time for the periodic measurements necessary for a real understanding of the effect of salinity on the distribution of species.

FAUNA OF THE ESTUARIES.

Rivers Tamar, Tavy, and Lynher.

An account of the Tamar and Lynher and their fauna has already been given by Percival (1929). Some of his identifications, as I show on page 656, are probably incorrect.

In the following summary of my collecting the species are arranged in the order adopted in the Plymouth Marine Fauna (1931). The localities are considered in order from the most to the least saline, and the rivers in the order Tamar, Tavy, Lynher. Their position is shown in Fig. 1. For most of the identifications I am entirely responsible. Some specimens of the following species have, however, been examined, and their identification confirmed, by experts to whom I wish here to express my deep gratitude. *Heterotanais örstedii*† was referred to Dr. J. H. Schuurmans Stekhoven of Utrecht; *Cyathura carinata, Idotea viridis,* and *Paragnathia formica* to Professor W. M. Tattersall; *Gammarus duebeni, G. zaddachi,* and *G. chevreuxi* to Mrs. Sexton; and *Melita pellucida* and *Leptocheirus pilosus* to Dr. K. Stephensen of Copenhagen.

ISOPODA.

**Cyathura carinata* (Kröyer). Tavy, Mt. Jessop, in mud-flat on river bank: Lynher, Sconner Creek, in mud.

**Paragnathia formica* (Hesse). Tavy, Mt. Jessop, under stone: Lynher, Wivelscombe Lake, Sconner Creek, in "salting cliff."

**Sphaeroma rugicauda* Leach. Tamar, Kingsmill Lake, salting pools; Clifton Marsh, salting pools; Whitsam, open creek; Haye, creek above sluice: Tavy, Mt. Jessop, under stones: Lynher, Sconner Creek, salting pools and cliff; Wivelscombe Lake, salting pools.

**S. hookeri* Leach. Tamar, Crosspark Wood, creek above sluice: Tavy, Lopwell Ford, main channel and creek above sluice.

**Idotea viridis* (Slabber). Tamar, Neille Point, in weed on buoys: Lynher, Wivelscombe Lake, salting pools.

AMPHIPODA.

Melita palmata (Montagu). Tamar, Weston Mill Lake, near H.W.M. among weed; Neille Pt., mussel bed and buoy; Crosspark Wood, among *Obelaria gelatinosa*: Lynher, Rat I., pools and under stones; Wivelscombe Lake, in ditch.

**M. pellucida* G. O. Sars. Tamar, Haye, creek above sluice: Tavy, Blaxton (open) creek, among oak-leaves, etc.; Lopwell Ford, creek above sluice; Lopwell Ferry, main channel under stones.

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† Kröyer's original spelling of this name was Örstedii: any change beyond altering the capital to a small letter seems to me a breach of Article 19 of the Int. Rules of Zool. Nomenclature.

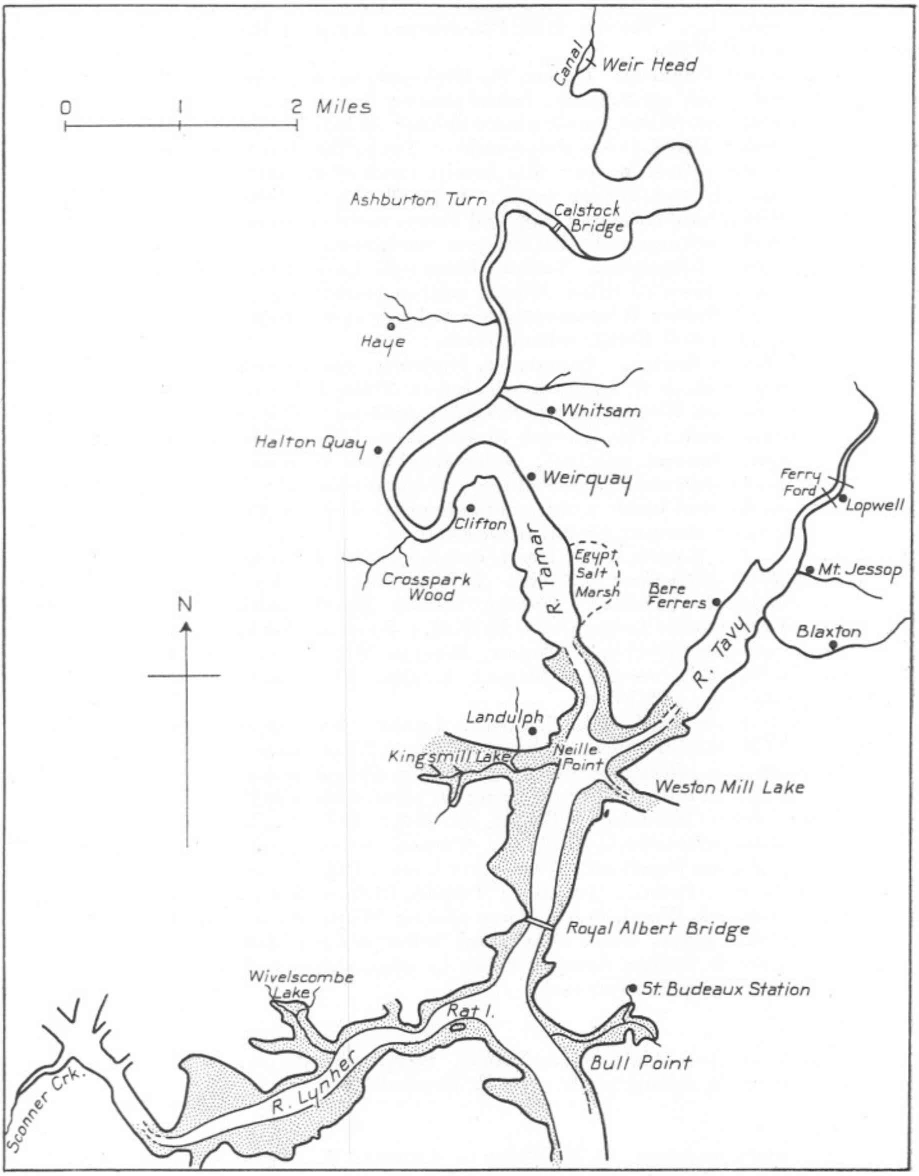

FIG. 1.—Map of Estuaries of Tamar, Tavy and Lynher.

Gammarus marinus Leach. Tamar, Clifton Marsh, and Crosspark Wood, in Fucus intertidally: Tavy, Blaxton Creek, Fucus at outflow: Lynher, Sconner Creek, Fucus; Rat I., under stones.

G. locusta (L.). Tamar, Bull Pt., buoys; Lynher, Rat I., under stones near L.W.M.

**G. chevreuxi* Sexton. Tamar, St. Budeaux, open creek; Kingsmill Lake, first creek on S. bank, below sluice; Landulph, creek above sluice; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek; Haye, creek above sluice: Tavy, Blaxton Creek, from outflow to nearly fresh water; Mt. Jessop, creek above and below sluice, main channel, and salting pools; Lopwell Ford, creek above and below sluice, main channel; Lopwell Ferry, main channel: Lynher, Sconner Creek, salting pool with *Scirpus maritimus*.

**G. duebeni* Lilljeborg. Tamar, Kingsmill Lake, first creek on S. bank, inside sluice; Clifton Marsh, salting pools; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek: Tavy, Mt. Jessop, and Lopwell Ferry, salting pools.

**G. zaddachi* Sexton. Tamar, St. Budeaux, open creek; Kingsmill Lake, first creek on S. bank, above sluice; Neille Pt., mussel-bed and buoy; Crosspark Wood, among *Obelaria gelatinosa*; Whitsam, more southerly open creek; Haye, creek above sluice: Tavy, Blaxton Creek, from main channel upwards, penetrating into permanently fresh water; Mt. Jessop, creek inside sluice, and main channel; Lopwell Ford, creek outside and inside sluice, main channel; Lopwell Ferry, main channel: Lynher, Sconner Creek, from Fucus.

G. pulex L. Tamar, Weir Head, derelict canal (fresh water).

Orchestia mediterranea A. Costa. Lynher, Rat I., under stones, H.W.M.

O. gammarella (Pallas). Tamar, Clifton Marsh, salting cliff: Lynher, Wivelscombe Lake, above H.W.M.; Sconner Creek, salting cliff.

Hyale nilssoni (Rathke). Tamar, Weston Mill Lake, H.W.M. in weed; Neille Pt., weed on buoys: Lynher, Wivelscombe Lake, among Salicornia and Fucus.

Microdeutopus gryllotalpa A. Costa. Lynher, Wivelscombe Lake, in ditch (J. Nicholson collected these in 1934: I have seen his specimens).

**Leptocheirus pilosus* Zaddach. Tamar, in *Cordylophora lacustris* on rocks, Whitsam and Ashburton turn; on piers, Calstock Bridge.

Jassa falcata (Montagu). Tamar, on buoys, Bull Pt., Neille Pt.

Corophium acherusicum A. Costa. Tamar, on buoys, Bull Pt., Neille Pt.

**C. insidiosum* Crawford. Tamar, on buoys, Bull Pt., Neille Pt.

**C. volutator* (Pallas). In mud: Tamar, Clifton Marsh, in salting pools; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek; Haye, creek above and below sluice; Ashburton Turn and Calstock Bridge, forming tubes in mud aggregated about the stolons of *Cordylophora lacustris*.

INSECTA.

**Aedes detritus* (Halliday). Tamar, Egypt marsh, and Clifton marsh, larvae in salting pools. (J. F. Marshall det.)

MOLLUSCA.

Limapontia capitata (O. F. Müller). Lynher, Wivelscombe Lake, salting pools. (Miss M. V. Lebour det.)

Of these species those marked with an asterisk may be considered the truly brackish-water species, which do not occur normally in fully marine or freshwater conditions. Of the remainder *G. pulex* is a freshwater species (whose presence in Tamar fresh water deserves notice since it is not found in all rivers), and the rest are marine.

From a study of the habitats chosen by the species of Gammarus, it appears to me (as has been remarked by previous workers) that *G. marinus* inhabits a higher tidal level than *G. locusta*, and penetrates farther up the estuary. I can, however, make no general statement about the ecological relationships of the three brackish-water species which would accord with all the facts observed while collecting in this and other estuaries.

The drainage creeks running into these estuaries are usually fitted with a sluice, which is closed by the pressure of the rising tide. Above the sluice the creek is not subject to any considerable influx of salt-water, although the soil may be impregnated with salt, but the level of water rises forming a "freshwater tide." Conditions below these sluices or in "open creeks" are subject to the same fluctuations as those in the main channel.

Two special habitats should be mentioned. (i) The buoys, the weed on which contains a characteristic fauna of which the most noteworthy species are *Corophium acherusicum* and *Jassa falcata*, both marine species. In 267 specimens counted at random from Neille Point buoys there were found :—

Corophium acherusicum	259	*Gammarus zaddachi*	2
C. insidiosum	3	*Melita palmata*	1
Jassa falcata	2		

Idotea viridis and *Hyale nilssoni* were also present.

(ii) The "Salting Cliff," or vertical face where the salt-marsh gives on to the mud-flats. *Paragnathia formica* is found practically nowhere else : *Orchestia gammarella*, *Sphaeroma rugicauda*, and *Carcinus maenas* are present in this and several other habitats.

River Plym.

All collecting from the Plym Estuary was done in the brackish-water ditches of Chelson Meadow on August 9, 1935. These drain by means of a sluice into the estuary of the Plym, at a point where it is practically an arm of the sea. Near the sluice the ditches contain a dense growth of *Ruppia marina*, from which the following species were washed :—

Sphaeroma hookeri, abundant.
Melita palmata, a few.
Leptocheirus pilosus, common.
Corophium insidiosum, abundant.

This fauna persisted in the larger ditches for some distance from the sluice. It was replaced in fresher water by the following :—

Sphaeroma hookeri, abundant.
Gammarus chevreuxi, abundant.
Corophium insidiosum, a few.

These three species penetrated, but not commonly, into water which contained a freshwater flora and insect larvæ.

Gammarus zaddachi was not seen, and only one specimen of *G. duebeni* (in nearly fresh water). On occasions the latter species has been recorded as common, and *Corophium volutator* is known to be present.

River Exe.

Five collections were made in brackish water on July 21, 1935.

1. Countess Wear, bed of main stream under bridge, tidal. *Phragmites communis* on bank, Enteromorpha sp. and *Potamogeton ?pectinatus* in stream.

Gammarus zaddachi abundant, together with several *Limnaea pereger* and a few Asellus sp.

2. Countess Wear, in a tidal ditch to W. of R. Exe.

G. zaddachi, a few. *G. pulex*, common.
Succinea putris (Gastropod) and *Haemopis sanguisuga* (Leech) also present.

3. A pond formed behind a sluice on the upper of two streams running through the Powderham Estate. *Scirpus maritimus* and Fucus sp.

Sphaeroma hookeri, 20–30. *Gammarus zaddachi*, abundant.
Jaera marina, 2. *Leptocheirus pilosus*, 2.
Hydrobia ulvae was also present.

4. Dawlish Warren, stream with freshwater tide, drying out at low water, exposing mud flats. These species, except for *Corophium volutator*, were washed from Fucus and Enteromorpha.

Heterotanais örstedii form *örstedii*, 15 ♂♂, ♀♀ abundant.
Cyathura carinata, 1 (presumably from mud around Fucus roots).
Leptocheirus pilosus, common. *Gammarus duebeni*, common.
Melita pellucida, several. *Corophium volutator*, common in the mud.

5. The same stream below the sluice.

Leptocheirus pilosus, 1. *Gammarus* sp., 2.
Melita palmata, 6.

River Taw (*Caen River*).

On August 4, 1935, several collections were made on the estuary of the Caen River, a confluent of the Taw on its right bank. The results are enumerated below from the mouth upstream, that is in order of descending salinity, with the exception of a few isolated waters which are placed at the end of the section. Their position is shown in Figure 2.

1. Sand at L.W.M., at confluence with R. Taw.

Eurydice pulchra, a few. *Haustorius arenarius*, a few.
Bathyporeia sp. indet., estimated at 4,000 per sq. m.

It seems that conditions at this point are nearly marine.

2. Outside sluice of small stream.

Gammarus chevreuxi, 1.
Orchestia ?gammarellus, 3 juv.

3. Salting cliff.

Paragnathia formica, 13.
Sphaeroma ?hookeri, 1.

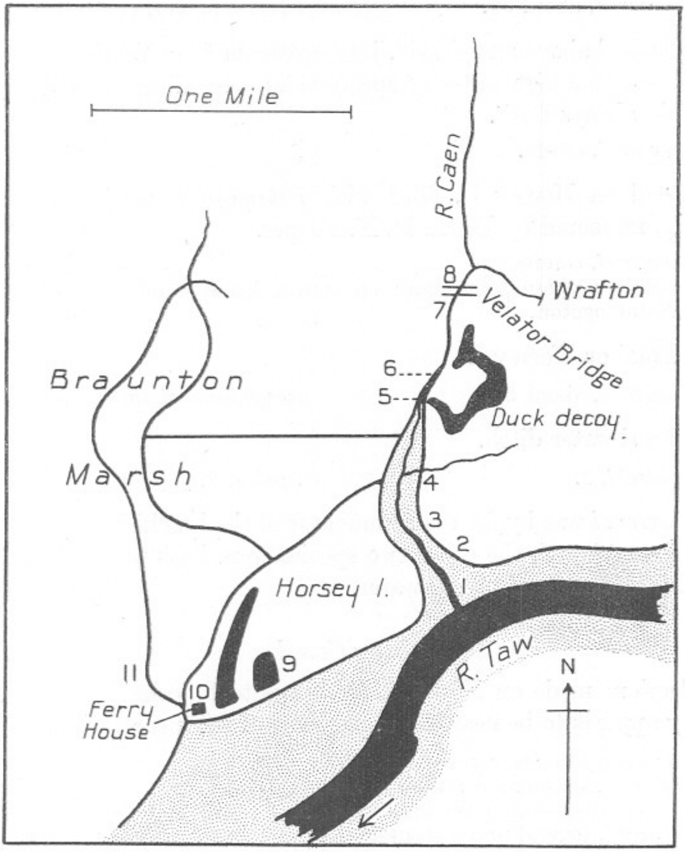

FIG. 2.

4. Open stream, above sea-wall.

Cyathura carinata, 1.
Sphaeroma hookeri, 1.
Melita pellucida, a few.
Gammarus chevreuxi, several hundred.
G. duebeni, a few.

4a. The same, below sea-wall.

G. marinus, 9.
G. chevreuxi, 1.

5. S.W. end of Duck Decoy Pond.

G. chevreuxi, 30.
Palaemonetes varians, 3.
Anopheles maculipennis (mosquito), 3 larvæ.
Corixa sp., sticklebacks, water-mites.

This water is presumably nearly fresh.

6. From Fucus at half tide.

Sphaeroma hookeri, 1.	*G. chevreuxi*, 3.
G. marinus, 5.	*G. zaddachi*, 2.

7. Channel below Velator Bridge (Enteromorpha and sewage).

G. chevreuxi, about 30. [*Corophium volutator*, common in mud.]

8. Channel above an 8-ft. sill, just upstream from Velator—entered by tide at extreme high water of spring tides, according to local boys, but probably always fresh.

G. chevreuxi, 50–60.

9. Pond on Horsey I., filled with *Potamogeton pectinatus*. Salinity $10{\cdot}7^{\circ}/_{\circ\circ}$, measured by Dr. L. H. N. Cooper.

G. chevreuxi, common.
Leptocheirus pilosus, abundant on stems, leaves, and especially roots of Potamogeton.

10. Pond on Horsey I.

G. chevreuxi, about 30. *Corophium volutator*, about 20.

11. Freshwater ditch.

G. zaddachi, 2. *G. pulex*, 9.

G. chevreuxi was by far the commonest of the brackish-water species of Gammarus (though the other two species were both present), and penetrated into completely fresh water.

River Camel.

Collections made on May 5, 1935, opposite Egloshayle Church. This locality appears to be near the upper limit of salt penetration.

Paragnathia formica, common in salting cliff.
Sphaeroma rugicauda, common in salting pools.
Gammarus chevreuxi, a few under stones.
G. zaddachi, several under stones.

River Towy.

Ferryside and Carmarthen are about 7 miles apart: my collecting was done on August 25, 1935, half-way between them, on an extensive salting, intersected by streams coming from high ground to the East. A short distance upstream from this salting, rocky shores came down to L.W.M., near which *Cordylophora lacustris* grew on the rocks. The locality resembled the Tamar between Clifton and Whitsam.

Heterotanais örstedii f. *örstedii*, 1♂, about 20♀♀ in *Cordylophora lacustris*.
Paragnathia formica, 4 in salting cliff.
Sphaeroma hookeri, 2 in salting cliff.
Melita pellucida, 2 among Enteromorpha in open stream.

Gammarus zaddachi, about 30 among grasses, etc., above a sluice; about 20 among Enteromorpha in open stream.
G. duebeni, 15 in hanging grass in open stream.
Orchestia gammarella, 3 in salting cliff.
Leptocheirus pilosus, about 12 in *Cordylophora lacustris*.
Corophium volutator, 5 in salting cliff.

It is surprising that *Heterotanais örstedii*, whose connexion with *Cordylophora lacustris* has been previously noted by Gurney (1907), was not found in the far greater quantities of this hydroid collected from the Tamar. *Gammarus chevreuxi* was specially looked for in the Tavy, and therefore may be presumed to be absent.

BRACKISH-WATER CRUSTACEA IN ENGLAND.

Definition.

It is not possible to define the term "Brackish-Water Species" in terms of salinity, since the changes of salinity to which an animal is subject depend as much on its habits as on the position of its habitat along the estuary. It is possible, however, in the fauna of an estuary to distinguish certain species which belong more properly to fresh water (e.g. *Gammarus pulex*), or to the sea (e.g. *G. locusta, G. marinus, Melita palmata*, etc.), than to brackish water, although such distinctions are not always clearly marked, and may have only local significance.

If such as these are omitted, there remain 14 brackish-water species of Tanaidacea, Isopoda, and Amphipoda in England, of which I have collected all, except *Corophium lacustre*, from the south-western estuaries.

Literature.

The most important lists of brackish-water Crustacea in Britain are included in the following papers:—

Gurney (1907); Rivers Bure, Yare and Waveney, Norfolk.
Serventy (1935); River Deben, Suffolk.
Omer-Cooper (1916); Christchurch Harbour, Hants (Tanaidacea and Isopoda only).
Percival (1929); Rivers Tamar and Lynher, Devon and Cornwall.

A great number of comparable lists have been compiled for brackish water on the coasts of the Baltic and North Sea. A bibliography of these and a summary of their contents are given by Sick (1933).

Some of these lists contain errors for which I here suggest corrections, either after examining specimens myself, or on the authority of other writers, or (with less assurance) on circumstantial evidence contained in the original paper.

GURNEY (1907). *Gammarus duebeni* refers in part to *G. zaddachi*, Serventy (1935, p. 292). *Microdeutopus* (=*Coremapus*) *versiculatus* on p. 427 and Table II refers to *Leptocheirus pilosus* : I have examined specimens in the British Museum. *Leptocheirus* sp. also refers to *L. pilosus*, Norman (1908). *Corophium grossipes* refers in part to *C. volutator* (pp. 417, 421, 427 part, 435 part, Table II part) and in part to *C. lacustre* (pp. 423, 427 part, 435 part, Table II part). I base this conclusion on circumstantial evidence. *C. volutator* burrows in the mud of estuaries, and *C. lacustre* builds tubes, usually among *Cordylophora lacustris*, in regions of low salinity, and was abundant in collections of this hydroid made for me in Heigham Sound in 1935. *Gnathia maxillaris* refers to *Paragnathia formica*, Monod (1926), and *Heterotanais gurneyi* to *H. örstedii* f. *gurneyi*, Monod (1924).

Serventy (1935). *Heterotanais gurneyi* refers to *H. örstedii* f. *gurneyi*.

Omer-Cooper (1916). *Paragnathia halidaii* refers to *P. formica*, Monod (1926).

Percival (1929). Percival's specimens are not available, and the following corrections are based on what seems to me satisfactory circumstantial evidence. All the species to which I suggest his names apply have been collected by me in the Tamar estuary in localities similar to those which he records. For *Anthura gracilis*, a marine species, read *Cyathura carinata*, a burrower in estuarine mud : for *Sphaeroma serratum* possibly read *S. rugicauda* : for *Idotea baltica* read *I. viridis*, which was common in the Zostera of St. John's Lake : for *Gammarus locusta* read *G. zaddachi*, at least in the less saline parts of its range : for *Corophium crassicorne* read *C. acherusicum*, which was present in the mussel-bed and abundant on the buoys at Neille Point.

Poisson and Remy (1926). Canal de Caen, France. For *Corophium acutum* var. *chevreuxi* read *C. lacustre*. I have examined specimens sent me by Mme Leroux.

Tesch (1922). Zuider Zee, Holland. For *Corophium grossipes* read *C. volutator* (a synonym), and for *C. crassicorne* read *C. lacustre*. Tesch's figures, though crude, seem to refer to *C. lacustre*, and Redeke (1922 and 1932) records *C. lacustre* from the Zuider Zee.

Schlienz (1923). Elbe, Germany. For *Leptocheirus hirsutimanus* read *L. pilosus*. He found his Leptocheirus in *Cordylophora lacustris*, which is the favourite habitat of *L. pilosus* : at Plymouth *L. hirsutimanus* is a marine species.

Table I has been compiled from the papers of Gurney (1907), Serventy (1935), and Omer-Cooper (1916), with such alterations in identification of species as I have suggested. The presence of species in the Tamar is based entirely on my own collecting : the presence of *Corophium volutator* in Chelson Meadow (Plym) is based on the Plymouth Marine Fauna (1931).

TABLE I.

	Norfolk, Gurney (1907).	R. Deben, Serventy (1935).	Christ Church Omer-Cooper (1916).	R. Tamar, etc.	R. Plym.	R. Exe.	R. Taw.	R. Camel.	R. Towy.	Other British Records (list incomplete).
TANAIDACEA.										
Heterotanais örstedii										
f. *örstedii* Kröyer.	—	—	×	—	—	×	—	—	×	
f. *gurneyi* Norman.	×	×	—	—	—	—	—	—	—	
ISOPODA.										
Cyathura carinata (Kröyer).	×	×	×	×	—	×	×	—	—	
Paragnathia formica (Hesse).	×	×	×	×	—	—	×	×	×	R. Welland (G.I.C.).
Sphaeroma rugicauda Leach.	×	×	—	×	—	—	—	×	—	See Omer-Cooper and Rawson (1934), pp. 34–36.
S. hookeri Leach.	—	—	—	×	×	×	×	—	×	See Omer-Cooper and Rawson (1934), pp. 36–38.
Idotea viridis (Slabber).	×	—	×	×	—	—	—	—	—	
AMPHIPODA.										
Melita pellucida G. O. Sars.	×	—	—	×	—	×	×	—	×	Benfleet, Essex (G.I.C.).
Gammarus chevreuxi, Sexton.	—	—	—	×	×	—	×	×	—	Warwickshire, Pentelow (1931).
G. duebeni, Lilljeborg.	?×	×	—	×	×	×	×	—	×	Essex (G.I.C.). R. Tees, Alexander, etc. (1935)
G. zaddachi, Sexton.	×	×	—	×	—	×	×	×	×	Tewkesbury, Glos; R. Test, Hants; R. Frome, Dorset; Benfleet, Essex (G.I.C.). R. Tay, Bassindale (1933). Essex, Palmer (1933). R. Tees, Alexander, etc. (1935).
Leptocheirus pilosus Zaddach.	×	×	—	×	×	×	×	—	×	
Corophium volutator (Pallas).	×	×	—	×	×	×	×	—	×	Numerous.
C. insidiosum Crawford.	—	—	—	×	×	—	—	—	—	
C. lacustre Vanhöffen.	×	—	—	—	—	—	—	—	—	

Distribution in England.

For all these species, except *Gammarus chevreuxi*, records have been published of occurrences abroad. In Southern England most of them seem to be present in every sizeable estuary. A few do not range over the whole of S. England.

Heterotanais örstedii was not found in England west of the Exe, though in the Tamar and Taw suitable habitats were carefully searched. According to Monod (1924) the two forms *örstedii* and *gurneyi* may live together.

Gammarus chevreuxi was present in the Tamar, Plym, Camel, and Taw, but not in the Towy, Exe, Frome (Dorset), Test (Hants), New England Creek (Essex), or at Benfleet (Essex). Collecting, except in the Frome and Test, was calculated to find this species if present. It is almost certainly absent from the Norfolk rivers and the Deben investigated by Gurney and Serventy. Its presence in inland brackish water near Coventry is well authenticated, Pentelow (1931).

Corophium insidiosum is so far known in England only from the Tamar, Chelson Meadow, and Plymouth Sound. Abroad it has been collected from Denmark, Germany (Kiel Canal), and Italy (Lake of Venice).

C. lacustre is so far known in England only from the Norfolk Broads. It is found abroad in France, Holland, Germany, and North America.

Habitats of Certain Estuarine Species.

Heterotanais örstedii builds tubes on hydroids and weed.

Cyathura carinata burrows in mud. *Paragnathia formica* makes burrows in salting cliffs, but I have found it under stones, cf. Monod (1926). The two species of Sphaeroma are not rigidly attached to one habitat, but live among weed, under stones or in holes in salting cliffs. *S. rugicauda* is especially common in salting pools, and *S. hookeri* in large brackish-water ditches as at Chelson Meadow (Plym). *Idotea viridis* lives on weed, especially on Zostera spp. and Ulva sp.

Melita palmata lives among weed, and is often abundant under stones : *M. pellucida* was chiefly found where there was much decayed land or freshwater vegetation among which it sheltered. The various species of Gammarus shelter among weed, dead leaves or twigs, or under stones.

Orchestia gammarella is found near high-tide mark along sea coasts and estuaries, sheltering under decaying vegetation or stones : it is also found on salt marshes and in holes in the salting cliff. I have found it in fresh water on the cliff near Kynance Cove, 200 ft. above sea-level.

Leptocheirus pilosus builds tubes, especially on *Cordylophora lacustris*, but also on any weed growing in suitable water. *Jassa falcata* builds tubes, especially on buoys.

The species of Corophium build tubes. *C. acherusicum* lives most often on buoys: *C. insidiosum* among weeds in water of rather high salinity (*ca.* 20°/₀₀). *C. volutator* builds its tubes in mud, usually on the intertidal mud-flats, or the floor of salting pools or creeks. At Ashburton Turn and Calstock its burrows are made in mud aggregated round the base of *Cordylophora lacustris*. It is frequently found in mud which has settled on horizontal piles. On the Towy I found it in holes in the salting cliff. *C. lacustre* builds tubes on weeds in water of low salinity, especially among *Cordylophora lacustris*.

NOTES ON THE IDENTIFICATION OF GAMMARUS SPECIES.

Seven species of Gammarus are known from England.

G. marinus Leach, marine.
G. locusta (L.), marine.
G. campylops Leach, marine.
G. chevreuxi Sexton, brackish-water.
G. duebeni Lilljeborg, brackish-water.
G. zaddachi Sexton, brackish-water.
G. pulex (L.), freshwater.

I have collected all of these except *G. campylops*. It is probable that there are other species, both marine and estuarine, in Great Britain which are as yet unnamed. Since also the known species are often confused with one another, records should always be critically examined by later workers, if possible with the help of specimens deposited in some trustworthy and accessible institution.

The species about which most confusion has arisen is *G. zaddachi*, which has been frequently recorded as *G. locusta* or *G. duebeni*.

Usually I found *G. zaddachi* easy to distinguish by the criteria listed by Sexton (1912), especially when there were numerous adult specimens available for examination. Younger specimens were not always identifiable unless accompanied by adults. Of these distinctions the most useful is the arrangement of hairs in graduated clusters on the first antenna, and especially on the basal joint; these vary greatly in length from one locality to another, but the general arrangement is characteristic. Other important characters are: (i) hand larger in the second gnathopod than in the first gnathopod, especially in ♂ (in *G. duebeni* the difference in size is slight): (ii) in adult ♂♂ the basal joints of the fifth and sixth pereiopods are only slightly expanded, and the hind corner is free only in the fifth pereiopod. Sexton based her statements on specimens from Bremerhaven, Hamburg, and Ireland. I have found them to be true also for specimens from Devon and Cornwall.

Poulsen (1932) gives a list of features which he states are characteristic of *G. zaddachi*. A number of these were not found in the type material which Mrs. Sexton kindly allowed me to examine, and were not in agreement with statements made in her original description. In particular, Poulsen states that the hind corner of the basal joint of the fifth pereiopod is pointed : I have always found it rounded. Further that the urosome of *G. zaddachi* is not hairy. I have found it always hairy and sometimes, as in the type German material, very hairy. Possibly Poulsen was examining some other species.

Gammarus duebeni is a very stout species, and usually of a muddy greenish- or reddish-brown colour. *G. zaddachi* is more slender, and its colours are more clear. The length and density of the setae on the antennae, limbs, and urosome of *G. duebeni* are very variable, as in *G. zaddachi*, but there are never more than a few small tufts of hairs (not graduated) on the basal joint of the first antenna.

I am not able to distinguish between the habitats of the three brackish-water species, *G. chevreuxi*, *G. duebeni*, and *G. zaddachi*. I found all three in every sort of brackish water in the rivers investigated, and sometimes one and sometimes another penetrated farthest upstream. I found all in fresh water—*G. chevreuxi* in the Taw ; *G. zaddachi* in the Taw (Braunton Marsh), the Tavy (Blaxton Creek), and the Avon at Tewkesbury ; *G. duebeni* up to 200 ft. above sea-level in streams running into the English Channel at Kynance, Cornwall, and nearby, and in similar situations in Anglesey.

There is a great deal of investigation still needed into the systematics, ecology, and physiology of Gammarus, even of the British species.

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A Double-tailed Eulalia.

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With 4 Figures in the Text.

INTRODUCTION.

WHILE examining a bowl of rock dredgings from the Mewstone Grounds near Plymouth, on 10th December, 1926, my attention was attracted by a handsome Phyllodocid worm which had evidently crawled out of a crevice in the broken rocks. On closer investigation the worm proved to be of an unfamiliar species and, of much greater interest, to possess a small secondary tail arising ventrally rather more than two-thirds of the way down the body (Fig. 1). Scale drawings, made at the time from the living animal, have recently been carefully checked by examination of the preserved specimen; only a few slight alterations have been found necessary.

A fairly large number of naturally occurring double-tailed and a few double-headed annelids have previously been recorded, especially among earthworms. A number of other double-tailed or double-headed worms have been produced artificially during regeneration experiments. In nearly every instance, however, the bifurcation is lateral and, with tails especially, very few dorso-ventral bifurcations have been obtained. The worm described in this paper is therefore of considerable interest in that the branching is of the latter type. This bifurcation will be considered first and the specific identity of the worm discussed afterwards.

THE BIFURCATION.

From the head to the 175th segment (the buccal segment carrying the first pair of tentacular cirri is, of course, counted as the first) the worm is perfectly normal. At the posterior ventral border of segment 175 the secondary tail arises. Its first few segments come off almost at right angles to the main body axis, but almost immediately the tail bends back until it is parallel with the primary tail above. In life the secondary tail was generally dragged along below the primary one, but occasionally it would be twisted to the right or to the left as shown in the drawings. It is composed of 28 segments and a pygidium and is about 5 mm. long.

It appears to be a newly grown structure ; its segments are smaller than those of the worm trunk immediately preceding, otherwise they are normally formed. The terminal pygidium has two caudal cirri and an anus.

Viewed from above it will be seen from Figs. 1 and 2 that at the place where the secondary tail arises the main body of the worm perceptibly narrows. The worm is widest about half-way from the head, and for a good many segments before it bifurcates the body width decreases gradually ; this is varied in life by the contractile movements used in crawling. At the fork the main body narrows abruptly owing to the comparatively small size of segments 176 to 179. Succeeding segments are of normal width (except for a slight slenderness of 180, 181 and possibly 182) continuing the interrupted gradual taper of the body to the anus. It should be noted that in Figs. 2 and 3 the normal segments of the primary tail are drawn as shortened, and therefore widened, by longitudinal contraction. The primary tail consists in all of 87 segments.

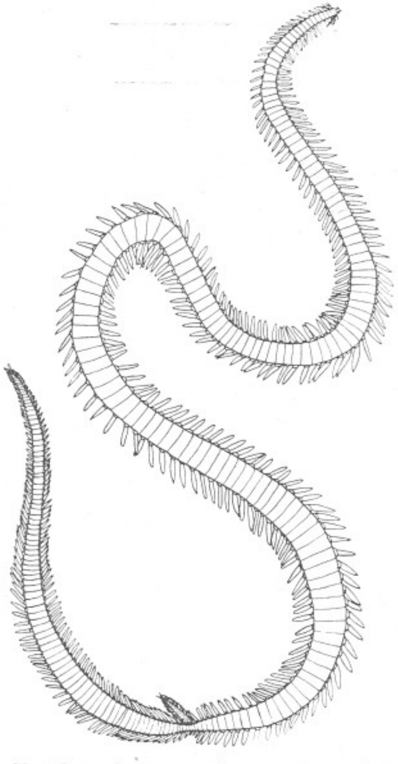
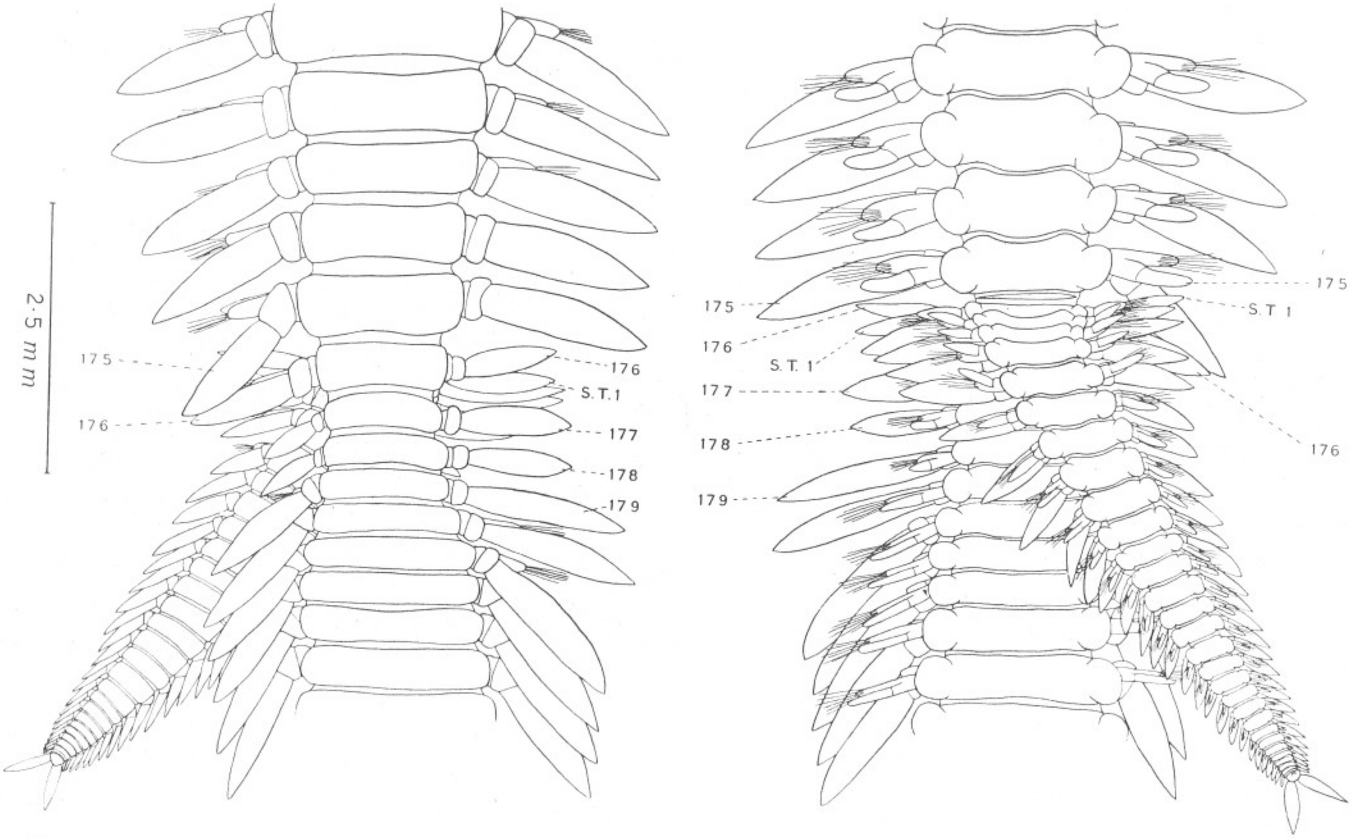


FIG. 1.—Sketch to show general proportions of the worm. From life × $1\frac{1}{2}$ approx.



Figs. 2 and 3.—Dorsal and ventral views of the secondary tail region. Drawn mainly from life. Main body segments 175–179 or their parapodia are numbered. The first segment of the secondary tail or its dorsal cirri are indicated by the lettering S.T. 1.

The parapodial details of the narrowed region provide a clue as to what has happened and will be considered in some detail.

Segment 176. The left parapodium was evidently normal in size or nearly so. Unfortunately it has broken off in the preserved specimen and therefore cannot be checked. The scar can be seen. The right parapodium is smaller than normal, but is complete with bristles and ventral cirrus.

Segment 177. The left parapodium consists only of a very small dorsal cirrus, the other parts of a normal parapodium being absent. The right parapodium, like the one in front of it, is of medium size and is complete with bristles and ventral cirrus.

Segment 178. The left parapodium again consists only of a very small dorsal cirrus, but the right parapodium is of medium size and is complete.

Segment 179. Both parapodia have normal dorsal cirri, but bristle lobes, bristles and ventral cirri are smaller than normal.

On the left ventral sides of segments 178 and 179 the body wall is ruptured. During life a number of eggs, of which the body was full, escaped through the hole, while in the preserved specimen a small portion of the gut protrudes.

Discussion.

There can be little doubt as to how the secondary tail and other abnormal structures came to be formed. It is almost certain that they were due to an injury, perhaps from a fish bite, that had removed a piece of tissue consisting of the ventral body wall of segments 176–179, the left parapodium of segment 176, all the parapodia of segments 177 and 178, and the ventral cirri and bristle lobes of segment 179. With it the nerve cord, together very probably with a ventral portion of the gut as well, would be removed in those four segments. The tail from segment 180 onwards would thus remain attached to the front part of the body only by a strip of dorsal body wall and a portion of the dorsal wall of the gut. For some reason the body did not break finally into two separate portions at this place, as it might very well have done ; instead the wound began to heal. Possibly the left side of the body wall of segments 177 and 178 was cut away at a higher level than on the right side where perhaps only the parapodia had been removed. This would account for the less completely regenerated parapodia on the left where more new tissue had to be formed before they could begin to grow again. It might also be responsible for the hole in the body wall on that side, the gap not yet having closed up. On the other hand the hole may be a new injury in what presumably would be weak new tissue, but I think the first explanation is the more likely.

If the hypothesis just advanced be correct, the appearance of a secondary tail is not at all surprising and might, indeed, have been predicted. We know from the work of others that in annelids regeneration of a new head or a new tail frequently takes place from the cut ends of a worm that has been divided into two portions, although the capacity to regenerate heads and tails varies with the level of the cut and in different species. If this Eulalia had been completely divided by its injury there is no doubt that the anterior portion would have grown a new tail in the ordinary way, and there would then have been nothing abnormal to record. It is merely that the old tail by remaining attached to the anterior portion has complicated the regenerative processes and brought about the formation of a double-tailed monster.

Holmes (1931) and others have demonstrated that in posterior regeneration the presence of the cut end of the ventral nerve cord at wound level is all important if normal regeneration is to follow. In some way the nervous elements govern organization of the new tissues into a properly formed new structure. In an injury such as has been postulated this necessary condition would have been fulfilled and regeneration of a tail would proceed from the region of the cut end of the cord at the anterior border of the wound. That a head did not simultaneously form near the severed nerve cord at the posterior border of the wound scarcely demands explanation, for we know (Berrill, 1928 ; Berrill and Mees, 1936) that in some worms the capacity to regenerate a new head is either confined to the anterior segments or does not exist at all, and Eulalia very likely belongs to one or other of these categories (Okada, 1934, p. 374). In Myxicola, however, Okada (1934) has shown that if the ventral nerve cord be transected artificially, in a manner similar to that which we have supposed to have happened in the present instance, a new head usually appears where the wound is made, generally more readily in the posterior region than in the anterior. In Myxicola it is the capacity to regenerate a tail from such a wound that appears to be almost entirely lacking. Very recently Zhinkin (1936) has produced in the Oligochaete Rhynchelmis secondary ventral tails in the middle of the body by operative removal of a portion of the ventral nerve cord, the operation resembling that of Okada on Myxicola. The artificial wound made by Zhinkin would be closely similar to the natural wound in my Eulalia. Incidentally Morgan many years before had supposed (1902, p. 372) that a double-tailed worm would result from such a mutilation.

I do not propose to mention individually the fairly numerous double-tailed worms with lateral bifurcation which have been described. A good bibliography of these can be found in Leloup (1931). In them it is the rule for the ventral nerve cord, and often the gut also, to fork and to pass into both branches of the worm. Dorso-ventral bifurcation, on the other hand, has rarely been seen, especially in naturally occurring examples, but

Andrews (1894) has described a number of bifid specimens of this type, all of the same species, *Podarke obscura*. They are closely comparable with my Eulalia. In them the intestine divided and passed into both branches, but the ventral nerve cord passed from the main anterior trunk into the ventral branch only. The dorsal branch contained its own ventral nerve cord which ended abruptly at the place where the bifurcation took place. Andrews came to the conclusion that the dorsal branch was the original tail of the worm and that the ventral branch was a new structure formed after injury to the ventral nerve cord. His operative experiments made in an attempt to prove this gave negative results. As we have seen Zhinkin has since been successful in an Oligochaete.

In my specimen the internal anatomy cannot be definitely determined without sectioning and I have preferred to keep the specimen intact. There can be little doubt, however, that it is closely similar to what Andrews found in Podarke, and this conclusion is supported by the results of stimulation experiments made on the worm while it was alive. By work on an annelid Bailey (1930) has shown that " impulses for locomotor movements travel only in the ventral nerve cord " and that a cut through the cord stops the passage of a contraction wave down the body. On this principle it is possible to test for places of interruption in the cord. When the primary tail of the Eulalia was anywhere stimulated with a needle the whole of it would contract, but the wave of contraction did not pass forwards beyond the bifurcation or into the secondary tail. Stimulation of the latter structure brought about a contraction that spread into the worm body anterior to the place of forking, but which did not affect the primary tail. Stimulation of the worm anterior to the bifurcation caused a contraction that did not spread to the primary tail. From these observations it seems a reasonably safe conclusion that the ventral nerve cord of the anterior part of the body is continued into the secondary tail, and that the cord of the primary tail is isolated from the rest of the worm. This agrees with the arrangement in Andrews' specimens of Podarke and with his similar stimulation experiments. Incidentally his paper was not seen by me until after my worm had been preserved.

The arrangement of the gut in my Eulalia is not known, but very probably it bifurcates and supplies both tails, each of which has an anus. Faeces can be seen inside that portion of the gut which protrudes in segments 178 and 179.

Finally it may be advisable to mention that although McIntosh gives a figure (1908, Plate XLIX, Fig. 1) which appears at first sight to represent a *Phyllodoce lamelligera* Linn. bearing a secondary tail essentially similar to that of my Eulalia, I consider this figure to be merely an unfinished drawing of a normal worm. In his text McIntosh says nothing whatever about the peculiar position in which the tail is represented. Okada

(1934, p. 374), however, seems inclined to interpret the figure as that of a worm with a secondary tail. If Okada were now to substitute my record for this very doubtful one from McIntosh his argument would still hold good.

THE SPECIFIC IDENTITY OF THE WORM.

The specific identity of the worm is puzzling. It definitely belongs to the genus Eulalia, but I have not been able to decide as to the species. It is quite unlike any Eulalia I have seen during ten years of watching and I cannot satisfy myself that it agrees with the published description of any species. At the same time I am reluctant to propose a new species on the basis of this single specimen, already abnormal in part; indeed, I do not consider such a course advisable in the present unsatisfactory state of the systematics of the genus itself. The worm would not have been mentioned but for the interest aroused by its secondary tail, and I therefore do not feel called upon to do more than to give a full description of it, leaving its status to be decided on some future occasion.

In the preserved and somewhat contracted condition the worm measures about 13 cm. long with a maximum width (excluding the feet) of about 2 mm. There are 262 segments between head and pygidium, 4 of which are abnormal where the secondary tail of 28 segments arises. The body tapers towards both ends.

The prostomium is well rounded, being broader than long. In the preserved condition the anterior portion bearing the tentacles is more distinctly constricted off from the posterior portion by a transverse groove than it was during life. Four of the five tentacles are relatively long, but the fifth or median tentacle appears as though the tip had been cut off accidentally. This tentacle is set level with the front of the eyes. The eyes are large, brown-black in colour.

The first segment bears a pair of tentacular cirri; their proportions are indicated in Figure 4. The dorsal tentacular cirri of the second segment are very long; the ventral cirri are shorter and rather flattened. The fourth pair of tentacular cirri are nearly as long as the preceding dorsal cirri. In the preserved specimen all cirri are somewhat contracted. In Bergstrom's formula the tentacular segments are expressed as follows :—

$$1+\mathrm{O}\frac{\mathrm{ol}}{\mathrm{a1}}+\mathrm{B}\frac{\mathrm{ol}}{\mathrm{aN}}$$

This is based on a dissection of the left side where bristles cannot be seen on the second segment, but it is just possible they have fallen out. Bristles cannot be seen on the right side of this segment either, but as this side has not been dissected it is more difficult to be certain that none is present.

The parapodia vary little from one end of the body to the other. The dorsal cirri are large, leaf-like and pointed. The bluntly rounded ventral cirri do not project beyond the end of the bristle lobe, at least in the preserved state. The bristle lobe has well-rounded lips.

The bristles have swollen denticulate ends to their shafts. On each side one tooth is more prominent than the others. The slender curved blade is finely toothed along its inner edge.

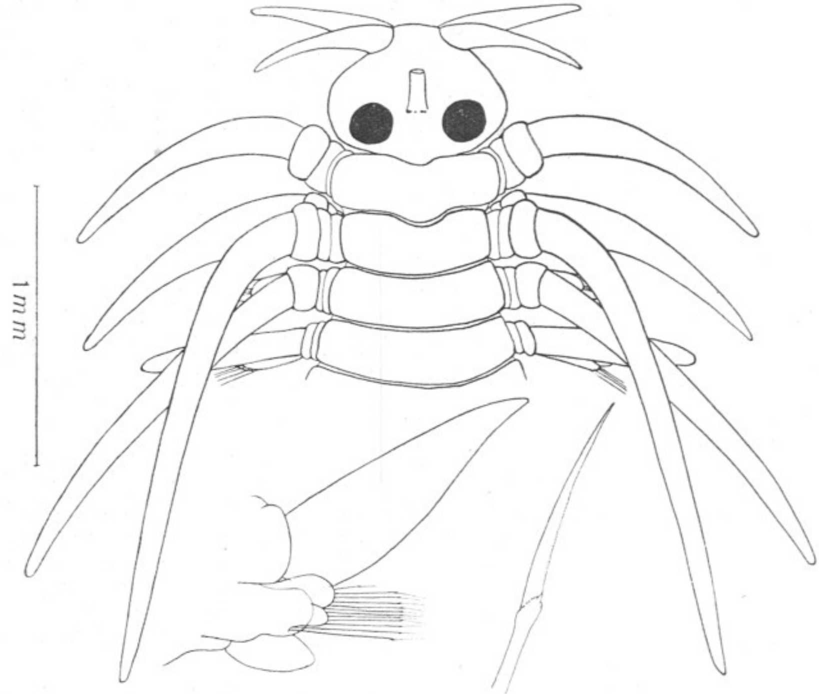


Fig. 4.—Head of the double-tailed Eulalia, from life. The scale is given alongside. Below are drawn an eighty-second parapodium ×25 approx. and one of its bristles×310 approx. after mounting in Farrant's Medium.

The tiny pygidium carries two large anal cirri similar to those on the secondary tail (Figs. 2 and 3).

The proboscis is, unfortunately, not everted.

In life the prostomium, tentacles and tentacular cirri were yellow. The dorsal surface of the body anteriorly was brownish yellow changing to green farther back, to become rapidly yellow again in the last thirty segments. The green colour was due to the body being filled with large numbers of green eggs underlying the yellowish skin. The inter-segmental folds were blue-green, giving a transversely barred effect. An ill-defined dusky band ran down the mid-dorsal surface from the head ; it gradually became lighter than the surrounding colours and continued to the tail as a faint band of lighter shading. The dorsal cirri were bright yellow, sometimes with a green tinge and with a few brown specks on most of them. The bristle lobes and ventral cirri had also one or two brown spots, and a few were present on the sides of many segments close to the insertions of the parapodia. Ventrally the colour was similar to that dorsally, except that two dark blue-green bands ran along on each side of the middle line over the greater length of the body.

The colour pattern of the secondary tail resembled that of the main body. It was greenish near its insertion, owing to contained eggs, but turned to yellow towards its extremity.

The preserved specimen (in alcohol) is very pale pinkish brown. The dark brown spots mentioned above can be seen.

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"Organic" Phosphorus in Sea Water from the English Channel.

By

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The amount of phosphorus in sea-water in organic combination has in recent years received considerable attention. For its determination various methods have been proposed of which the most promising is that of Kalle (1935). The writer has examined a method in which sea-water was evaporated in a platinum dish with sulphuric acid to remove halides, the resultant melt being dissolved in water and treated successively with permanganate and sulphite, made up to a known volume and its phosphorus content determined colorimetrically. This method promised well as a reference method by which others could be checked, but it was very tedious particularly as only a limited amount of platinum ware was available. As a routine method Kalle's modification of Winkler's procedure is much more promising but here it has not given results as concordant as could be wished, the main source of error being a rather large reagent blank which it has not proved possible to reduce. The total content of phosphorus and arsenic, calculated as phosphorus, as found by Kalle's method, appears to be somewhat less than by the evaporation-permanganate oxidation method. One sample gave 1·20 mg.-atom by the permanganate method and 1·00 mg.-atom per cubic metre by Kalle's. This suggests that there may be incomplete oxidation either of arsenite or of organic phosphorus compounds. When a solution of Waksman's ferri-ligno-protein complex (which may well be typical of some of the more resistant organic constituents of sea-water) was added to sea-water, so as to give 120 mg./m^3 of added iron, and then oxidized by bromine water as in the method for "total iron" (Cooper, 1935), only 40% of this iron was set free. It would thus appear that any practicable method of oxidizing organic material in sea-water without prior evaporation is likely to be incomplete. Nevertheless the possibility that iron or phosphorus, that cannot be set free by such drastic processes, has any immediate biological value is remote, so that Kalle's method may quite well give a figure for total biologically available phosphorus (+arsenic).

To reduce arsenate to arsenite and so to render the colorimetric determination of phosphorus free from interference by arsenic, Kalle advocates thiourea. In trial experiments with known amounts of arsenic *in concentrations likely to be found in sea-water* the writer has been unable to effect any reduction whatever with thiourea, with bisulphite, with "Analytical Reagent" zinc or with a special activated zinc containing small percentages of cadmium, copper and tin. Dr. Kalle has very kindly supplied a sample of his own thiourea, but no better success was achieved with this. At high dilutions complete reduction of arsenate to arsenite and the converse oxidation are known to be difficult to bring about and to be very dependent upon the pH value of the solution. The precise conditions for the reduction, which Kalle has evidently found, are difficult to reproduce and investigators intending accurately to determine total phosphorus should make certain that they have succeeded in removing arsenic present.

The conditions governing the arsenate-arsenite equilibrium in sea-water may themselves be of biological interest since to a limited extent for a limited range of species arsenic is able to replace phosphorus (cf. Atkins and Wilson, 1927).

In Table I are given analyses of total phosphorus+arsenic, $\Sigma(P+As)$, in samples of sea-water either unfiltered or filtered through Schleicher and Schüll's filter paper No. 589 (Blueband) as recommended by Kalle. Judging from subsequent work in this laboratory on iron, a membrane filter ought to prove more efficient. The organic phosphorus+arsenic content of unfiltered water from Stations E1 and L4 in early spring and July appears to be very constant. The arithmetic mean of all determinations is 0·44 mg.-atom/m.^{3} and it is of interest that the arithmetic mean of all Bôto's determinations (1935) of organic phosphorus by Kalle's method off the coast west and south of Portugal between the surface and fifty metres in August and September, 1934, average 0·30 mg.-atom/m.^{3} and that the arithmetic mean of Seiwell's results (1934) between the surface and fifty metres for thirteen stations in the Western North Atlantic in February and March averaged 0·46 mg.-atom. Kreps and Osadchih (1933) by a somewhat different method found in the Barents Sea an annual mean of only 0·24 mg.-atom organic phosphorus (including arsenic) per cubic metre. An examination of all the records shows that organic phosphorus+arsenic in the surface layers of the North Atlantic averages about 0·4 mg.-atom per cubic metre. Around Iceland with an earlier provisional method, Kalle (1933) found values for the surface which were all consistently much higher, averaging 1·1 mg.-atom/m.^{3} In an interesting set of analyses by his present method for a September station in the North Sea he found (mg.-atom/m.^{3}) :—

PO_4–P.	ΣP in unfiltered water.	ΣP in filtered water.	Org. P in unfiltered water.	Org. P in filtered water.
0·17	0·89	0·53	0·72	0·36

Arsenic was said to have been removed by thiourea.

Off Plymouth in July, 1935, results were also obtained on filtered water, but the two sets of analyses cannot be regarded as conclusive. Work here in 1934 had shown that seldom was more than 0·03 mg.-atom P/m.^{3} present as plankton caught in a silk net with 200 meshes to the linear inch, while Harvey's investigations have also shown that nannoplankton able to pass such a net was unlikely to be present in such bulk as to equal the net catch. The origin of such a large organic phosphorus fraction removable by filtration through filter paper is therefore still unknown.

Rakestraw and Lutz (1933) carried out direct determinations of arsenic on the waters in the neighbourhood of Woods Hole ; the arithmetic mean of all their results from the surface down to fifty metres was 0·19 mg.-atom per cubic metre. Again, in waters from seventy metres in the English Channel in November, 1921, the Government Chemist found 0·25 mg.-atom/m.^{3} (Orton, 1924). Thus about 0·2 mg.-atom/m.^{3} arsenic is present in sea-water, probably mostly as arsenite, which after oxidation in any of the methods used for determining total and organic phosphorus should yield arsenate which behaves like an equivalent amount of phosphate in colorimetric determinations.

The inference is therefore that at least one-half of the so-called organic phosphorus is really arsenite (cf. Atkins and Wilson, 1927) and that the quantities of phosphorus in organic combination present in the surface layers of the Atlantic are not in general such as to play any large part in the food chain in the sea.

The measurements of " organic phosphorus " by Kreps and Osadchih (1933) and by Seiwell and Seiwell (1934) evidently include arsenic since no steps were taken to remove it.

SUMMARY.

Determinations of organic phosphorus (so called) have been made in waters from off Plymouth. The amount varies little with the time of year and averages 0·44 mg.-atom per cubic metre. This is of the same order as determinations in other parts of the North Atlantic. About one-half of this " organic phosphorus " is considered really to be arsenite.

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TABLE I.

Total and Organic Phosphorus (including Arsenic calculated as Phosphorus).

MILLIGRAM-ATOMS PHOSPHORUS PER CUBIC METRE.

Date.	Station.	Depth	PO$_4$–P.	Analyses on unfiltered water.		Analyses on filtered water.	
		m.		Σ(P+As)	Org. P+As	Σ(P+As)	Org. P+As
12-ii-34*	L4	0 & 25‡	0·39	0·84	0·45	—	—
	E1	0, 5 & 50‡	0·32	0·64	0·32	—	—
26-ii-35†	L4	0	0·39	0·79	0·40	—	—
		25	0·42	0·86	0·44	—	—
		45	0·42	0·87	0·45	—	—
		Average§	*0·41*	*0·84*	*0·43*	—	—
	E1	0	0·42	0·82	0·40	—	—
22-iii-35†	L4	0	0·37	0·77	0·40	—	—
		5	0·32	0·84	0·52	—	—
		25	0·39	0·79	0·40	—	—
		45	0·39	0·79	0·40	—	—
		Average	*0·37*	*0·80*	*0·43*	—	—
	E1	0	0·52	0·97	0·45	—	—
		5	0·37	0·81	0·44	—	—
		50	0·35	0·87	0·52	—	—
		67	0·35	1·10	0·75	—	—
		Average	*0·36*	*0·88*	*0·52*	—	—
4-vii-35†	L4	0	0·04	0·42	0·38	0·14	0·10
		5	0·02	0·58	0·56	0·29	0·27
		25	0·17	0·53	0·36	0·50	0·33
		45	0·20	0·53	0·33	0·50	0·30
		Average	*0·13*	*0·53*	*0·40*	*0·45*	*0·29*
	E1	0	0·07	—	—	0·30	0·23
		5	0·05	—	—	0·35	0·30
		15	0·07	—	—	0·30	0·23
		25	0·12	—	—	0·48	0·36
		50	0·22	—	—	0·81	0·59
		Average	*0·16*	—	—	*0·59*	*0·43*

* Analyses on 12-ii-34 by evaporation—permanganate oxidation method.

† Analyses in 1935 by Winkler-Kalle method.

‡ Mixed sample from depths stated.

§ Average content of water column; for definition and method of computation see J. Mar. Biol. Assoc., N.S., 1933, Vol. 18, p. 722.

The Seasonal Abundance of the Pelagic Young of Teleostean Fishes in the Plymouth Area. Part IV. The Year 1936, with Notes on the Conditions as shown by the Occurrence of Plankton Indicators.

By

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Naturalist at the Plymouth Laboratory.

With 4 Figures in the Text.

In continuation of the three previous reports on the seasonal abundance of the pelagic young of teleostean fishes (Russell, 1930, 1935 and 1936) the corresponding data for the year 1936 can now be given. These are published in the same form as in the previous reports to which reference should be made. The dates on which the collections were taken are given in Table I and the monthly average catches for the young fish in Table II. No observations were available between October 12th and December 16th, but this does not materially affect comparison with other years because normally the young fish present at that time of year are very few in number. As in previous years the results are based on half-hour oblique hauls with the 2-metre ring-trawl. In Fig. 1 is given the curve for the average catches for each fortnight for all young fish, excluding Clupeids, and superimposed upon this the corresponding curve for the average of the period 1930 to 1934 inclusive (see 1935, Fig. 1).

Two features are at once noticeable in this figure for 1936; first, the almost complete absence of the usual peak of the young of spring spawners, and second, the increase in the numbers of the young of summer spawners as compared with those in the years 1934 and 1935. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive (see 1935, Table II), excluding Clupeids, was 115 in 1936, as against 79 in 1934 and 37 in 1935.

Below are given for the more important species the sums of the average monthly catches for the year 1936 divided by the corresponding average sums for the period 1930 to 1934 (see 1936, p. 601). In the second column are given the figures for the best year divided by the worst year in the period 1930 to 1936 inclusive.

	1936/Av. / 1930–34.	Best / / Worst.
G. merlangus . .	0·07	23·6 (1932/1936)
G. minutus . . .	0·07	40·3 (1931/1935 & 36)
Onos spp. . . .	0·62	13·0 (1930/1935)
Arnoglossus spp. . .	0·24	11·5 (1931/1934)
S. norvegicus . .	0·32	5·4 (1932/1935)
P. limanda . . .	0·33	14·0 (1931/1935)
P. microcephalus . .	0·13	20·5 (1932/1935)
S. variegata . . .	0·27	5·9 (1932/1936)
Callionymus spp. .	0·31	3·4 (1930/1936)
S. scombrus . .	0·59	11·2 (1930/1935)
Gobiid spp. . .	0·47	39·7 (1930/1935)

The year 1936 has thus been the worst year recorded for the period 1930 to 1936 for *G. merlangus*, *S. variegata* and Callionymus spp.* For *G. merlangus* the best year, 1932, was 23·6 times greater than 1936.

The phosphorus available at the beginning of the year 1936 was still low, deviating −11% from the mean content for the winters 1923–24 to 1934–35 (data kindly supplied by Dr. L. H. N. Cooper).

Figs. 2 and 3 give the data on the occurrence of plankton indicators at Plymouth in 1936 in continuation of those given in the last report (1936, p. 599, Figs. 2, 3). Fig. 2 shows that until August in 1936 there was a distinct preponderance of *Sagitta elegans* over *S. setosa*. This is, however, in no way comparable with the predominance of *S. elegans* in 1930 since the upper half of this figure shows that its numbers were very low. Accompanying *S. elegans* there have also been a few of its associated indicators, e.g. Aglantha, Euphausian larvae, and *Themisto gracilipes* (see Fig. 3). *S. setosa* occurred in fair numbers temporarily in February during a period of strong easterly gales. A remarkable feature of the year 1936 has been the return of the siphonophore, *Muggiaea atlantica*. This species disappeared after the year 1924 and was replaced thereafter by *M. kochi* (Russell, 1934). In 1936 *M. kochi* did not appear after January. There have been indications of the occurrence of oceanic water. On March 16th Dr. M. V. Lebour gave me a medusa from the plankton which, while not identifiable for certain, was most likely a young stage of the Laodiceid, *Chromatonema rubra*. This is a deep-sea medusa. On March 26th and 31st specimens of the oceanic scyphomedusa Pelagia also appeared in the ring-trawl collections. It is interesting to note that these animals appeared immediately after the sudden decrease of *S. elegans* in March. This appearance of oceanic animals together with the occurrence

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* In the corresponding table for 1935 (see 1936, p. 601) Callionymus spp. 0·20 should read 0·34; the average for the period 1924–29 had been used in error instead of that for 1930–34.

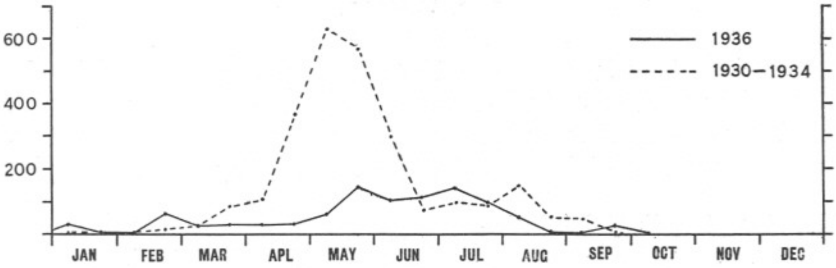

Fig. 1.—Curves showing the average catches in half-hour oblique hauls with the 2-metre ring-trawl for each fortnight for all young fish, excluding Clupeids, in 1936 (————) and the same averaged over the period 1930 to 1934 inclusive (– – – –).

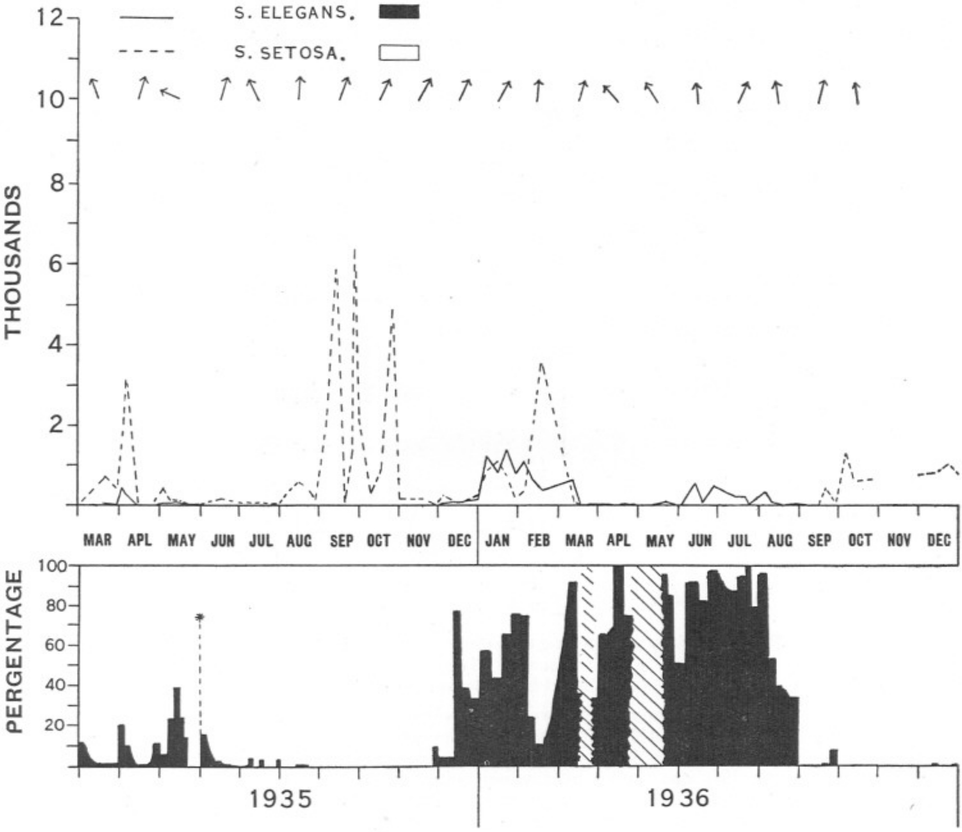

Fig. 2.—Above, curves showing the actual abundance of *S. elegans* (————) and *S. setosa* (– – – –) in half-hour oblique hauls with the 2-metre ring-trawl during the period March, 1935, to December, 1936.

Below, the percentage composition of the Sagitta populations during the same period; *S. elegans*, black; *S. setosa*, white; no Sagitta, cross-hatched.

At the top of the diagram the arrows indicate the mean direction (true) of the flow of water through the Straits of Dover for each month as indicated by the Carruthers Current Meter working from the Varne Lightship, kindly supplied by Dr. J. N. Carruthers. (Continued from Russell, 1936, p. 599, Fig. 2.) (*=*S. setosa*, 1; *S. elegans*, 2.)

of Muggiaea throughout the second half of the year possibly explains the preponderance of *S. elegans* and also its low numbers. Such water as has filled the western end of the English Channel has not come from the west, where the water is rich in *elegans*, but from the south-west and has carried away with it small quantities from the boundary of the *elegans* water proper. I am indebted to Dr. H. W. Harvey for the information that the western end of the English Channel filled with water of low salinity early in the year. This appears at first in conflict with the occurrence of oceanic plankton animals, but it must be realized that along the French coast whence this water probably comes the steep-to coast will allow the

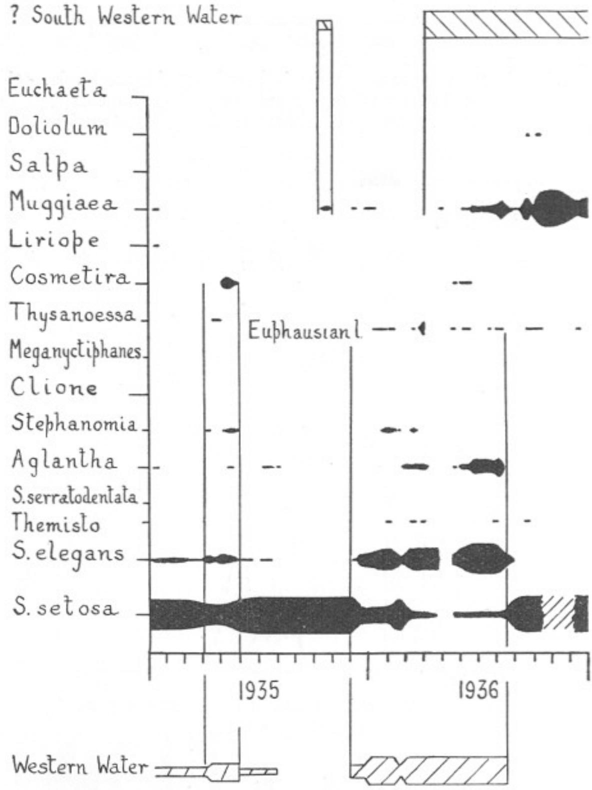

FIG. 3.—Diagram showing the occurrence of the various plankton indicators in collections off Plymouth during the years 1935 and 1936. (Continued from Russell, 1936, p. 599, Fig. 3.)

The Muggiaea species were *M. kochi* up to January, 1936, and thereafter in 1936 *M. atlantica*. The cross-hatching indicates a period during which no standard collections were made. *M. atlantica* was shown by tow-net collections to be numerous off Plymouth during that period. The Doliolum species was *D. nationalis*.

occurrence of oceanic plankton animals well inshore. It is possible that the improvement in the numbers of the young of summer spawning fish may bear some relation to these water movements.

From September until the end of the year *S. elegans* was almost completely replaced by *S. setosa*, while the presence of some south-western water was also indicated by the persistence of Muggiaea. An unusual record on December 31st, 1936, was that of the Scyphomedusan, *Discomedusa lobata* Claus, which has never before been recorded in these waters.

In Fig. 4 are shown the temperatures at L5 (surface) and E1 (bottom) in the early months of the year. Compared with other years 1936 was a late year, and the occurrence of such of the young of spring spawners as were taken was in agreement with this. It can, however, hardly have been the cause of the disappearance of the usual peak of young of spring spawners. Neither can their disappearance be accounted for by the depredations of ctenophores as was suggested for 1929 (1935, p. 166, Fig. 7). Ctenophores were very scarce in 1936 until September, when there was a sudden invasion, chiefly of Pleurobrachia, whose numbers were as follows :—September 15th, 3 ; 22nd, 2940 ; 29th, 14,020 ; October 6th, 1740 ; 12th, 3. Mr. P. G. Corbin has told me that Pleurobrachia were present in large numbers at E1 on September 18th, apparently already moving in towards the Eddystone.

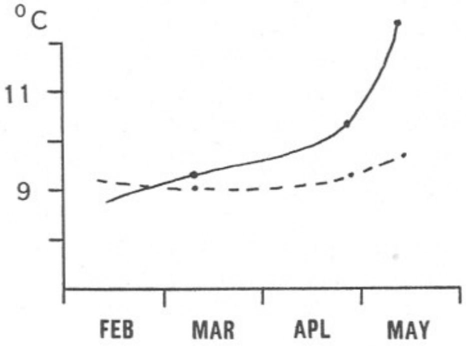

FIG. 4.—Temperatures in February, March, April and May for the year 1936. ——— surface at L5 ; – – – – bottom at E1.

We can thus at present only account for the failure of the production of the young of spring spawners as being due to the prolonged period of poverty in nutrient salts that has continued since 1932. In 1935 the spring peak was already considerably smaller than normal. If a renewed total annual abundance of young fish is to take place it must presumably await an influx into the English Channel of water rich in nutrient matter from the west in the winter months.

The year 1936 has been outstanding for the prolonged abundance of the eggs of the pilchard. These appeared first in numbers on March 31st and were last seen on October 12th, after which collections ceased until the middle of December. Their occurrences were as follows (approximate numbers, when counted, in brackets):—March 31st, many (2500): April 7th, few; 15th, few; 22nd, many (1750): May 4th, many (1430); 13th, very many; 20th, many: June 2nd, many (2000); 12th, many; 16th, very many (8000); 26th, many (3300): July 13th, very many (17,400); 24th, very many (5750); 29th, few: August 17th, present; 28th, present: September 1st, present; 9th, few; 15th, many (1500): October 6th, present; 12th, many (3160). The numbers of surviving young, however, do not appear to have been high.

It can now be stated that as in previous years the curve of the abundance of young whiting in the plankton still follows that for the landings of whiting (cf. 1935, p. 169, Fig. 8; 1936, p. 602). The landings of whiting by British sailing trawlers in area VII, d–e, in the English Channel fell in 1935 to 2·0 cwt. per 100 hours' fishing, and the sum of the average monthly catches of young whiting dropped to 13. This is excessively low when compared with 308 in 1932.

My thanks are due to Capt. V. Lord and the crew of the S.S. *Salpa* for their continued care in making these collections.

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TABLE I.

DATES ON WHICH COLLECTIONS WERE MADE, 1936.

All 2 miles east of Eddystone unless otherwise stated.

(No observations between October 12th and December 16th.)

Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
1	5	12	7	4	2	13	5	1	6‡		16
7	12*	16	15	13	12	22†	11	9	12		21*
14	18*	23	22	20	16	24	17	15			31
21		31	28	27	26	29	28	22			
29								29			

* Haul taken at L4–L5.

† Haul taken 4 mi. S.S.E. of Mewstone.

‡ Haul taken 4 mi. E. × S. of Prawle Point.

TABLE II.

Average Monthly Catches of Post-larvae per Half-hour Oblique Haul with 2-metre Ring-trawl, 1936.

(No observations between October 12th and December 16th.)

	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total Young Fish	67	654	75	38	167	375	251	65	14	63		94	1863
Ditto, less Clupeids	21	27	30	31	104	111	112	29	14	6		2	487
All Clupeid spp.	46	627	45	7	63	264	139	36	+	58		92	1377
Clupea harengus	–	–	–	–	–	–	–	–	–	–		92*	92
Gadus pollachius	–	–	1	1	–	+	–	–	–	–		–	2
Gadus merlangus	–	–	3	1	7	2	–	–	–	–		–	13
Gadus minutus	–	+	1	1	1	4	–	–	–	–		–	7
Gadus luscus	12	1	2	–	–	+	+	–	–	1		+	16
Gadus callarius	–	–	–	–	–	–	–	–	–	–		–	–
Onos spp.	–	–	12	5	12	2	1	–	+	–		–	32
Molva molva	–	–	–	–	–	–	–	–	–	–		–	–
Merluccius merluccius	–	–	–	–	–	–	+	–	–	1		–	1
Raniceps raninus	–	–	–	–	–	–	1	–	–	–		–	1
Capros aper	–	–	–	–	–	–	–	–	–	–		–	–
Zeus faber	–	–	–	–	–	–	–	–	–	–		–	–
Arnoglossus sp.	–	–	–	–	–	3	2	2	1	–		–	8
Rhombus laevis	–	–	–	–	–	–	–	–	–	–		–	–
Rhombus maximus	–	–	–	–	–	–	+	+	–	–		–	+
Scophthalmus norvegicus	–	–	+	1	8	9	1	–	–	–		–	19
Zeugopterus punctatus	–	–	+	1	2	3	1	–	–	–		–	7
Zeugopterus unimaculatus	–	–	–	–	+	–	+	–	–	–		–	+
Pleuronectes limanda	–	+	+	2	12	4	–	–	–	–		–	18
Pleuronectes flesus	–	–	–	+	1	–	–	–	–	–		–	1
Pleuronectes microcephalus	–	–	–	–	1	2	–	–	–	–		–	3
Solea vulgaris	–	–	–	–	1	+	–	–	–	–		–	1
Solea variegata	–	–	–	1	6	12	3	–	–	–		–	22
Solea lascaris	–	–	–	–	–	–	–	–	+	–		–	+
Solea lutea	–	–	–	–	–	1	+	–	–	–		–	1
Serranus cabrilla	–	–	–	–	–	–	–	–	–	–		–	–
Caranx trachurus	–	–	–	–	–	–	+	1	8	1		–	10
Mullus surmuletus	–	–	–	–	–	–	–	–	–	–		–	–
Morone labrax	–	–	–	–	–	–	–	–	–	–		–	–
Ammodytes sp.	7	22	5	2	–	–	–	3	1	–		–	40
Ammodytes lanceolatus	–	–	1	4	2	4	4	2	–	1		–	18
Cepola rubescens	–	–	–	–	–	–	–	+	–	–		–	+
Callionymus spp.	–	–	3	12	50	52	49	2	1	1		–	170
Labrus bergylta	–	–	–	–	1	1	–	–	–	–		–	2
Labrus mixtus	–	–	–	–	+	1	+	–	–	–		–	1
Ctenolabrus rupestris	–	–	–	–	–	1	9	8	–	–		–	18
Crenilabrus melops	–	–	–	–	–	2	2	1	–	–		–	5
Centrolabrus exoletus	–	–	–	–	–	–	–	–	–	–		–	–
Trachinus vipera	–	–	–	–	–	–	+	1	+	–		–	1
Scomber scombrus	–	–	–	–	–	1	8	4	–	–		–	13
Gobiid spp.	2	1	–	–	1	4	10	1	–	1		1	21
Lebetus scorpioides	–	–	–	–	–	+	+	–	–	–		–	+
Blennius ocellaris	–	–	–	–	–	–	–	–	–	–		–	–
Blennius pholis	–	–	–	–	–	+	1	+	–	–		–	1
Blennius gattorugine	–	–	–	–	–	2	18	5	+	–		–	25
Chirolophis galerita	+	1	1	–	–	–	–	–	–	–		–	2
Agonus cataphractus	–	1	–	–	–	–	–	–	–	–		–	1
Trigla spp.	–	–	–	–	–	1	1	–	1	2		–	5
Cottus sp.†	–	+	2	1	–	–	–	–	–	–		–	3
Liparis montagui	–	–	–	–	–	–	–	–	–	–		–	–
Lepadogaster bimaculatus	–	–	–	–	–	1	+	–	–	–		–	1
Lophius piscatorius	–	–	+	–	–	+	1	–	–	–		–	1
Young Pipe-fish	–	–	–	–	–	1	–	–	1	–		–	2

* On Dec. 16th there was a catch of 274; this was immediately after a heavy gale and the contents of the catch were typical of a night haul. This average may therefore be unduly weighted.

† While I was in Copenhagen last year Dr. A. Fr. Bruun kindly drew my attention to a paper in which he described the young stages of what he presumed to be *Cottus lilljeborgi* (Public. Circ. No. 88, 1925). A re-examination of a number of specimens in my collections has shown that they agree with Bruun's figures for *C. lilljeborgi*, although the adult has not yet been recorded here. These post-larvae had previously been included under the name *C. bubalis*.

The Biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.).

By
C. M. Yonge, D.Sc.,
University of Bristol.

With 6 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE genus Aporrhais comprises a small number of species which are easily recognizable owing to the greatly expanded outer lip of the shell, and which occur in the North Atlantic from West Africa to the Arctic. The animals are of especial interest on account of their habits and also of their close relationship to the tropical family Strombidae, the two most important genera of which, Strombus and Pterocera, are characteristic members of coral reef faunas, the latter in the Indo-Pacific, the former in both this region and the Atlantic.

Two species of Aporrhais occur in the Norwegian fjords, *A. pes-pelecani*, which is also a member of the Plymouth fauna, and *A. serresiana* (=*A. macandreae*) which is an inhabitant of deeper water and is found only off the northern shores of Great Britain. This paper is the result of observations carried out on these two species at the Bergens Museum Biological Station at Herdla during the month of August, 1936. The author wishes to express his sincere thanks to the Director of the Station, Professor A. Brinkmann, for his great kindness and help and also to Amanuensis D. Rustad for much assistance. Acknowledgements are also due to the Colston Research Society of the University of Bristol for financial assistance.

APORRHAIS PES-PELECANI.

This species (Fig. 1) is characterized by a solid shell, the spire of which is longer than the expanded lip or "body." The latter is prolonged into four conspicuous digitations and a fifth which is only very slightly developed. The terminal or "caudal" digitation is notably stout and, owing to lateral dilation, blade-like (see Fig. 1). The point is directed downwards as shown in Fig. 2. This downward curve increases with age because, after the attainment of full size with the complete formation of the expanded lip, further shell formation is confined to an increase in thickness (very well-marked in the most worn shells), while, for reasons which will be made clear later, the frontal upper surface of the tip of the terminal digitation is worn away.

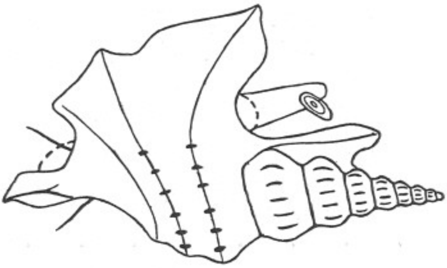

FIG. 1.—*Aporrhais pes-pelecani*, seen from above when moving over a hard surface. The head, except for the tentacles, is obscured by the blade-like terminal digitation. The operculum is attached to the upper side of the posterior end of the foot. The broken lines mark the positions, when the animal is buried, of the inhalent and exhalent apertures. × 1½.

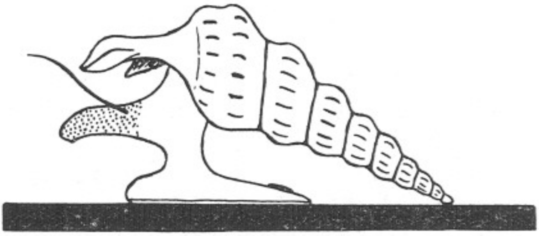

FIG. 2.—*A. pes-pelecani*, lateral view from left side showing the mode of progression over a hard surface.* The animal is raising the shell off the ground by extending the "neck," the body and shell will then be moved forward. × 1½.

The exposed regions of the animal are yellowish-white with red

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* Weber (Z. vergl. Physiol., II, 109 ; 1924) has described and figured this arhythmical movement in Chenopus (= Aporrhais) and also in Conus and Strombus.

speckling which often extends over the foot, including the sole. The snout and head are thickly speckled with scarlet, while the tentacles are mingled yellow and scarlet. The foot (Figs. 1 and 2) is narrow and very extensile and carries the small, elongated operculum (Fig. 1) on the upper surface near the posterior end. It is united to the body by a thick " neck " or stalk (Fig. 2). The head is prolonged into the characteristic proboscis, the mouth opening at the end of this and consisting of a perpendicular slit. The tentacles (Figs. 1, 2 and 4) are long and slender when fully expanded and at the base of these, situated on prominent bulbs, are the eyes (Fig. 4).

(*a*) *Habitat and Habits.*

A. pes-pelecani is found on comparatively firm muddy gravel bottoms. In the neighbourhood of Herdla it was most abundant near Rossland on a bottom of this type at a depth of some 20 metres. It is characteristic of the shallower depths in which such bottoms occur; both Forbes and Hanley (1853) and Sars (1878) give the vertical distribution as from about 5 to 100 fathoms.

The animal is, in the words of Jeffreys (1867), " shy, slow and backward in its movements." When placed in a dish of sea-water the animals soon expand, locomotion taking place by a series of somewhat ungainly movements. The body is first raised by extending the " neck " (as shown in Fig. 2) which may stretch to a length of 1 cm., especially when faced with obstacles. Then, the foot remaining motionless, the body and the shell are carried forward in one convulsive movement for a distance up to about 8 mm. The shell and body then fall and the foot glides forward for the same distance, after which the "neck" is again raised and the process repeated. When placed upside down the animals can right themselves. This they do by extending the foot and head to the maximum extent around the base of the terminal digitation on the side away from the expanded lip. Extension proceeds until the foot is placed firmly on the substratum and, with the aid of the purchase so obtained, the shell is righted by a convulsive contraction of the body musculature.

It is interesting to compare these movements with those of the related " spider-shell " of the tropical Indo-Pacific, *Pterocera crocata*, which, although very much larger, has a shell of somewhat similar type. This animal lives on sandy areas on coral reefs. As previously observed (Yonge, 1932), it progresses by a series of sudden movements not unlike those of Aporrhais, but in this case not with the aid of a creeping sole, which has been lost, but by means of the stout operculum, long and very sharp, which is dug into the sand before each movement, after which it is dragged forward and pushed into the sand again.* In this case the animal

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* Parker (J. Exp. Zool., XXXVI, 205; 1922) records similar progression in *Strombus gigas*.

can right itself by extending the foot around the same side of the shell as in Aporrhais until the operculum is hooked under the shell where this rests on the ground. Then, by a convulsive movement, the animal turns over.

When *A. pes-pelecani* was placed in a vessel containing a thick layer of gravelly mud it soon became apparent that the animal is actually specialized for burrowing and that progression on the surface must normally be of rare occurrence. After moving about for a short time on the surface the animals invariably began to burrow. The process is interesting. The terminal digitation, in shape admirably fitted for this, is first pushed beneath the substratum. Then, as a result of a succession of movements, the animal gradually progresses at first obliquely downward and then horizontally beneath the surface. The movements, which at first occur at intervals of between 40 seconds and one minute, become less frequent as the obstacles to progression increase. At each movement the animal turns over a little to the right side (that with the expanded lip) and the shell, as indicated by the movement of the mud above it, is raised. The action is clearly the same as when the animal is moving on the surface. As the animal sinks below the surface a small mound is raised in front of it and it is when this is some 5 mm. above the highest point on the terminal whorl of the shell that the direction of movement becomes horizontal. The upper surface of the apical whorls of the shell are still uncovered but lie in an elongated depression into which material falls from the sides and particularly from the mound raised in front. Finally, by a combination of the effect of continued forward movement and the falling in of material from all sides the shell is completely covered, as indicated in Fig. 3.

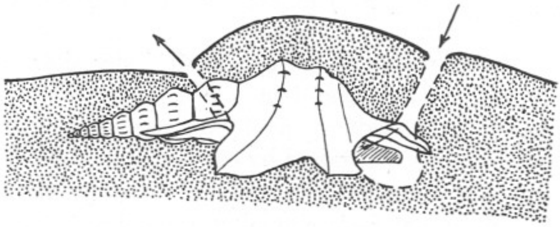

FIG. 3.—*A. pes-pelecani*, semi-diagrammatic representation of the position of the animal when buried, from the right side. The inhalent and exhalent apertures are indicated by arrows showing the direction of the currents. × 1½.

At this stage further movements can still be detected though with little or no progression. Each movement, by causing a raising and lowering of the expanded lip, results in the ejection of water from under the hinder margin of the expanded lip. In this way a temporary opening is formed in the gravel. There is no other opening at this stage. These movements probably serve to clear away the softer mud before the animal finally settles down ; they may also clear a space below the expanded, horizontally disposed lip.

Finally all movements cease. An inhalent opening is then made by the highly extensile proboscis which extends around the right-hand side of the terminal digitation, in front of the expanded lip, and upward until it breaks the surface. It then moves round actively in all directions curling back over the opening, so that the inhalent opening, at first irregular in outline, becomes finally rounded and some 2 mm. in diameter. Mucus is secreted by numerous unicellular glands in the wall of the proboscis (demonstrated in sections) and this consolidates the wall of the inhalent opening. The proboscis is then withdrawn, turned backward under the expanded lip and protruded upwards around the edge of the bay at the hinder end of the lip. An exhalent opening is formed in exactly the same manner as the inhalent one, the positions of both being shown in Fig. 3. The function of these becomes at once apparent when carmine is added to the water around them, a steady flow of water passing into the anterior one and out by way of the posterior one. The formation of two siphonal openings by the same agency, and at such considerable distance from one another—an animal of shell length 3·8 cm. had siphonal openings 2·3 cm. apart—has not, as far as can be ascertained, been observed in any other animal. It provides a most interesting example of adaptation in a burrowing Gastropod. The formation of siphonal tubes consolidated with mucus is also unusual in Mollusca although, during the same period at Herdla, it was found that the lamellibranch, *Thracia pubescens*, forms siphonal tubes in somewhat the same manner (Yonge, 1937).

After the inhalent and exhalent apertures have been made and consolidated the proboscis is withdrawn and only very occasionally protruded through them again, apparently to strengthen the lining of the tubes. It can always be induced to protrude by obliterating either of the openings which it promptly proceeds to reconstruct. The animals remain motionless beneath the surface, the only indication of their presence the two small openings, for long periods. One animal remained so for three days before uncovering itself, when it moved about for a short distance and then burrowed again. The proboscis can presumably range about at will under the surface of the expanded wing and both in front of and behind this, and it is to be assumed that the animal remains in one position so long as sufficient food can be obtained within this area.

(*b*) *Currents in the Mantle Cavity.*

The powerful inhalent and exhalent currents which enter and leave the apertures constructed by the proboscis reveal the presence of strong ciliary currents within the mantle cavity. It is also clear that, living buried beneath mud, the animals must be exposed to great danger from silt blocking the mantle cavity and must possess adequate mechanisms for dealing with this. The nature of the various ciliary mechanisms was revealed when the mantle cavity was opened, by cutting along the right side, as shown in Fig. 4.

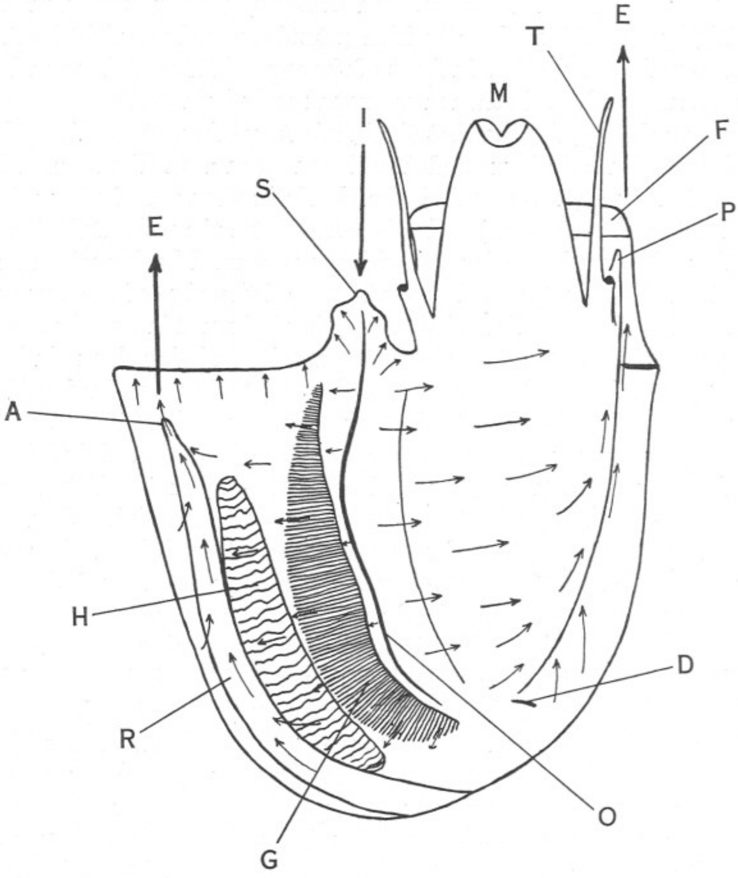

Fig. 4.—*A. pes-pelecani*, mantle cavity opened along the right side, seen from above. × 5. A, anus; D, opening of the male reproductive duct; E, exhalent current; F, anterior margin of foot; G, gill; H, hypobranchial gland; I, inhalent current; M, mouth; O, osphradium; P, penis; R, rectum; S, siphonal extension; T, tentacle with eye on bulb at base. Arrows indicate direction of ciliary currents.

The respiratory current is created by lateral cilia on the gill filaments, each of which consists of an elongate triangle, broadest at the base but slightly flattened at the tip. The large size of the gill (G) explains the powerful nature of this current. The inhalent current (I) enters on the left side of the head, where the mantle is extended to form a short siphonal process (S). The exhalent current (E) leaves the mantle cavity on the right side (topographically behind the other).

In the intact animal the siphonal process when distended is considerably larger than it appears in Fig. 4. It then extends for some distance forward under the terminal digitation and around the adjacent edge of the bay on the front edge of the expanded lip of the shell. The largest particles which are carried in with the inhalent current come in contact with the surface of the mantle in this region and are caught in powerful outwardly directed ciliary currents which also extend all around the edge of the mantle, as indicated by the arrows in Fig. 4.

The osphradium (O) is unusually elongated. It arises a short distance anterior to the extreme posterior end of the gill (G), running parallel to the base of this for some two-thirds of its course then diverging somewhat to the right and extending for some distance anterior to the gill along the middle line of the siphonal extension. The line of the osphradium marks the extreme left-hand side of the mantle cavity and therefore the middle line of this when it is cut open and extended as in Fig. 4. Under these conditions the ciliary currents on the mantle carry particles in opposite directions on either side of the osphradium. On the right-hand (ventral) side particles are carried over the floor of the mantle cavity to the exhalent region where they pass forward alongside the genital groove. On the dorsal side (left side in the figure) particles are carried to the gills, in between the filaments of which the water passes, where they are carried to the tip by the frontal cilia and thence, over the surface of the large hypobranchial gland (H) which secretes large quantities of mucus, to the region of the rectum (R) where they pass forward. The two mucus-laden streams of particles from the ventral and dorsal surfaces of the mantle cavity thus combine on the right or exhalent side of the mantle cavity and pass out, together with faeces discharged by the anus (A) at the side of the head. They are then carried downwards over the " neck " region into a groove running around the base of the foot in which all this waste material is conveyed backwards. All material which drops on to the foot is also carried into this tract.

The powerful respiratory currents, necessary possibly in view of the probably lowered oxygen tension in the water immediately in contact with mud containing much organic matter, are thus provided by the lateral ciliation on the filaments of the very well-developed gill. Disposal of material in suspension is brought about by three agencies. (1) Largest particles are immediately carried to the edge of the inhalent region, in essentially the same manner as similar material is ejected from the inhalent cavity of Lamellibranchia (see Kellogg, 1915 ; Yonge, 1923, 1926). (2) Somewhat lighter particles, which settle to the surface farther within the mantle cavity, are carried across the floor of the mantle cavity to the exhalent region. (3) The lightest particles of all, which are retained in suspension, are carried to the tip of the gills when the water passes through this and are then entangled in mucus secreted by the hypobranchial gland before passing out with the medium particles and the faeces by way of the exhalent opening.

(c) *Feeding.*

The animals will feed on the surface as readily as when buried and so the process can be observed. The proboscis continually moves about, being capable of extension from base of tentacles to tip up to a length of 1 cm., while the mouth continually searches the ground for food. The lateral lips are very sensitive and repeatedly open, exposing the small, but powerful, radula and the jaws (capable of firmly seizing a needle inserted into the mouth) which are protruded between them. Aporrhais has been described as a carnivore (Woodward, 1875), but is actually, as will be shown, a specialized herbivore. The presence of animal matter (shredded out tissues of bivalves) may even cause the animals to move away, sometimes backwards, or this may first be tasted and the proboscis then withdrawn sharply, the animal passing elsewhere. Finely cut up pieces of Fucus were not accepted, but fine green algae, such as shredded strips of Enteromorpha, were taken readily. This was seized by the jaws and radula and swallowed whole. The radula consists of a single hooked and denticulate tooth with three laterals, the first two transverse and the third claw-shaped (see Woodward, 1875, Fig. 100). A radula of this type has usually been considered characteristic of carnivorous Gastropoda (e.g. by Digby (1902) in Chytra and Limnotrochus), but is actually adapted for seizing, as opposed to scraping, which is the more usual method of feeding in herbivorous Gastropoda. The radula of Aporrhais, as Woodward has pointed out, most closely resembles those of Strombus and Pterocera (both herbivorous, Yonge, 1932) and of the Heteropod Carinaria, a carnivore which is specialized for seizing larger members of the zooplankton. This misapprehension as to the true significance of this type of radula is probably responsible for the statements that Aporrhais is a carnivore.

The animal presumably feeds normally by collecting, by means of the extensile proboscis, all particles of plant matter which occur in the mud in the region below and around the expanded lip. This material will consist largely of detritus of vegetable origin, the remains of algae or of diatoms which have dropped from the surface, together with bottom-living diatoms. Hunt (1925) in his work on the food of the bottom fauna around Plymouth classified *Aporrhais pes-pelecani*, together with one other Gastropod, *Turritella communis*, as a selective deposit-feeder. He did so as a result of examination of the stomach contents which he found always consisted of "roughly sorted bottom material."

(*d*) *The Alimentary Canal.*

Further evidence as to the nature of the food is provided by a study of the gut. A straight and comparatively wide oesophagus carries material into the large and complex stomach (Fig. 5). Into the lumen of this projects a stout crystalline style, 8 mm. long and 1 mm. wide in an adult animal. This structure, the presence of which was noted by Digby (1902), is secreted within a wide style-sac (S) in restricted communication with the first portion of the intestine (I). The head of the style bears, in life, against a similarly well-developed gastric shield (G). The presence of these organs immediately indicates that the animal is herbivorous, because, for reasons given elsewhere (Yonge, 1930), the presence of a crystalline style is incompatible with that of an extracellular protease, and, as already noted, the only possible substitute for this mechanical triturition by the radula, is absent. A second structure of great significance in the stomach is the series of parallel ridges which constitute

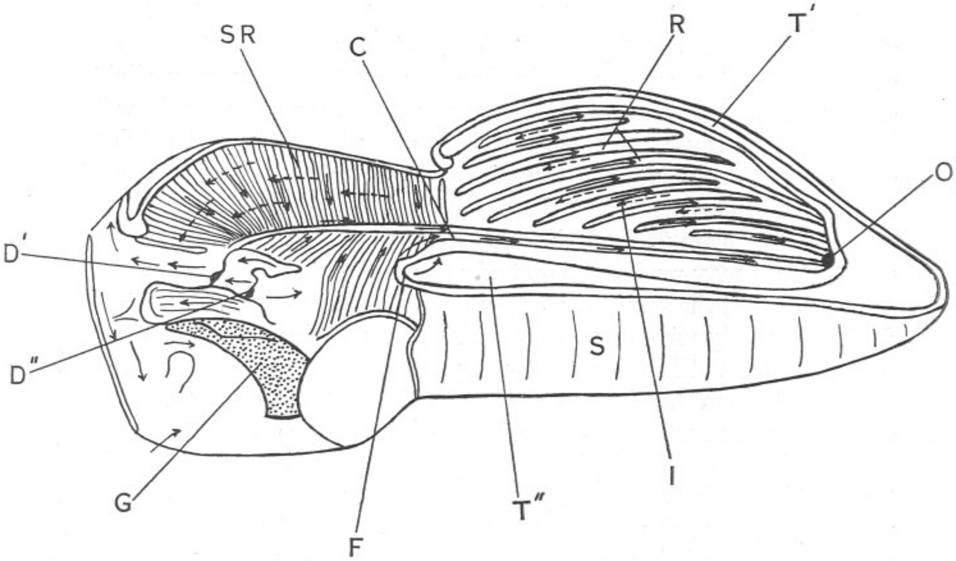

FIG. 5.—*A. pes-pelecani*, stomach with initial region of intestine and style-sac opened along mid-dorsal side. ×9. C, channel leading into initial region of intestine from sorting region in stomach; D′, D″, ducts into digestive diverticula; F, flap guarding entrance from oesophagus; G, gastric shield; I, initial region of intestine; O, opening into second region of intestine; R, ridges in initial region of intestine; S, style-sac; SR, sorting region; T′, T″, typhlosoles which separate style-sac from intestine. Arrows indicate direction of ciliary currents.

a sorting region (SR). Fine particles are carried over these ridges from summit to summit (as indicated by the broken arrows in Fig. 5) and so passed to the vicinity of the openings of the two ducts into the digestive diverticula (D′, D″), while larger particles pass into the grooves between the ridges and are conveyed by different ciliary tracts into a channel (C) which carries them rapidly into the first portion of the intestine.

The stomach of Aporrhais thus bears a remarkably close resemblance to that of a typical Lamellibranch in the presence of a style with an associated gastric shield and of a complicated sorting region (identical in function with those of Modiolus (Nelson, 1918), Mya (Yonge, 1923), Ostrea (Yonge, 1926) and Ensis (Graham, 1931)). It resembles the stomach of Pterocera and *Vermetus novae-hollandiae* (Yonge, 1932) in the presence of a style, but a sorting mechanism is absent or only very slightly developed in these animals. In Pterocera such an organ is probably of no importance, because the food, which is exclusively of plant origin, is exposed to the action of a powerful cellulase—absent (as experiments proved) in Aporrhais—which breaks down the larger food masses. In Vermetus the more finely divided nature of the food (collected by ciliary mechanisms) may render elaborate further sorting unnecessary.

The action of the stomach, therefore, is to convey fine particles into the ducts of the digestive diverticula and larger ones into the first portion of the intestine. There is an outward passage of particles along the floor of the ducts from the digestive diverticula (indicated by arrows in Fig. 5) and an inward movement above this. It is therefore possible for material to be carried in, and for the indigestible remnants of intracellular digestion to be later expelled. Muscular movements may also assist in this ; the walls of the stomach were observed to make frequent contractile movements even after being opened out, and this applied particularly to the flap which separates the two ducts and that which guards the entrance from the oesophagus (F). Within the stomach circulation of particles will be assisted by the rotation of the style, the dissolution of which will bring about extracellular digestion of starch. Sections of the digestive diverticula revealed the absence of secreting cells. The cells are presumably concerned exclusively with intracellular digestion as in other herbivorous Prosobranchia, such as Patella (Graham, 1932), and in all Lamellibranchia.

The intestinal regions of the gut are three in number and are concerned exclusively with consolidating the particles passed on from the stomach into firm faecal pellets. The regions consist of a wide initial region (I, Fig. 5) which is largely separated from the adjacent style-sac (S) by two typhlosoles (T′, T″), a narrow " small " intestine which ramifies for some distance through the viscera, and a terminal, much wider "rectum" (R, Fig. 4), which runs along the right side of the mantle cavity to open at the anus (A) in the exhalent region.

The channel (C) into which material is passed from the sorting region of the stomach is continued throughout the wide initial region of the intestine, which also possesses an interesting series of ridges (R) which run obliquely around it as shown in Fig. 5. On the summits of these powerful ciliary currents carry material into the opening into the "small" intestine (O) towards which the ridges converge. In the grooves between the ridges less powerful currents beat in the opposite direction. There is a great production of mucus in this region of the intestine and the purpose of the ridges and grooves with their different tracts of cilia is apparently that of thoroughly mixing the particles with mucus. Muscular movements play an important part in this process, continual contractions, causing the temporary obliteration of the grooves, being frequently observed even after this region had been opened out. The material passed into the opening of the "small" intestine is thoroughly mixed into a homogeneous mass with large quantities of mucus.

The "small" intestine has a narrow lumen with no typhlosole, but with a fine groove on one side which probably represents the continuation of the channel in the stomach and initial region of the intestine. A powerful anally-directed ciliary current is present in this groove. The faeces are here consolidated into a firm, continuous thread with an outer envelope of mucus. In this form they enter the wide "rectum." The groove with its powerful ciliary current is continued and provides the propulsive force towards the anus. The remainder of the wall of the rectum is ciliated, but the direction of the currents could not be determined with accuracy. When carborundum was placed upon this surface it merely trembled to and fro. The same action is always observed when similar particles are placed on the surface of the style-sac epithelium of any Lamellibranch (or style-bearing Gastropod), indicating that in the rectum also the cilia may only act when material is pressed tightly against them (Yonge, 1926). Additional evidence is provided by a similar velvety appearance of the surface of the living epithelium in both rectum and style-sac and by a general resemblance of both epithelia in section. It is certainly true that both epithelia have the same function, that of moulding material into a rod-like form. In the rectum of Aporrhais the fine threads which enter from the "small" intestine are converted into elongated, thick pellets, each of which contains a twisted coiled mass of these finer threads enclosed in a second, thicker envelope secreted by the walls of the rectum. Thus it is in the form of large pellets, which cannot foul the water in the mantle cavity, that the faeces are expelled from the anus.

APORRHAIS SERRESIANA.

This species provides an interesting contrast in structure and habitat to *A. pes-pelecani*. The shell, illustrated in Fig. 6, attains a slightly greater size than that of *A. pes-pelecani*, but is somewhat more delicate, notably in the expanded lip. Owing to the greater length of the terminal digitation in this species (compare Figs. 1 and 6) the spire is shorter than the " body " of the shell. The expanded lip is much larger than in the other species and there are five, instead of four, prominent digitations, which are prolonged into fine points instead of ending bluntly. The terminal digitation is notably long and narrow, being straight and pointed instead of broad and blade-like as it is in *A. pes-pelecani*. The animal is more delicate than that of the other species and the tissues are white and translucent except for the head and proboscis. The former possesses a triangular patch of red on the dorsal surface, while the latter is speckled with scarlet along the dorsal surface, with a white line, widening near the tip, running along the middle line. The tentacles are translucent with an opaque white band running along the upper side. They are also longer and more extensile than those of *A. pes-pelecani*, being capable, in a fully grown animal, of extending to a length of 1·5 cm.

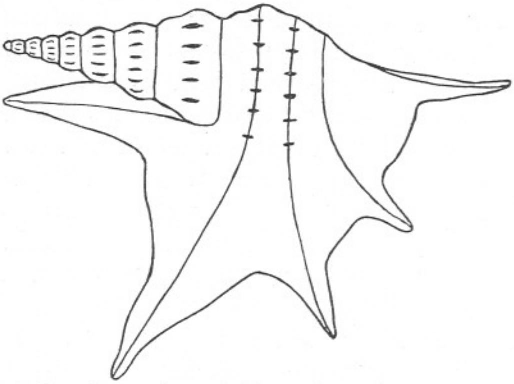

FIG. 6.—*A. serresiana*, shell seen from above, the great extent of the expanded lip is shown, also the five sharply pointed digitations, the terminal one being notably fine. × 1½.

A. serresiana is an inhabitant of deeper water than *A. pes-pelecani*. Sars (1878) states that the vertical distribution is from 80–300 fathoms. It was collected in greatest numbers, although it is never so abundant as *A. pes-pelecani*, at depths of about 200 metres in the Herdla fjord, where it was the only species of the genus taken. At intermediate depths, notably about 60 metres at Ypsøsund, both species were taken in proportions of roughly seven *A. pes-pelecani* to one *A. serresiana.* Neither species was as abundant as they are in shallower or greater depths respectively.

The distribution of the two species is clearly dependent on the nature of the bottom. *A. pes-pelecani*, as already stated, occurs on comparatively firm bottoms of muddy gravel, but *A. serresiana* is an inhabitant of softer bottoms of fine mud found in deeper water.

The habits of *A. serresiana* are the same as those of *A. pes-pelecani.* It moves in the same manner over the bottom of a glass dish and burrows into soft mud. When placed on muddy gravel taken from the normal habitat of *A. pes-pelecani*, one specimen burrowed into the side of a small mound and moved slowly horizontally under the surface. No attempt was made to push downwards nor was there the same "shouldering" action as in the other species. Only with much greater effort and over a much longer period did the animal finally bury itself. *A. serresiana* is definitely less powerful than *A. pes-pelecani* and possibly in its natural habitat tends to sink in the mud and then push forward rather than actively to burrow downwards. The shape of the shell can be related to the needs of the animal. The elongated, pointed terminal digitation is well adapted for pushing through soft but closely compacted mud, while the greater extent of the expanded lip and the lighter shell prevent it from sinking too far below the surface.

When *A. pes-pelecani* was placed on soft mud it moved about less easily than the other species, tending to flounder in it and being hampered by great accumulations of mud in the mantle cavity and on the foot. The animal made no attempt to burrow in the mud, but rather tended to raise the body as far as possible clear of the bottom. The animal was most clearly not adapted for life on such a bottom.

Examination of the genital organs of *A. serresiana* failed to reveal the presence of a brood-pouch for incubating the young, so it is probable that pelagic larvae are produced similar to those of *A. pes-pelecani* described by Lebour (1933). If this is so then the survival of the young of the two species, after they descend at metamorphosis from the surface waters, must depend on the type of bottom on which they fall (itself usually dependent on the depth). Young *A. pes-pelecani* which settle down in deep water will be unable to exist on the soft mud, and young *A. serresiana* will be similarly unable to burrow, and so find adequate protection, on stiff muddy gravel bottoms at moderate depths. In certain intermediate regions both species will be able to exist, though conditions will be ideal for neither and the population of both will be correspondingly sparse.

Both in the form and solidity of the shell and in the strength of the body the two species are clearly adapted for a similar mode of life on different types of bottom and the fact that these occur at different depths explains the differences in the horizontal distribution. The reduced pigmentation of the body in *A. serresiana* is presumably the result of the reduced light in the greater depths where it lives.

DISCUSSION.

The genus Aporrhais consists of Gastropods adapted for burrowing in mud and collecting beneath the surface of this detritus of plant origin by means of an extensile proboscis. The manner in which they maintain contact with the water above represents a further adaptation of the proboscis and one which, so far as our present knowledge extends, appears to be unique amongst the Gastropoda. The mode of life resembles more that of a Lamellibranch than of a Gastropod, the majority of mud-living species of which are carnivorous, such as Buccinum, Murex or Nassa, which plough their way through the mud in the search for prey. It is, however, possible that Turritella, which as shown by Hunt (1925) has similar stomach contents, and just possibly Cerithium and Caecum, may prove to live in a somewhat similar manner to Aporrhais. The interesting freshwater genera, Chyta and Limnotrochus, from Lake Tanganyika have similar feeding and digestive organs (Digby, 1902), but nothing is known of their habits. They are certainly related to Aporrhais and to the Strombidae.

The characteristic expanded lip of the shell in the fully grown animal is not necessarily primitively an adaptation concerned with the burrowing habit. In the first place young specimens of *A. pes-pelecani* in which the terminal whorl has not yet been formed, and also older specimens in which the terminal whorl is present but the expanded lip has still to be formed, were both found capable of burrowing like the adults. These will also burrow, although with certain difficulty, when the terminal digitation has been broken off. In the second place a similar expanded lip occurs in the allied Strombidae—very well developed in Pterocera, less so in Strombus, but absent in Rosellaria—none of which live in the same manner. In Pterocera (Yonge, 1932) this flattening of the shell enables the animal to move about on the surface of the sand *without* sinking into this and to keep the right side up despite the ungainly, jerking movements referred to earlier in this paper. Strombus possesses somewhat similar habits; those of Rosellaria are unknown to the author. It appears not impossible that the expanded lip of Aporrhais may originally have been evolved in connexion with a similar mode of life, but that the animals later took to life on mud instead of sand and then to burrowing in this with consequent changes in the form of the terminal digitation and in the breadth and flatness of the lip. There can be little doubt that both are of importance to the adult animals, the terminal digitations in the manner described for the two species, and the horizontal shelf provided by the lip in the increased area over which the proboscis may browse unimpeded and, in *A. serresiana*, possibly by the increased resistance to sinking in the softer mud.

The powerful water currents through the mantle cavity due to the great development of the gill, and the elaboration of the ciliary mechanisms for disposing of sediment carried in with the respiratory current (the latter better developed in *A. serresiana*) are both of them adaptations to the mode of life. They have an added interest because they indicate the manner in which ciliary feeding in Gastropods such as Crepidula (Orton, 1912) and *Vermetus novae-hollandiae* (Yonge, 1932) may have evolved. The mechanism for rejection of large particles from the inhalent opening may have become modified to form the food pouch in Crepidula, and the rejection currents in the exhalent region to form the food channel. The further flattening of the tips of the gill filaments and the appearance of cilia carrying particles forwards in this region would convert the gill into the food-collecting organ of Crepidula, or *Vermetus novae-hollandiae*. It is hoped to develop this argument in more detail elsewhere.

The mode of feeding is very similar to that of Pterocera, the radula and jaws having a similar selective action and the teeth of the radula being few in number to permit of seizing instead of rasping. The form of the gut is that of an herbivorous Gastropod, most notably in the presence of a well-developed crystalline style and gastric shield which, as shown elsewhere, occur in herbivorous Gastropoda which " feed by ciliary mechanisms, or by the slow but almost continuous action of a radula " (Yonge, 1932). It is certain that, if it is to obtain adequate supplies of vegetable detritus having food value, Aporrhais must constantly be feeding. The differences between Aporrhais and Pterocera consist in the presence of a powerful cellulase in the latter—necessary because fresh algae, not decomposing detritus, are swallowed intact and there is no means of mechanical triturition—and the presence of an elaborate sorting mechanism in the stomach of the former—the result of the varied size of the particles collected by the proboscis and the necessity of ensuring that only the smallest of these shall pass into the ducts of the digestive diverticula for intracellular digestion. The remainder of the gut in Aporrhais is concerned exclusively with the elaboration of faeces, of profound importance, as Graham (1932) has emphasized in Patella, in Gastropoda (and other Mollusca, Yonge, 1935) in which the anus opens into the mantle cavity, fouling of which must be rigidly prevented.

NOTE ADDED IN PROOF. Since this paper appeared in proof, Mr. R. Winckworth, in the course of a most helpful letter on the nomenclature of the northern species of Aporrhais, has pointed out that Kobelt (1906,

p. 17) considered *A. serresianus*, described by Sars (1878, p. 198, pl. xii, fig. 7), to be merely a deep-water form of *A. pes-pelecani* and so re-named it *A. pes-pelecani sarsii*. The significant differences recorded in this paper between the form of the shell, the form and pigmentation of the exposed portions of the body, and the reactions to different types of bottom, in *A. pes-pelecani* and *A. serresiana* lend little support to this view. Moreover, the fact that both were taken in the same haul of the dredge at intermediate depths, appears convincing evidence that *A. serresiana* is a true species.

SUMMARY.

1. *Aporrhais pes-pelecani* occurs on muddy gravel at moderate depths and is specialized for burrowing in this.

2. The mode of burrowing is described and also the formation of mucus-lined inhalent and exhalent openings by the proboscis.

3. There is a powerful respiratory current through the mantle cavity which also possesses three sets of ciliary currents for disposing of sediment carried in with this.

4. The animal is a specialized detritus feeder selecting only material of plant origin. The radula consists of one central and three lateral teeth on each side, an indication that it is used for seizing as opposed to scraping, *not* that the animal is carnivorous.

5. The stomach possesses a well-developed ciliary sorting mechanism. The large crystalline style and gastric shield indicate that the animal is herbivorous, but there is no cellulase.

6. The intestine is divided into three regions which are concerned exclusively with the gradual elaboration of the large elongated faecal pellets.

7. *A. serresiana* occurs in deeper water on a soft mud bottom. The differences in the form of the shell and the strength of the body between this species and *A. pes-pelecani* can all be correlated with the difference in habitat of the two species.

8. The form and the mode of life of both species are compared with those of the allied Strombidae of tropical coral reefs, and the ciliary mechanisms in the mantle cavity with those of ciliary feeding Gastropoda.

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Larval and Post-larval Lima from Plymouth.

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With 4 Figures in the Text.

Two species of Lima are known from Plymouth : *Lima hians* (Gmelin), the commonest species, inhabiting small patches of stones with muddy gravel at extreme low-tide mark on the north side of the Breakwater, where many individuals may be found together, and *Lima loscombi* Sowerby, found on the coarse grounds west of the Eddystone, Rame–Eddystone Grounds, Mewstone Grounds, Stoke Point Grounds and south-west of the Eddystone (see Marine Biological Association, Plymouth Marine Fauna, 1931). The latter is a much smaller species than the former, not so highly coloured, and much rarer. Although it is often difficult to obtain *Lima hians*, as it is only accessible at very low tides, it occurs in numbers in the locality cited.

Whilst investigating the lamellibranch veligers in the plankton one was found which stood out from the rest on account of its triangular wedge-shaped shell, most of the lamellibranchs being round or oval in their free-swimming stages. In 1914 Odhner, describing some veligers from Rovigno in the Adriatic, showed that *Lima inflata* Lamarck has a similarly shaped shell and his figures and descriptions agree in essentials, both in animal and shell, with those from Plymouth. Miyazaki (1935) reared the larvae of *Lima brasilanica* Adams and Reeve from artificial fertilizations up to the late veliger stages in Japan, but his latest veligers were much rounder than either *Lima inflata* or the Lima from Plymouth.

The Plymouth veligers were picked out from the fresh plankton and placed in plunger-jars with some food consisting of small flagellates and diatoms. The water in the plunger-jars was from outside the Breakwater and was not sterilized nor filtered : it must thus have contained minute plant food. The veligers grew well and soon lost the velum, reaching a stage when they were easily recognizable as Lima. As they are much commoner in the inside plankton than in the outside, it seems almost certain that they belong to *Lima hians*, although it has not been possible to rear them farther than to a shell breadth* of 2 mm., at which stage

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* The breadth of the shell is measured from the umbo to the ventral margin, the length from the anterior to the posterior margin.

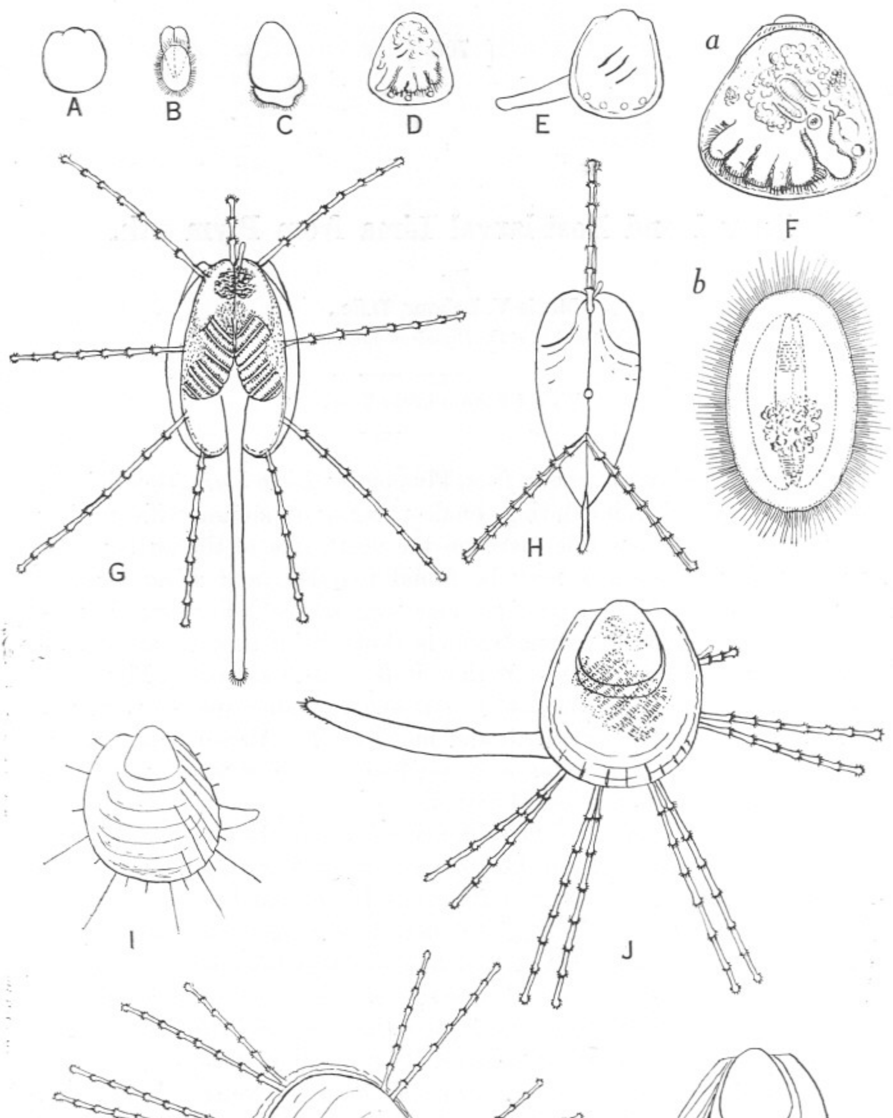

Fig. 1.—Lima larvae and post-larvae.

A. Smallest larva from plankton, 0·08 mm.
B. Veliger, 0·16 mm.
C. Veliger, 0·24 mm.
D. Veliger, 0·30 mm. showing rudiments of tentacles.
E. Latest veliger, 0·32 mm. (*a*, lateral view, velum withdrawn; *b*, swimming, from above).
F. Post-larva, having lost velum, 0·35 mm. across.
G, H, J, K: Post-larva grown in plunger-jar from veliger, shell 0·64 mm. breadth. (G, from above, valves open; H, from above, valves closed; J, side view; K, side view crawling).
I. Young Lima, 1 mm. across, grown in plunger-jar.
L. Young Lima, 1·28 mm. across, grown in plunger-jar, showing eyes through the shell.

the animal was still almost colourless and the shape and markings not distinctive of either species.*

These Lima veligers occurred in the plankton from August to April. They were completely absent in the early summer and reached their maximum abundance about October, when it was possible to pick out 70 to 90 specimens from one tow-net haul. They occurred most plentifully in the tow-nettings from inside the Breakwater or just outside it, although often present in small numbers in the outside waters as far as Station L4 (half-way to the Eddystone) or slightly beyond this.

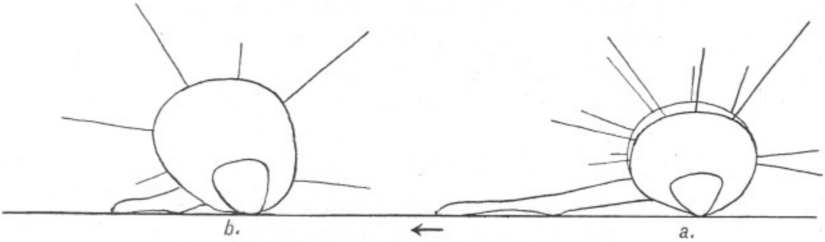

FIG. 2.—Post-larval Lima crawling. (*a*) Valves open. (*b*) Valves closed.

Besides the unusual shape of the larval shell it is the very peculiar method of progression in the young bottom stages that makes Lima so specially interesting. The adult animal is provided with a mass of long and contractile ciliated tentacles. In the very young bottom stages only a few of these tentacles are developed and they are used to help the animal as it crawls. This, however, is not done by their action on the ground surface, for they are stretched out freely into the water ; it seems rather that they are used to balance the body as described below.

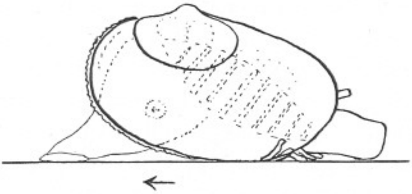

FIG. 3.—Post-larval Ensis, showing the usual method of crawling in lamellibranchs.

The smallest veliger seen in the plankton is almost round and is about 0·08 mm. in length and breadth (Fig. 1, A), having a straight hinge with toxodont teeth. This corresponds well with Odhner's youngest larva (1914). Later larvae (Fig. 1, B–D) have a broader shell, gradually becoming wedge-shaped with the widest part ventral. They sometimes

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* Since this was written, Mr. R. Winckworth has examined these reared post-larval shells and pronounces them to be, almost certainly, *Lima hians*.

vary in breadth in relation to the length, but usually the greatest length is about equal to the breadth. Just before metamorphosis the shell measures about 0·32 mm. in breadth (Fig. 1, E). At this size it loses the velum and goes down to the bottom. Three or four roundish prominences are to be seen just inside the mantle edge which are the beginning of the tentacles. The velum is large and overlaps the ventral shell margin. The foot, as is well known in the adult, has the peculiarity of being twisted in the opposite direction from all other known lamellibranchs, and this shows even in the early bottom stages, as has been noted by Odhner (*op. cit.*).

When the velum is lost the shell grows, especially in breadth, the tentacles lengthen, increase in number and become ringed and ciliated. The animal takes up its position on the bottom with its hinge and anterior margin downwards, the posterior and ventral margin upwards. The foot, which is long and flexible, emerges antero-ventrally; the tentacles are extended and the valves open, showing the gills and mantle-margin (Fig. 1, G). The mantle-margin is thin and filmy, being enlarged ventrally as a soft veil-like outgrowth. The tentacles arise from just inside the margin. The ciliated foot is extended to its greatest extent and attached to the bottom: the tentacles also extend outwards and the valves are far apart. The muscles of the foot contract; the valves close; the pairs of tentacles, still extended, come together, and a sudden movement takes place in a leech-like manner, the animal being brought up to the fixed position of the foot (Fig. 2). This very extraordinary method of progression is unknown in any other genus. Odhner (*op. cit.*) described the movement of the very young bottom stages of *Lima inflata*: the foot directed backwards, the young shell creeping backwards, with the mouth posterior to the foot; but in the young Lima from Plymouth the tilt of the shell goes much farther and the hinge is almost on the bottom. Thus the direction of movement is antero-ventral and not actually backwards, although the mouth is behind the foot and the foot is twisted in the opposite direction to that of the ordinary lamellibranch young which crawls with the dorsal margin uppermost and the foot moving forwards (Fig. 3). This position with the hinge and anterior margin downwards and ventral and posterior margin upwards is the natural resting position of the adult Lima and also its position when it crawls. A figure (Fig. 4) is given here showing a small *Lima loscombi* in a bowl which always took up its position with its valves open, gills exposed and tentacles more or less outstretched. Jeffreys (1863, Vol. II, p. 89) quotes Canon Norman's description of *Lima hians* which when tired of swimming lies on its back, the valves expanded. In the recent paper by Studnitz (1931) there are good figures and descriptions of the normal position of the adult *Lima hians* and of the twisted foot in relation

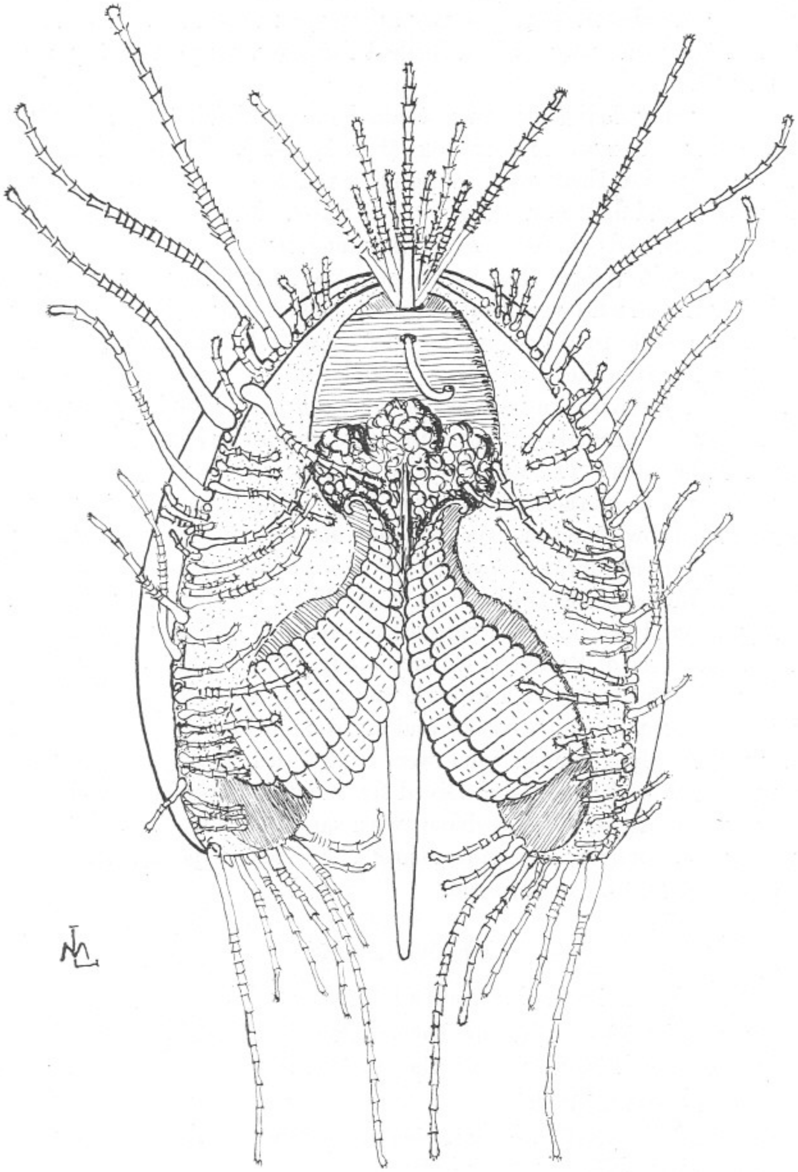

FIG. 4.—*Lima loscombi*, from Eddystone Amphioxus grounds, 8 mm. broad, in natural position on bottom.

to the other organs. He also describes, to a certain extent, the creeping movement with the position of the shell, but in the adult the enormous mass of tentacles must necessarily affect the movement and cannot be used in the same way as is described for the very young stages from Plymouth.

As the young shell grows, more tentacles are added between the others, some being longer with many rings (Fig. 1, G–K). In specimens reared in a plunger-jar there were 17 pairs of tentacles in one shell 1·5 mm. in breadth, and at 2 mm. there were 25 pairs. In the adult *Lima hians* there are hundreds, *L. loscombi* having much fewer.

The smallest veliger seen in the plankton must be very young and probably not much larger than the first shelled stage. Unfortunately it was not possible to collect adults with eggs and fertilization could not therefore be attempted.

All the free-swimming stages have shells glass-like in transparency with colourless animals, a faint pink tinge appearing in the young stages 2 mm. in breadth. The velum is bordered by very powerful cilia. Gills begin to appear in the latest veliger stage. The stomach is usually full of green or brown food and the digestive gland is of a conspicuous brown colour. There is a large otocyst at the base of the foot containing several otoliths. In specimens from 1 mm. in shell breadth there are well-formed red eyes round the inside of the mantle margin, looking very like those in similar stages of Pecten or Chlamys (Fig. 1, L).

Up to 2 mm. in breadth growth was quick, for veligers of 0·16 mm. grew to 0·32 mm. in a few weeks, and in two months they reached 1·5 mm. In two and a half months some were 2 mm. in breadth, but they never grew after this although some lived for months at this stage. Some of these were removed to glass dishes with sand and put under circulation, but they did not grow and made no nests. The oldest specimens at present alive are about four months old.

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A Comparison of the Biology of *Echinus esculentus* in different Habitats. Part III.

By

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With 3 Figures in the Text.

GENERAL.

In an earlier paper (Moore, 1934), an account was given of the season of spawning and the seasonal changes in the gonad volume of urchins from various depths in the Isle of Man. In order to compare these with urchins from a more southerly locality, monthly samples were taken in 1934–5 from 2 miles N. to N.N.E. of the Eddystone, in 27–28 fathoms, and in 1935–6 from $2\frac{1}{2}$–3 miles S. to S.S.W. of Revelstoke Point in 17–22 fathoms. The samples consisted of about fifty urchins each time, and the gonads of these were examined by smears in the usual way, their condition being recorded as the percentage of each sex which were respectively unripe, ripe, spawning or spent. The gonad volumes were expressed as the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$ (Moore, 1934, p. 871). These results, together with temperature observations kindly supplied by Dr. H. W. Harvey, are shown in Fig. 1. Unfortunately no temperature observations are available for the actual grounds on which the samples were taken, but they may be assumed to be very similar to those at station L4 which is half-way between Rame Head and the Eddystone. At this station temperatures were available up to August 1935 only, so the observations for station E1, 10 miles SW. of the Eddystone, are also included. Although at this deeper station the temperature range at the bottom is less extreme than at L4, yet at the critical period of spawning there is little difference. An eleven years' mean temperature curve for E1 is also included from which it will be seen that the summer of 1934 was distinctly cold and the following winter rather warm, while the summer of 1935 was normal, and the following winter rather cold. Whether there is any connexion between these temperature differences and the observed differences in the gonads in the different years is doubtful.

SEASONAL GONAD CHANGES AT PLYMOUTH.

As has already been stated, the degree of ripeness of the males is less easily defined with accuracy than that of the females. Considering the latter, therefore, it will be seen that practically no ripe females were found before the beginning of February in either year, and few before the beginning of March. Spawning commenced about the end of March in 1935 and the end of February in 1936, the time corresponding approximately with the time of lowest sea temperature. The date on which 50% of the urchins were spent, taking both sexes together, was May 3rd in 1935 and April 25th in 1936, corresponding to sea temperatures of about 9·7 and 9·2° C. The temperatures at a corresponding period in spawning in the Isle of Man were 7·0° C. in 1931 and 7·8° C. in 1932. Spawning takes place, therefore, at a higher temperature at Plymouth than in the more northerly locality, and falls at about the middle of the range of 4–16° C. given by Runnström (1927) for the normal development of *Echinus esculentus* larvæ.

The growth of the gonads at Port Erin was found to be very different on the two grounds "Breakwater" and "Breast." On the latter, at a depth of 17–20 fathoms, the gonads never filled up to a value of more than 0·4 for the ratio $\frac{10\times\text{Gonad volume}}{\text{Test volume}}$. The gonads gradually regained size after spawning until they were at a maximum size about August, after which they remained constant until the winter and then shrank considerably, only regaining their full volume immediately before spawning. This winter shrinkage of the gonads was definitely not a second spawning, and seems more likely to have been associated with lack of food at that time. On the "Breakwater" ground, where the urchins live about low-water mark, the gonads filled up to a much greater size, with a ratio of nearly 2·0 compared with 0·4 on the Breast ground, and with no winter drop in volume. It seems probable that the greater abundance of food is here the controlling factor.

The Plymouth material appears to be of the Breast type, as might be expected from the depth from which it was taken. The gonad volume ratio was at a value of between 0·4 and 0·5 in the summer of 1934, but dropped somewhat in the winter, rising again only immediately before spawning in 1935. At their maximum the females attained a value of 0·7, being considerably bigger than the males of a corresponding test size, a phenomenon which was observed on both grounds at Port Erin also. After spawning in 1935 the gonads filled up slightly, but never reached nearly so great a size as they did the previous year, and the spawning in 1936 was extremely poor, the drop in volume of the female gonads being from 0·7 to 0·2 in 1935 and only from 0·3 to 0·2 in 1936.

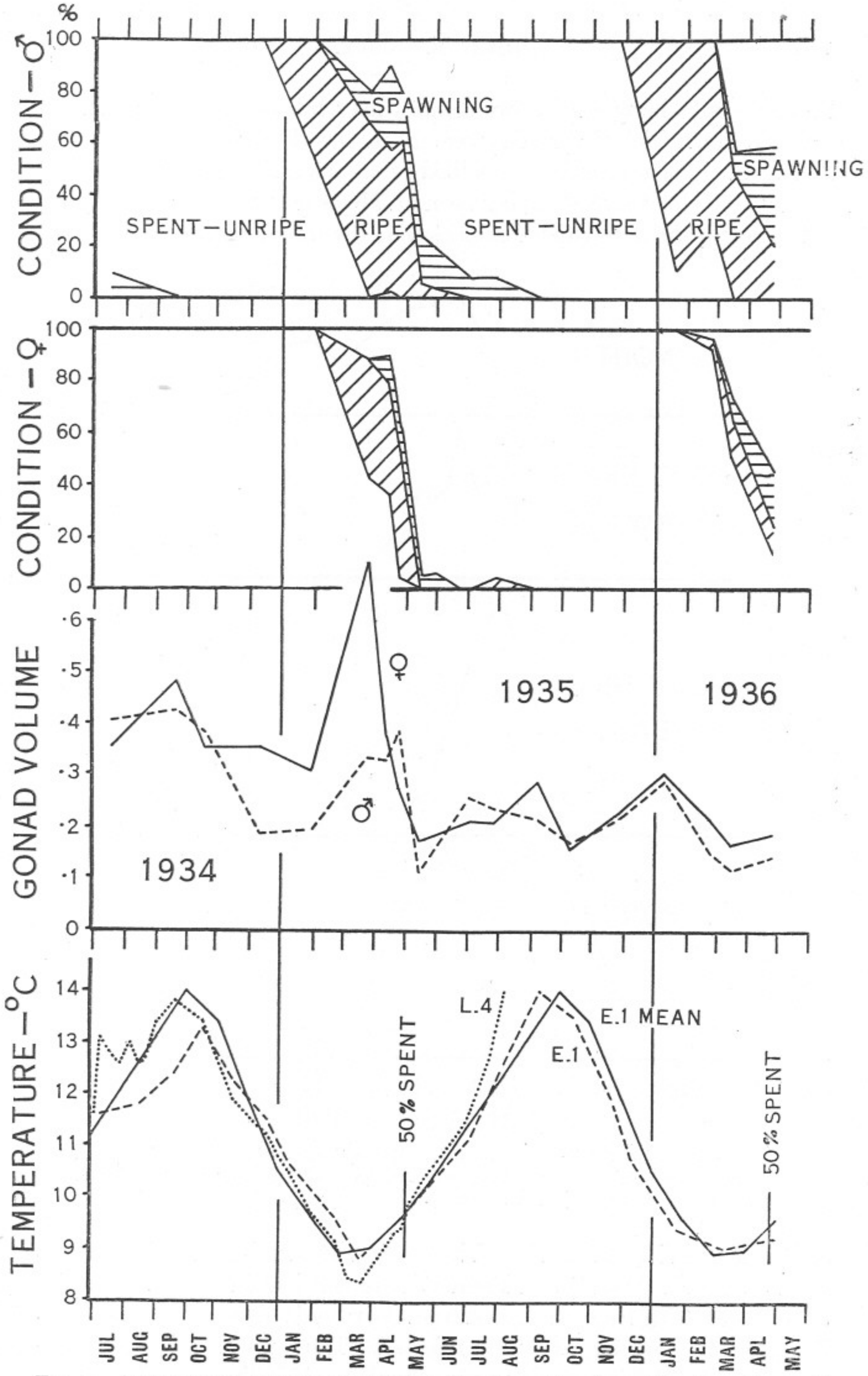

Fig. 1.—Seasonal changes in the conditions of male and female urchins from Plymouth and of their gonad volumes as indicated by the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$. Temperatures at the bottom at Stations L4 and E1 during the period under observation, and an eleven years' mean temperature curve for E1.

The difference between the two seasons may be due to the shift in the grounds from which the urchins were taken, but the two grounds are very similar in character and it seems likely that the differences were, in part at any rate, due to 1936 having been an abnormal year.

There appears to be a definite increase in the size of urchins southwards, as indicated in Fig. 2. It should be noted that in this figure the samples from Port Erin (Breast) and Plymouth are deficient in the smaller sizes, the curves having been abstracted from the records of gonad examinations for which the smaller sizes were rejected. Those for Port Erin (Breakwater) and for Millport are, however, complete. At Millport and Port Erin, specimens were never recorded over 121 mm. in breadth, corresponding

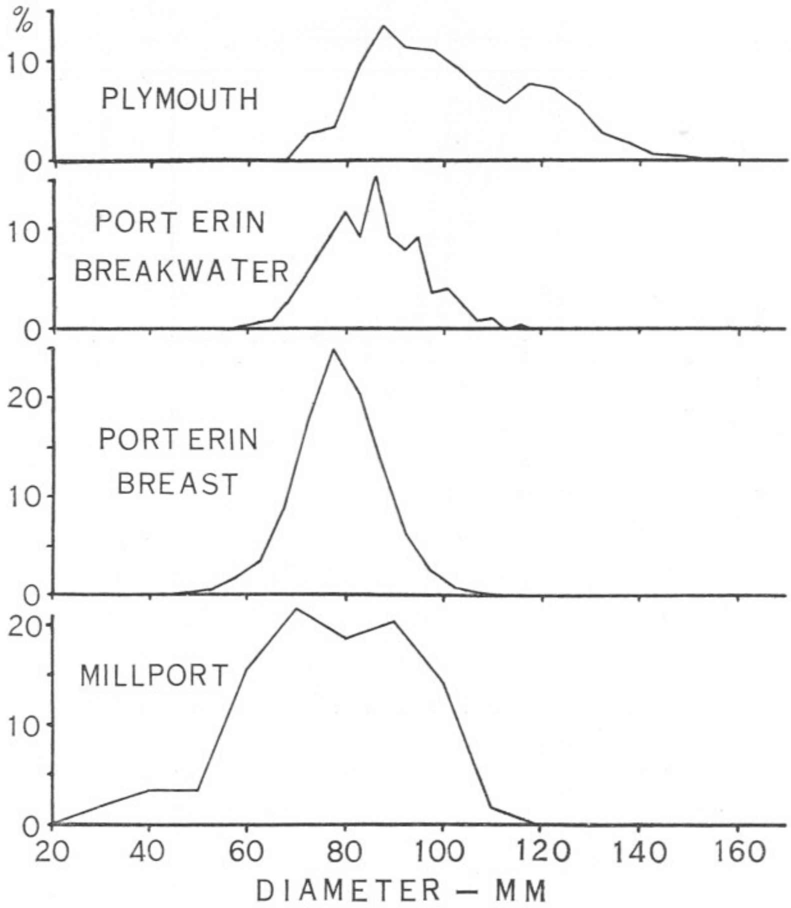

FIG. 2.—Mean size distribution curves for all samples examined from Plymouth, Port Erin (Breakwater and Breast) and Millport, showing greater size of urchins in the south (see text below).

to a volume of about 800 c.c. (external), whereas urchins were frequently taken at Plymouth with a diameter of 150 mm., corresponding to a volume of about 1800 c.c., and still larger specimens have been recorded.

DEPOSITION OF PIGMENT.

In colour also the Plymouth urchins resemble most closely the Breast urchins, the violet colouration of the test which was so frequent on the Breakwater, but rare on the Breast, having never been noted at Plymouth. Violet colouration of the spines is, however, frequently seen. The violet pigment is probably derived from some food, possibly algal, which is obtained more readily in the alga-covered littoral and sub-littoral zone than in deeper water. Griffiths (1900) has described a violet pigment with lipochrome properties from the integument of *Echinus esculentus*, while MacMunn (1885, 1889) has given the name Echinochrome to a reddish pigment occurring in the elaeocytes in the perivisceral fluid of *Strongylocentrotus lividus*, *Echinocardium cordatum* and *Echinus esculentus*. Later workers have studied a similar pigment found in the test, and McLendon (1912) and Cannan (1927) have described the same or a similar pigment from Arbacia at Woods Hole.

Dr. K. G. Stern (personal communication) when working on *Echinus esculentus* at Plymouth, found that this red pigment, which he calls Echinorubin, and which was similar to, although apparently not identical with that of McLendon and Cannan, was present in the elaeocytes of the body fluid and also in the test, but was present in far the greatest quantities in the walls of the intestine. The pigment appears to be absorbed into the intestine with the food, transferred to the elaeocytes in the body fluid, and finally excreted into the outer surface of the shell where it is deposited. I am indebted to Dr. Stern for permission to publish these notes on the amounts of pigment found by him in the intestines. The extraction with solvents of a large number of the latter, sent to him at intervals throughout the year, proved that the red pigment which was so abundant in the intestines in the summer and autumn, was absent from them in the winter and spring, its place being apparently taken by a brown oily substance. Table I shows the yields of echinorubin obtained by him from the intestines of the Plymouth urchins, but it must be realized that these are only notes on the yields obtained in the preparation of the crystalline substance, and not in any way quantitative analyses.

The tests of urchins from both grounds at Port Erin and also those from Millport showed the deposition of the red pigment, and of the violet one when present, in the period between about April and December (Moore, 1935). As, however, shell growth was confined to the period between November to January and the end of March, there being no further growth during the summer months, and since pigment laid down in the surface of the plates will remain at the surface until overlayed by a layer of non-pigmented shell at the next period of shell growth, there can be no evidence of the precise time at which the pigment is deposited beyond the fact that this occurs between the limits of about April and December. Since the pigment is now shown to be the same as that which is present in large quantities in the intestine during summer and autumn, it seems probable that the annual summer rings of pigment in the test represent periods of feeding on some particular diet, or quite possibly the main periods in which the urchin is feeding at all. On the other hand, the females from the Breakwater at Port Erin continued to show gonad growth right up to the time of commencement of spawning, and on all grounds where there is a drop in gonad volume in winter there is a corresponding rise just before spawning, presumably correlated with an increased supply of food at that time. It is noteworthy, however, that on the Breakwater ground, where algal food is abundant throughout the entire year, and where there is no winter drop in gonad volume, the pigment rings were sufficiently clear to be counted in only 46% of the urchins as compared with 79% on the Chickens ground farther offshore. And with regard to the source of the pigment, Awerinzew (1911) has shown a close correlation between algal and urchin pigments in the case of *Strongylocentrotus draebachiensis*. This species varies in colour from yellowish green to deep reddish purple, and it was found that urchins of the former colour occurred almost invariably on a substratum of sandy gravel while the reddish purple ones were found on the red calcareous alga Lithothamnion. Finally the reddish purple urchins soon began to lose their colour when taken into the aquarium. So it is very probable that here also the urchin is obtaining its pigment from the food that it eats.

TABLE I.

Date.	No. of urchins.	Yield of crude echinorubin crystals.	Notes.
1934.			
Sept.–	ca. 50	ca. 80 mg.	together yielding 50 mg. of recrystallized echinorubin.
Oct. 20	ca. 50	ca. 40 mg.	
Dec. 14	45	30 mg.	
1935.			
Jan. 11	ca. 50	35 mg.	
Feb. 2	ca. 50	trace only	extract yielded a brown oily substance.
April 18	?	trace only	
May 15	65	some	
May 23	18	none	

Deutler (1926) has demonstrated the presence of similar pigment bands in the plates of the urchin *Colobocentrotus atratus*. From these bands, he states, the age can be determined; and he shows that they are seen clearly in those echinoderms which feed at any rate to some extent on algæ, and which migrate into the littoral zone. He quotes a number of such urchins which live in the littoral zone, and some of which migrate in and out of it annually, and he suggests that the zonation of the pigment in their plates is due to a seasonal feeding rhythm which makes them deposit pigment in the summer at the time when they are feeding most.

If a large seasonal migration into and out of the algal region of the shore took place in *Echinus esculentus* this would necessitate such changes of diet as might well produce the observed seasonal differences in pigment, and some such migration has been suggested both at Millport (Elmhirst, 1922) and at Port Erin (Stott, 1931). The former, however, states that the migration is only from the actual intertidal zone down to a depth of one to two fathoms (where algæ are still very abundant), and so far as Port Erin is concerned I have never been able to satisfy myself that such a migration occurs at all. Certainly there is no such migration of the deep-water Chickens urchins which live at a depth of 35 fathoms and yet show clearly distinguished pigment zones. It must, therefore, be assumed that some seasonal rhythm of feeding occurs in both the littoral and the deeper-water urchins, and that the main difference between the two lies firstly in the greater food supply available in the littoral zone, resulting in larger gonads and absence of a winter drop in gonad volume, and secondly in a difference in the nature of the food as reflected in the greater frequency of occurrence of the violet pigment in the tests of the littoral urchins.

OUTLINE OF SEASONAL CHANGES.

Reid (1935) has recently brought together what is known of the relation of *E. esculentus* to its external environment, and in Fig. 3 an attempt is made to summarize the existing knowledge of its internal changes, e.g. growth, spawning, etc., and the seasons at which they occur. Since the information available is incomplete, and of necessity drawn from different localities, the results must be taken as a generalization only, from which any individual locality may diverge considerably.

At the beginning of the year the shell starts to grow, and continues to do so up to some time between April and June, the exact time varying with locality and year. At the same time, on the offshore grounds, feeding appears to have slowed down, and the gonad which is the main reserve of food material has been shrinking since October–November. It is replenished, however, in February and March, and about March, when the sea temperature is at its minimum, spawning commences with concurrent shrinking of the gonad. Spawning continues until about May, by which time the gonad is beginning to fill up again, and this it continues to do until about August. In the case of the females only from the Breakwater, gonad growth continued right up to the commencement of spawning the following year. Stott (1931) has shown that in the period between December and the end of March, the percentage of glycogen in the gonad is dropping, possibly being transformed into some other form of carbohydrate. The time of pigment deposition in the shell is not clearly defined but almost certainly follows closely the time when there is abundant pigment in the walls of the intestine, that is from about May to January, and this probably corresponds with the main feeding period. In August–September the sea temperature is at its maximum, and it is about this time that shrinkage of the gonads of the offshore urchins commences.

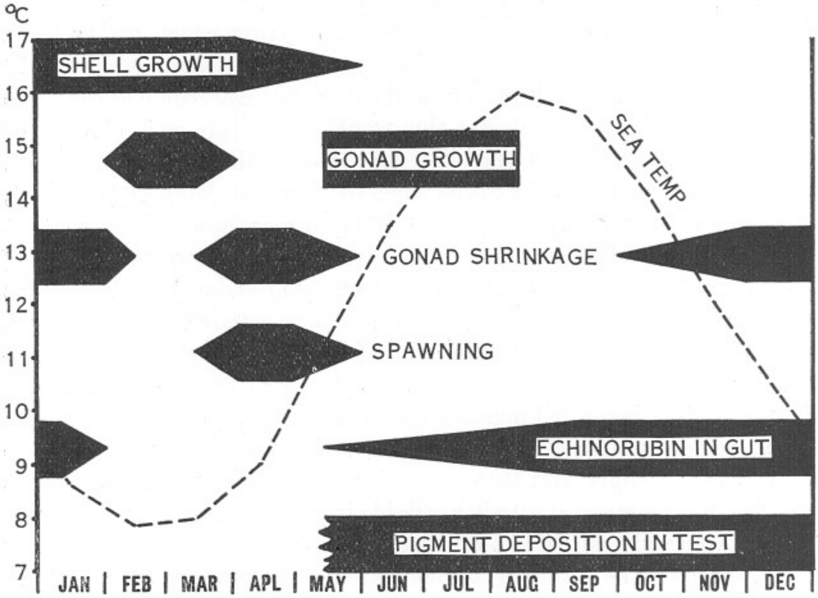

Fig. 3.—Generalized diagram of the seasons of shell growth, gonad growth, etc., in *Echinus esculentus*, with a sea temperature curve (for Plymouth).

SUMMARY.

1. Gonad examinations were made on monthly samples of *Echinus esculentus* from Plymouth in 1934, 1935, and 1936.

2. Spawning is from February–March to May, 50% spawning occurring at a temperature of 9·2–9·7° C. compared with 7·0–7·8° C. in the Isle of Man. There was a winter drop in gonad volume one year, but not the other.

3. The nature, distribution and source of the pigments in the shell are discussed, and it is shown that pigment is found in quantity in the intestine only in the summer and autumn.

4. The known facts with regard to the seasons of growth, spawning, etc., are brought together into a generalized diagram.

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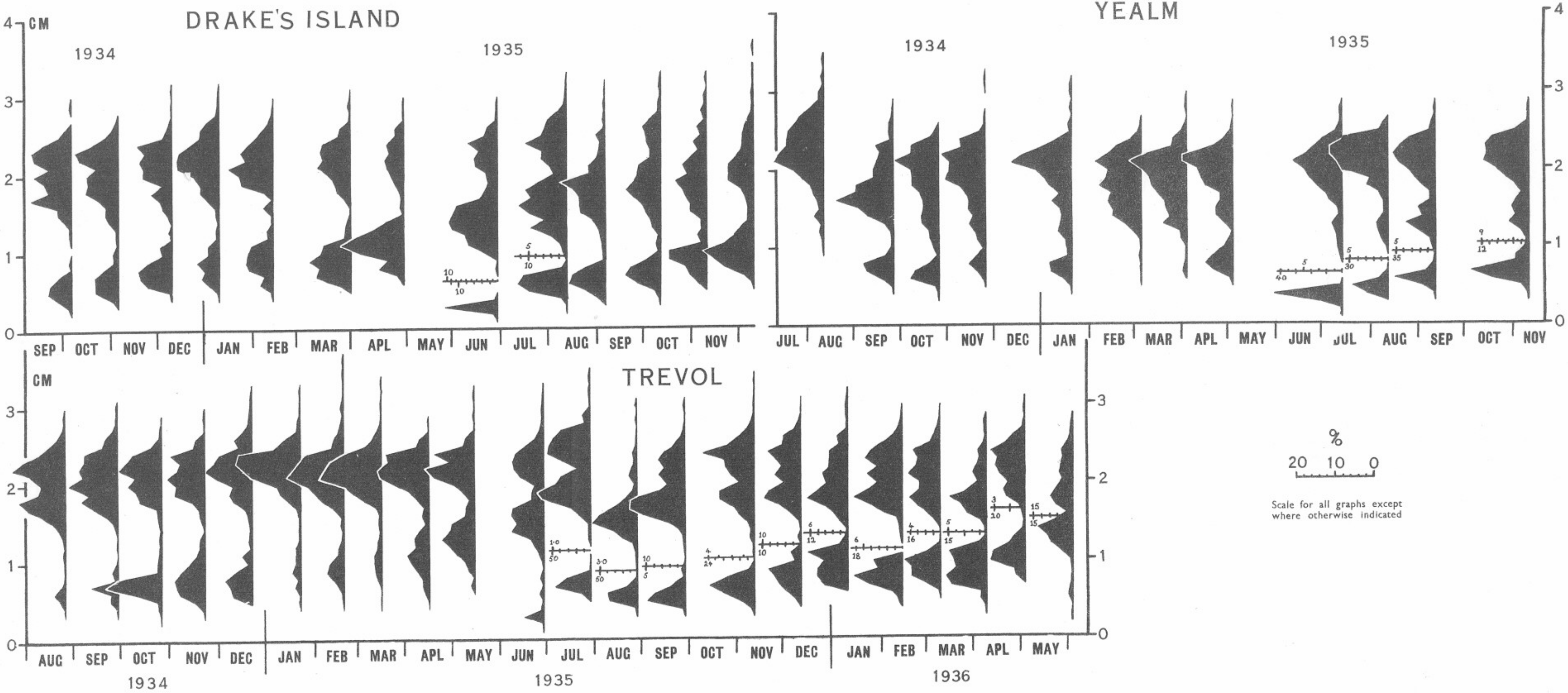

Scale for all graphs except where otherwise indicated

The Biology of *Littorina littorea*. Part I. Growth of the Shell and Tissues, Spawning, Length of Life and Mortality.

By

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With Plate III and 10 Figures in the Text.

CONTENTS.

MATERIAL AND METHODS.

THE Periwinkle, *Littorina littorea* (L.), is one of the most abundant gastropods on the shore, and can live under widely varying conditions. It is found on clean, alga-covered rocks, among small stones, on gravel, on soft mud, and rarely even on sand. It ranges from about high water of neap tides to extreme low water of spring tides, and in some places even slightly below this, although in most localities it is restricted to a much smaller part of the tidal zone. It occurs also from shores with high wave-exposure to sheltered and even polluted estuaries, where it is tolerant of considerable lowering of the salinity. The material for the present study was collected at intervals throughout 1934–1936 from three localities near Plymouth, the details of which are as follows.

Trevol. Level: mid-tide level. A mud flat in the middle of St. John's Lake, opposite Trevol Pier. The mud is soft, so that a man will sink six to twelve inches into it, and there is a sprinkling of dead shells on the surface. The smaller winkles in particular tend to cluster on these dead shells. In some parts there is a growth of Zostera and Enteromorpha, but on most of the ground there is no macroscopic algal growth.

Drake's Island. Winkles are abundant from about mid-tide level to between mean low water of neap tides and mean low water of spring tides. The area used for collection was a stony beach on the north side of the island, with a medium amount of Fucoid growth.

Misery Point, Yealm. The winkles are abundant about mean low water of spring tides, and very few are found above mean low water of neap tides. There is very little Fucoid growth, but the winkles cluster in very large numbers on such few fronds of Fucus as are present. There is a tidal stream of about 2½ knots past the point.

Single samples were also taken from four other localities for shape determinations (see p. 732).

A certain number of winkles are collected by fishermen from the Trevol and Yealm grounds, but mostly from slightly different positions from those used in the present work, so that the populations may be taken as being little influenced by them. There is no such collection on Drake's Island.

Two methods of sampling were used. The first, that of hand picking all the winkles visible on a fairly large area, yielded large numbers, but was not fully representative of the smaller sizes below about one centimetre in height. The second method consisted in sieving the entire surface sample of ground from a known area, down to about five centimetres in depth, but owing to the large amount of extraneous material collected this method could be applied to small areas only—in practice usually one square metre. The second method yielded a representative sample of all sizes of the population, with as many of the small sizes as were needed for measurement but did not contain anything like the one to two thousand of the larger sizes which were required. Where possible, therefore, the two methods were used and the size distribution of the larger sizes as determined from the large hand-picked sample combined with that for the smaller sizes as determined from the surface sample in the proportion indicated in the latter. This procedure was readily applicable on the mud at Trevol, where it was used from July, 1935, onwards. It was more difficult on the stony ground at Drake's Island and the Yealm, where it was applied on special occasions only; in general, only hand-picked samples were taken from these two grounds with the result that, while the mean height of the first year shells as determined from these samples is correct, their numbers relative to the older ones are too small. The same applies to the sample taken at Trevol before July, 1935.

The height of the smaller shells was measured to the nearest millimetre with sliding callipers. For the larger shells it was found necessary, if a second year peak was to be differentiated with any certainty in the size distribution curves, to measure between one and two thousand shells in each sample. For this purpose a machine was used which measured the height of each shell, and besides indicating its height in millimetres, counted the total number measured in each millimetre group. The average numbers measured per sample for each ground were 1,348 for the Yealm, 1,601 for Trevol and 706 for Drake's Island, the numbers being kept smaller at the latter locality owing to the limited size of the ground and the fear of seriously depleting its stock.

Samples were taken from each ground at approximately monthly intervals, and were used for size distribution analyses and also for shell and tissue weight determinations and for gonad examinations. At first twenty animals were taken at each millimetre interval of height and, after being boiled for about two minutes, the animals were removed from their shells with a pin, the twenty shells and twenty bodies being placed in weighed glass dishes. They were then dried in a boiling-water oven, the shells for one day and the tissues for three, and weighed. Monthly curves were thus obtained for each locality showing the relation of shell and tissue weights to shell height. After twelve months it was shown conclusively that there was no seasonal variation in shell weight, so the latter determinations were discontinued, and the mean values for the year assumed to hold for all further calculations (Fig. 6). In this part of the work the two sexes were not distinguished, but from July, 1935, onwards the material from Trevol was examined on extraction from the shells, and twenty each of males and females were set aside from each millimetre group for weighing. It was found to be quite possible to distinguish the sexes by the presence or absence of a penis, except in very small immature specimens, although in the non-breeding period the penis is reduced to a very small size.

From December, 1935, regular samples were examined from Trevol, and a few also from the other grounds, for the condition of the gonads. Smears were taken from the ovary and oviduct of the females and from the vesicula seminalis of the males, and the condition of the genital products recorded. In most cases samples were taken representative of each distinguishable year group on the ground in question.

Finally, for the determination of the growth of shells which were too old to come within the limit of distinguishable year-groups in the size distribution analyses, a number of winkles were collected from Drake's Island, marked at the apex with cellulose paint, and their lip notched with a carborundum wheel. They were then released on the ground from which they were taken and at intervals they were collected and the height and the spiral increment to the lip from the notch measured for each individual. They were then returned to the shore again as quickly as possible, care being taken to avoid high temperatures during the period when they were away from the shore ; it was usually found possible to collect them one day and to return them the next. The process of marking was calculated to produce as little disturbance as possible. The shells were rapidly dried in a current of air from an electric fan ; the apex of each was then dipped into cellulose paint and they were replaced in the air current until the paint was dry enough to handle. The edge of the shell was then notched with an electrically driven carborundum stone, and the winkles returned to running sea-water, the whole process not lasting more than half an hour. Cellulose paint was found to last fairly well on the shore and not to need renewing for several months at least.

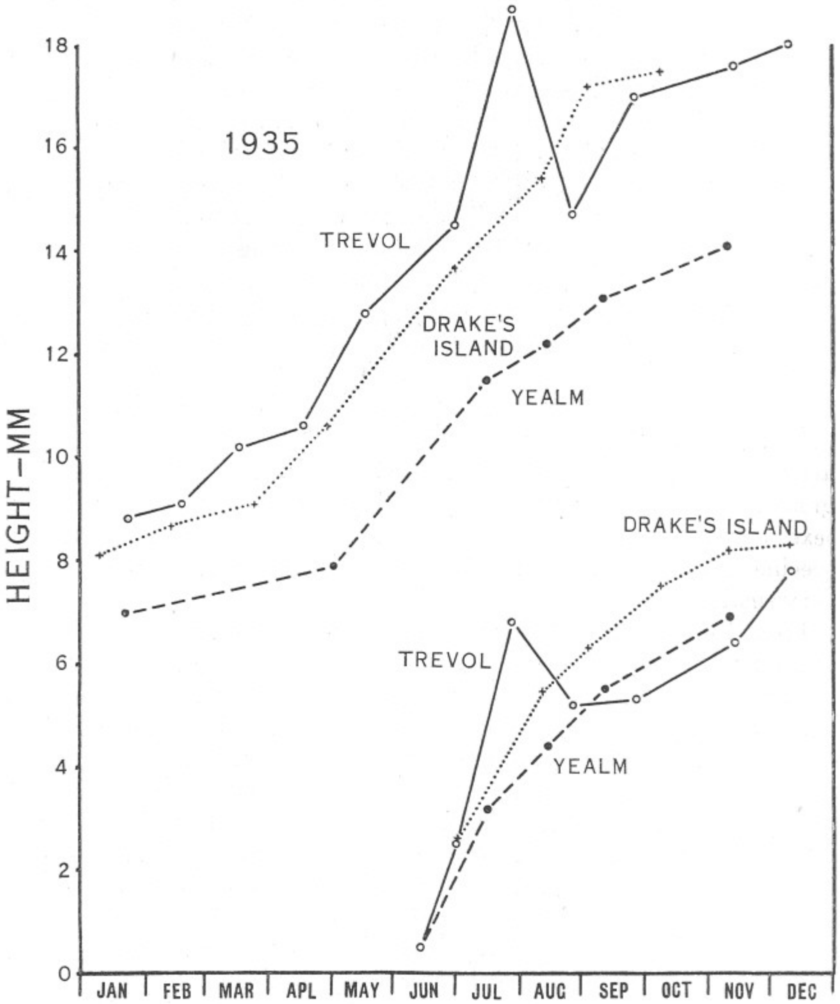

Fig. 1.—Growth of *L. littorea* on the three grounds in 1935.

In the first place 2,695 marked winkles were released on Drake's Island in September, 1934, and the returns obtained ranged from three to four hundred in the first few months down to about a hundred at the end of a year. Of these winkles, 1,700 whose sex was not determined, were marked with blue paint. The sex of the remainder was determined by relaxing them in a dilute solution of pilocarpine hydrochloride and noting the presence or absence of a penis. The males were then painted green and the females red. The measurements of the red and the green shells were kept separate for the determination of the relative growth-rates of the two sexes, but all colours were taken together for the general growth results.

SHELL GROWTH.

The size distribution curves for the three grounds are shown in Plate III. It should be noted that the proportion of first-year shells to older ones is too low up to a height of about one centimetre on all grounds except for the 1935 brood at Trevol. From these size distribution figures the mean size of the first and second year groups was determined wherever possible for each sample, and from these the growth curves shown in Figs. 1, 2 and 3 were drawn. Fig. 1 shows the relative growth in height on the three grounds in 1935. In their first year, growth on Drake's Island was considerably faster than that at the Yealm, while the growth at Trevol was rather erratic. For the second year animals, however, the rates for Trevol and Drake's Island are very similar while that for the Yealm is definitely less. The figures serve also to show the variation in growth on the same

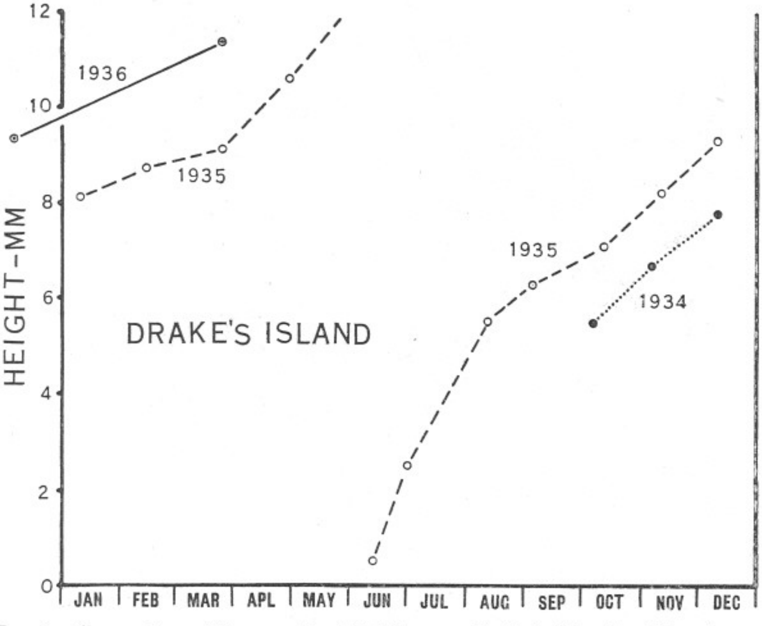

FIG. 2.—Comparison of the growth of *L. littorea* on Drake's Island in different years.

ground in different years (Figs. 2 and 3). At the Yealm there is no significant difference in the growth-rates in the years 1934, '35 and '36, but at Drake's Island the rate is definitely greater in 1936 than in 1935 and in 1935 than in 1934. At Trevol the reverse results are found, and the rate is less in 1936 than in 1935 and less again in 1935 than in 1934. The differences in successive years at Drake's Island and Trevol are of an order which might well be considered significant in correlation with, for example, sea temperature changes in the different years, and yet the winkles on the

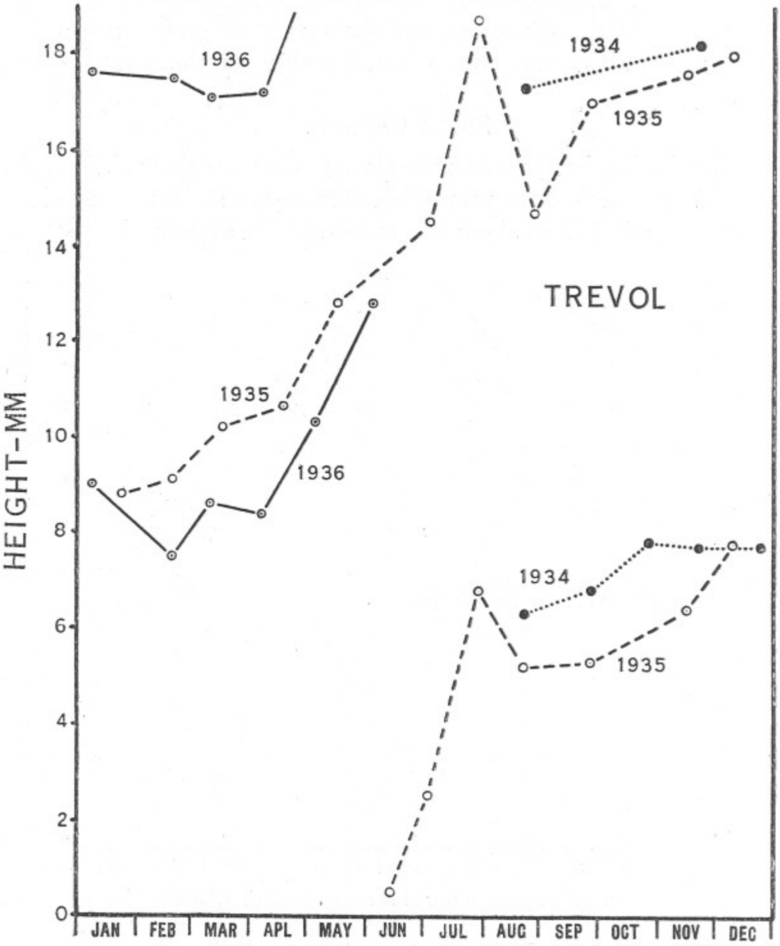

FIG. 3.—Comparison of the growth of *L. littorea* at Trevol in different years.

EXPLANATION OF PLATE III.

Size distribution curves for *L. littorea* for the three grounds.

different grounds show entirely different variations, thus emphasizing the danger of drawing conclusions from the study of a population from a single locality or for a single year only. The possible connexion between the observed local differences and the habitat is discussed later.

The size distribution figures are useful only up to an age of about two years, after which the successive peaks overlap too much to be distinguished, so for the growth of the larger sizes a method of individual marking was necessary. Such a method is possible only on a ground which is close to the laboratory, and where collecting is easy and there is no risk of the brightly coloured shells being picked up by fishermen, and for all these Drake's Island was ideal. A small number of marked shells were released at the Yealm also, but the returns were poor, and the results served only to confirm the much slower growth-rate there than at Drake's Island.

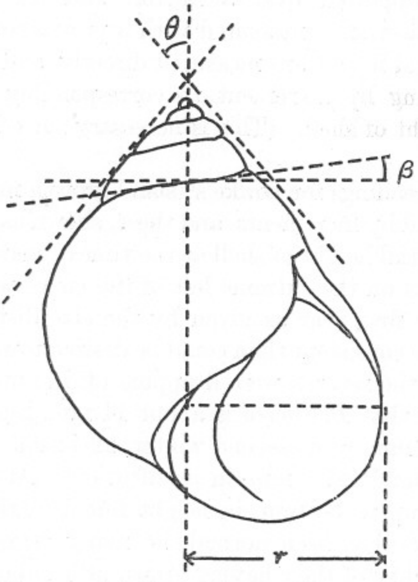

FIG. 4.—Diagram of *L. littorea* showing shell angles (see text).

The relation between the amount of growth measured in a spiral direction on the lip of a shell and the corresponding increase in the height of the shell is dependent on two fundamental shell angles, θ the half-apical angle (Fig. 4), and α the spiral angle (Moore, 1936, p. 72). θ is easily obtained by direct measurement, but α is more readily obtained from the formula

$$\tan \alpha = \frac{2{\cdot}72 \sin \theta}{\log \mathrm{R}}$$

where R = the ratio of the diameters of two successive whorls. The formula for the length of a plane logarithmic spiral is $\frac{l}{r} = \sec \alpha$, where l=the length, and r=the vector radius (Fig. 4). In the case of a spiral projected on to a cone such as we have in Littorina, a correction must be made, so that

$$\frac{l'}{r} = \sec \alpha . \sec \beta$$

where l′=the spirally measured length, and β an angle derived from α and θ, but most readily obtained by direct measurement (Fig. 4). If the shell is supported over a mirror, and the angle between a suture and its reflection is measured with a protractor, this is equal to 2β. The radius and height are measured directly, and so a curve can be constructed relating lip increment to corresponding height increment at any given height of shell. (This is necessary since both α and θ vary with shell height.)

The successive readings for Drake's Island growth material were in the form of heights and lip increments, and these, shown as height increments plotted against initial height of shell at the time of marking, are shown in Fig. 5. The points on the extreme left of the curve were obtained from the growth in the first year as given by the size distribution analyses. The results are less consistent than could be desired towards the end of the experiment when the returns were dropping off in number, but they are sufficient to show that *L. littorea* is about 14 mm. high in December of its first year, 17·4 mm. in its second winter, 22·4 mm. in its third winter, 25·4 mm. in its fourth, 27·3 mm. in its fifth, etc. At this rate the very large individuals up to 36 mm. in height found in this locality would, if their growth-rate has been normal, be many years old, but there is always the possibility of their having grown at an abnormally high rate, perhaps as a result of parasitization by cercariae. It may, however, be mentioned that Waters (1890) says that he kept individuals living for ten years in an aquarium.

In the above calculations the possibility of a different growth-rate in the males and the females has not been considered, since it would obviously have been impossible to determine the sex of the sixty thousand shells measured. The experiment on the growth of winkles of known sex on Drake's Island shows clearly, however, that there is such a difference. If we take the ratio of the amount of growth in the males to that in the females in each millimetre group at each period of collection, and from this obtain a mean value for each period, we get the results which are shown in Table I (p. 730).

Excepting the first month when the amount of growth was so small as to be difficult to measure, and therefore not very reliable, there is in all cases a definitely greater rate of growth in the females than in the males.

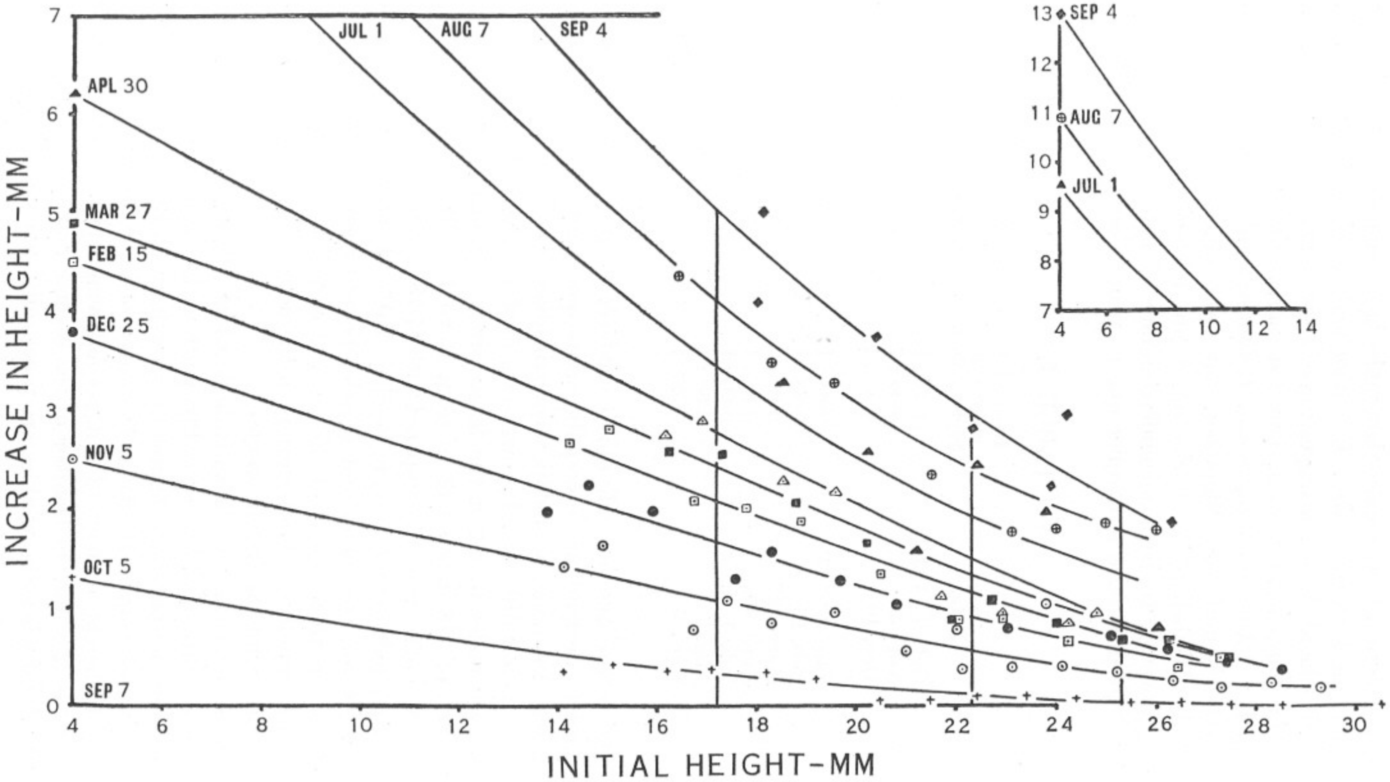

FIG. 5.—Growth of marked *L. littorea* at successive intervals of measurement on Drake's Island. Each point represents the mean for all individuals commencing growth within a given millimetre group.

A greater growth-rate in females than males has been indicated in the case of two Indian Littorinas also, *L. scabra* and *L. obesa* (Sewell, 1924). On the other hand there is a suggestion of a greater rate of growth in the males of *L. littorea*, at any rate in their first year, made by Linke, who says (1933, p. 4): "Auch die Jungen von *L. littorea* werden erst nach einem Jahr geschlechtsreif, das Männchen hat dann eine Schalenhöhe von 13 mm., das Weibchen eine solche von 8 mm. (Pelseneer, 1926)." This appears, however, to be a misunderstanding of Pelseneer's statement (p. 18): "Je dois faire remarquer que ce pénis n'est d'ailleurs jamais développé avant que les individus considérés aient comme dimension 13 millimètre de hauteur de coquille, alors que, pour un hauteur de 8 millimètres, des ovules sont déjà reconnaissables dans la glande génitale des ♀♀." Such a differential growth-rate explains the preponderance of females over males found in the larger sizes. Pelseneer (1926), in an examination of 516 individuals of from 13 to 15 millimetres in height, found 50·96% of females, as compared with 67·18% of females in a sample of 192 individuals over 2·2 cm. in height. Table II shows a similar condition at Trevol, the males and females being present in about equal proportions up to a height of 25 mm., after which the proportion of females rises rapidly to three-quarters of the population. Sewell found a similar result with the Indian species.

TABLE I.

Date.	Ratio of ♂ : ♀ growth since Sept. 6, 1934.	Number of specimens.
Oct. 5 1934.	(1·48 : 1)	131
Nov. 5	0·90 : 1	145
Dec. 10	0·82 : 1	334
Jan. 9 1935.	0·98 : 1	61
Feb. 15	0·83 : 1	97
March 27	0·91 : 1	76
April 30	0·84 : 1	84
July 1	0·60 : 1	17
Aug. 7	0·68 : 1	30
Sept. 4	0·52 : 1	12

There are practically no data available which allow of the comparison of the growth-rate of *L. littorea* at Plymouth with that in other localities. Wright (1936) has published figures for growth in the Blackwater estuary in Essex, which show a height in December of their first year of about 8 mm., and a height of about 12 mm. the following April. But his further figures of 21–22·5 mm. in October of the second year, and 23 mm. the following April when the winkles are practically two years old are read from size-distribution peaks which are most probably multiple, and which are based on the wholly inadequate numbers of 19, 44 and 7 individuals respectively. Hayes (1929) gives some figures for growth over a short period at St. Andrews, N.B., which showed a progressive decrease in growth-rate of adult winkles with increasing height above low water.

TABLE II.

Mean height. mm.	% of ♀♀.	No. of specimens.
15·8	47·5	202
16·8	50·0	214
17·8	46·3	317
18·8	54·6	317
19·8	50·9	320
20·8	48·1	318
21·8	45·1	315
22·8	42·6	317
23·8	51·7	311
24·8	48·7	288
25·8	59·0	251
26·8	68·9	106
27·8	77·8	36
29·8	76·9	26
	Total	3338

SHELL SHAPE AND WEIGHT.

Shell shape in *L. littorea* shows very much less variation from one locality to another than in *Purpura lapillus* (Moore, 1936), this being probably associated with the dispersal obtained by the pelagic eggs of the former, the young Purpura hatching and dispersing on the same ground as the adults. The spiral angle α (Moore, 1936, p. 72) appears to remain more or less constant up to a height of 1–1·5 cm., and thereafter to drop fairly steadily. The value for the small shells was about 82·6°, and the lowest value observed in large shells was 81·1°. The apical half-angle θ appears to rise slightly to a maximum at a height of about 1–1·5 cm., and, as in α, to fall steadily with further increase in height. Table III shows the values of α and θ at a height of 2·0 cm.

For a given height of shell, an increase in apical angle will tend to result in an increase in the shell weight, but since an increase in the spiral angle will tend to reduce the weight, and since these two angles vary in the same direction with increasing shell height, the weight does not show any great departure from a linear relationship with the cube of the height.

TABLE III.

Locality.	α	θ
Trevol	32·4°	82·46°
Hannafore Point, Looe	40·8°	81·95°
Polperro	38·9°	82·30°
Wembury, Church Reef	40·4°	82·08°
Charlestown	38·8°	81·72°
Drake's Island	41·4°	82·10°

Fig. 6 shows the shell weight–height relationship for the three Plymouth grounds. In *Purpura lapillus* a close correlation was found between sexual maturity and the changes in the fundamental shell angles, but this is not apparent in *L. littorea*.

MATURATION OF THE GONADS AND SPAWNING.

The anatomy of the gonads and genital apparatus has been described in detail by Linke (1933), and on pp. 38–40 he summarized the information extant on the eggs and the process of laying them. According to him spawning takes place in March, April and May, though in extreme cases there may be some spawning as early as January and as late as June ; and he states further that eggs of *L. littorea* have been found in the plankton as early as November. Spawning takes place chiefly on the flood tide and at night. Elmhirst (1923) gives the spawning season at Millport as January to July and rarely August, and states that young appear abundantly on the shore by April. Tattersall (1920) gives the breeding season as January to June with a maximum in April and early May, and states that the males become mature in early January, but that he did not find any females with the ovary ripe until the middle of February. He found spent males after the beginning of April.

The results obtained from gonad examinations of winkles from Trevol are very similar (Fig. 7). No ripe females were found before early February, but between then and mid-March spawning took place rapidly, although some females not yet completely spent were still to be found at the end of May. No fully ripe males were recorded before the beginning of January, but at that time most of the males contained a certain number of apparently ripe sperm, and were presumably capable of copulating. By early February all the males were fully ripe, and in May a few spent ones were found. The curves showing the seasonal variation in tissue weight on the different grounds (Figs. 8, 9, 10) indicate similar results, if the spring drop in weight is taken to represent loss due to spawning. At Trevol and Drake's Island the spawning appears to commence about the beginning of December, and at the Yealm perhaps slightly earlier, although no sample was taken there in December. At Trevol, where the tissue weights of the males and females were determined separately, the males show a drop in weight commencing about a month before the females, that is at the beginning of November, this earlier loss of weight being no doubt due to copulation which precedes spawning by a variable period. On all three grounds spawning appears from the tissue weight figures to have been practically complete by some time between mid-March and mid-April. Dr. M. V. Lebour's observations on the occurrence of the eggs and larvae of *L. littorea* in the plankton

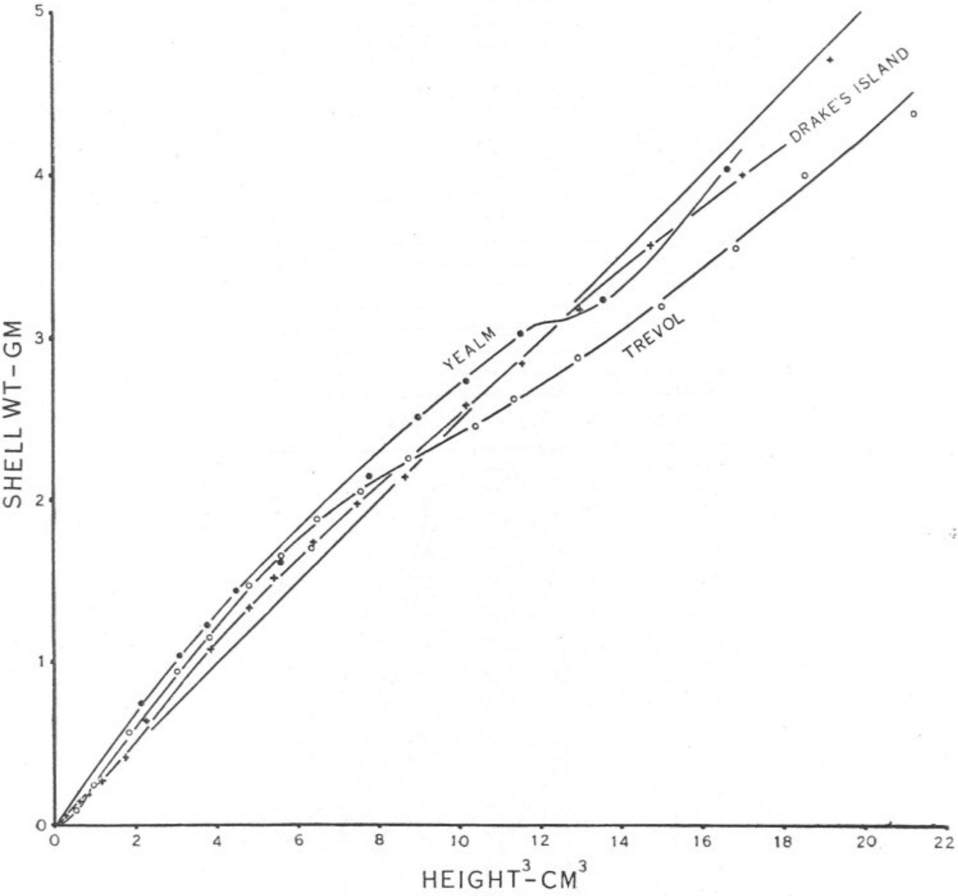

FIG. 6.—Relation of shell weight to height.

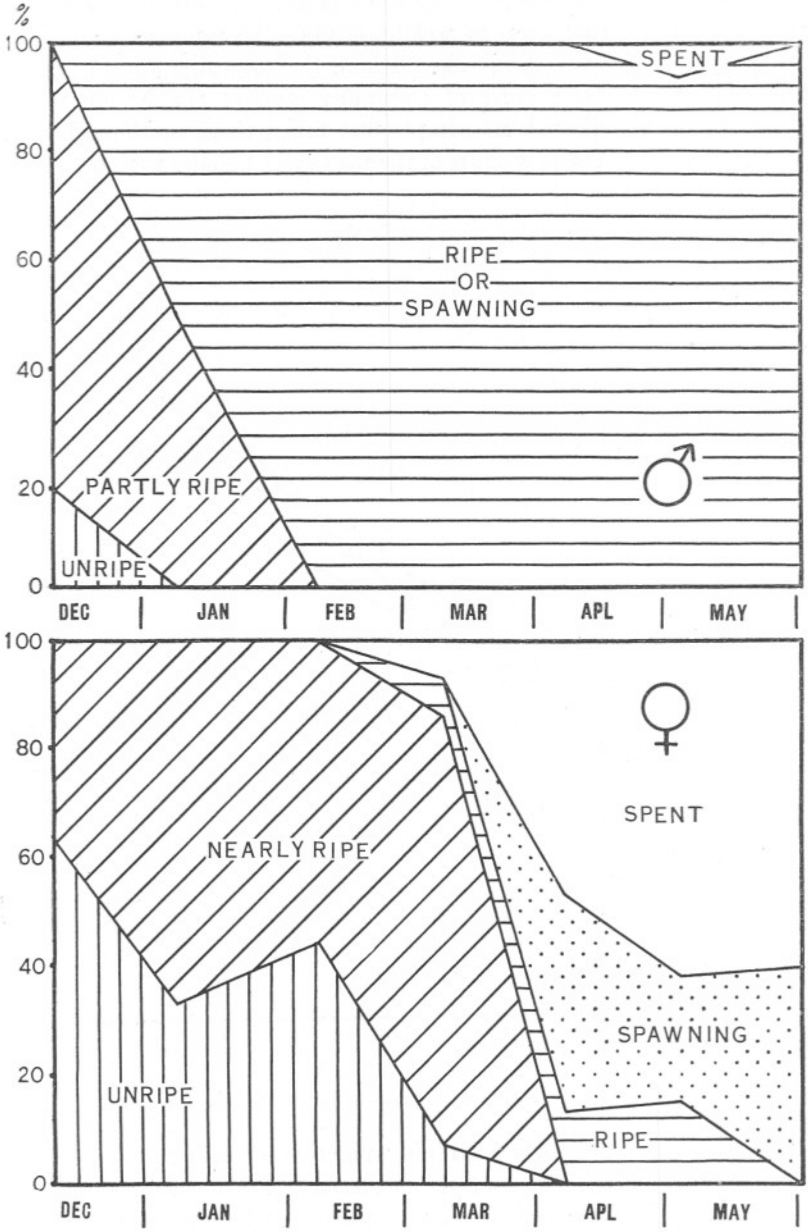

FIG. 7.—Gonad condition of *L. littorea* at Trevol in 1935–36.

round Plymouth, confirm these dates. She says (personal communication) that the first eggs are usually seen about the middle of November, and that a few may be taken as late as June, but that the greatest numbers are in February and March. With regard to the time of settlement of the young on the shore, the 1935 brood was specially searched for with a fine sieve at Trevol on May 17 of that year and none were found, but at the next visit on July 1 they were abundant. At Drake's Island the 1936 brood was not found on the shore on April 21, and was recorded as present, but not plentiful on May 19. On June 2, 1936, they were present in very small numbers only at Trevol. About the end of May to the end of June may therefore be taken as the main period of settlement of the young on the shore, and if this is so Elmhirst's statement of the abundance of newly settled young on the shore in April is open to question.

Fig. 8 shows a curve for mean monthly temperatures for the sea off Promenade Pier, Plymouth, for the years 1912–19 (Orton, 1920), and from this it will be seen that, if we take the spawning period as falling in the months February to mid-April, the corresponding sea temperatures will be from the winter minimum of about 8° C. to an upper limit of about 9° C., with a small amount of earlier spawning on a dropping temperature from about 10° C. downwards.

TISSUE WEIGHTS.

The tissue weight curves in Figs. 8, 9 and 10 were obtained as follows: From all three grounds, curves were available relating tissue weight to shell height, at intervals through the year (p. 723). Curves showing shell growth during the first two years of life, as indicated by the size distribution curves, were also available for all three grounds, and for Drake's Island the growth during subsequent years could be calculated from Fig. 5. The shell height curves were therefore drawn, using the cube of the height as being likely to have an approximately linear relation to weight, and the observed tissue weights then inserted for the shell heights corresponding to the successive seasons of sampling. As shell-height curves for only the first two years were available for the Yealm and Trevol, their subsequent growth was assumed to be similar to that at Drake's Island, but less throughout in the ratio of $\frac{\text{height (Yealm)}^3}{\text{height (Drake's I.)}^3}=0{\cdot}46$ for the Yealm, and greater for Trevol in the ratio $\frac{\text{height (Trevol)}^3}{\text{height (Drake's I.)}^3}=1{\cdot}22$ these being the observed ratios on the last dates on which accurate figures are available from size distribution curves, namely, November 11 (2nd year) for the Yealm, and July 30 (2nd year) for Trevol. It is fully realized that such figures for the third and subsequent years are only

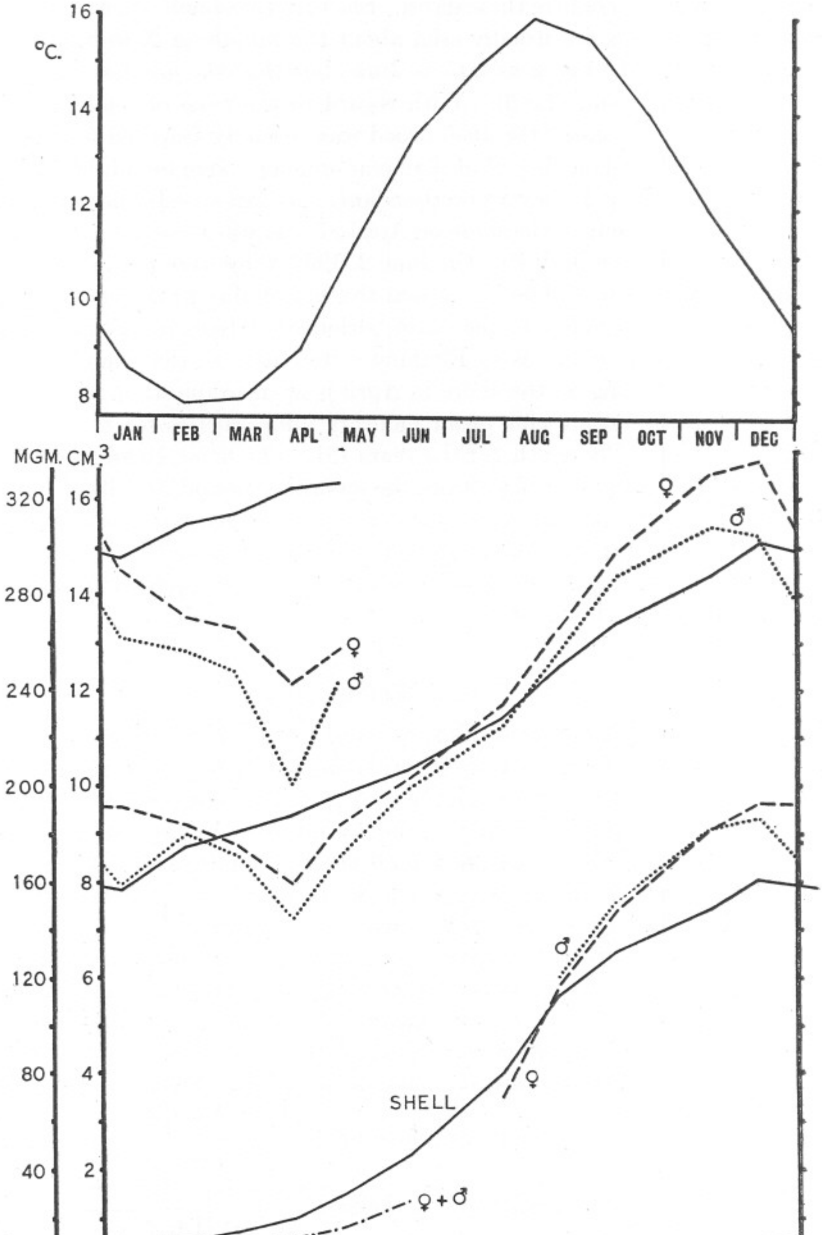

FIG. 8.—Monthly mean sea temperatures for Plymouth (1912–19); growth of the shell (height³) and of the tissues (dry weight) in the successive year-groups at Trevol.

rough approximations, but the purpose of the tissue weight curves is not to show the absolute tissue weight at any given time, but rather to show its seasonal variation, and the degree of this variation at different ages relative to the shell size, and to show also the differences, if any, in the seasonal variations in tissue weight in the two sexes. For this the shell heights used form an adequate framework. Separate data for the males and females are available only from Trevol, and even there only above an age of one year, the sexes not having been found separable externally in the younger stages. No account has been taken of the observation that the females grow somewhat faster than the males,

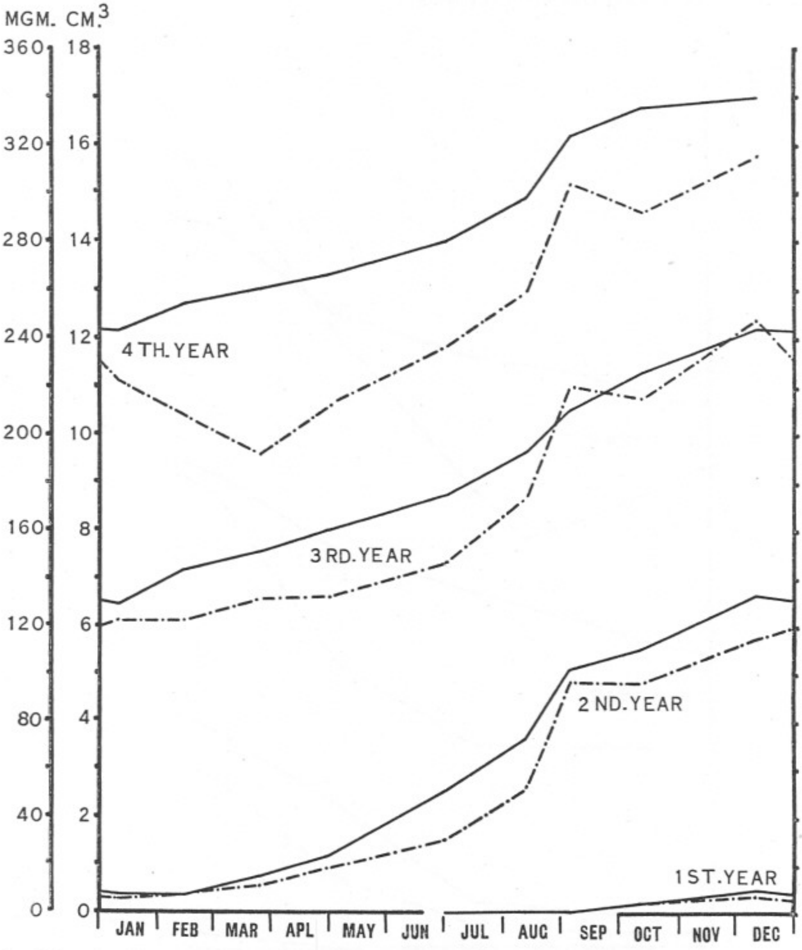

Fig. 9.—Growth of the shell (height^3) and of the tissues (dry weight) at Drake's Island.

since it would only have added complexity to the diagrams, but if the difference in growth of the two sexes is the same at Trevol as it is at Drake's Island, then it may be taken that the tissue weights for the females should be about 10% greater, and those for the males about 10% less throughout than those shown. This, however, has no effect on the general deductions drawn from the graphs.

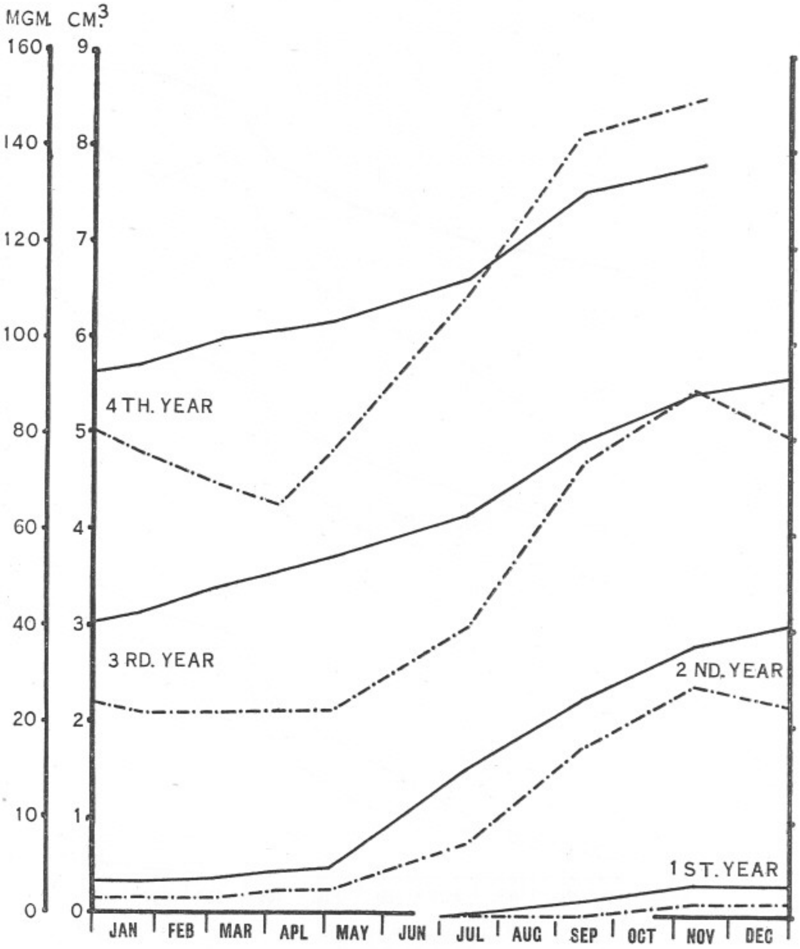

FIG. 10.—Growth of the shell (height^3) and of the tissues (dry weight) at the Yealm.

The relatively slow growth-rate of the Yealm winkles is rendered even more noticeable when, instead of being recorded in terms of height, it is shown in the more natural units of either tissue weight or height^3. It is then seen that the growth at the Yealm is only about half that of Trevol and Drake's Island. In shell growth then, Drake's Island and

Trevol are more or less similar, in contradistinction to the Yealm. With regard to tissue growth, however, there is a point in which Drake's Island and the Yealm differ markedly from Trevol. It was found by examination of samples of winkles from Drake's Island in December, 1935, and from Trevol and the Yealm in March, 1936, that on all grounds the 1935 brood, which were then 3–6 months old (since settling), were immature sexually, while the 1934 brood, then 15–18 months old, were all definitely mature. The tissue weight figures for Trevol confirm this, showing a marked drop in weight in the second spring, indicating presumably a considerable spawning when 18 months old, but on the other two grounds, and in particular on Drake's Island, there is indication of very much less spawning, and it is not until the winkles are 2½ years old that the loss of weight at spawning is really marked, and even then the weight loss is not as great as it is at a corresponding age at Trevol. The latter locality therefore appears to be markedly superior to the other two so far as production of larvae is concerned.

MORTALITY RATE.

The size distribution curves in which it is possible to separate the numbers of shells in the first, and sometimes also the second year groups from those of all older groups, allow of the calculation of the rate of mortality in those groups. This is, of course, possible only if the sample is an adequate one so far as those groups are concerned. After the shells are about one centimetre in height, the sampling may be taken to be adequate on all grounds. With the method of sampling used at Trevol, the first year groups also may be taken to be adequately sampled there from the spring of 1935 on. The method also assumes that the spat-fall is similar in different years. While this is almost certainly not strictly true, yet the general impression obtained is that the wide fluctuations observed in the spat-fall in different years in many lamellibranchs does not occur in this species, and that one year is substantially similar to another, at any rate in this region.

At the time when the young post-larval winkles are settling on to the shore, the loss by death will be to some extent counteracted by gain from the plankton so that the mortality rate cannot be estimated by this method, but by the end of July the gain from the plankton may be assumed to be negligible. In the two samples from Trevol on July 30 and August 28, 1935, the ratios of the numbers of 1935 group shells to all older ones was 8·6 : 1 and 8·4 : 1 respectively. Taking 8·5 : 1 as the mean value, then out of every 950 shells of all ages at that time, 850 are first year, and 100 are in their second or subsequent year. Of these hundred, $100\times\frac{1\cdot4}{2\cdot4}$ or 58 are in their second year (1·4 : 1 is the ratio in the second and subsequent years, see below). That is to say that, if the July–August rate were maintained for a year, only 58 animals would survive out of an initial 850 newly settled young. This gives a mortality rate of 94 per cent per annum for the months July and August, but if during this time there was any further settlement from the plankton, then the rate must be even higher, and during the period immediately after settlement the rate almost certainly is higher. It seems desirable to omit the samples in September, 1935, and in May, 1936, as being obviously not representative. Doing this, and working out the ratio of the 1935 group to all older shells for all samples from Trevol from September, 1935, to June, 1936, the mean value for the ratio comes to 1·7 : 1, and similarly, taking the mean value of the ratio of numbers in the 1934 group to all older ones in the period July, 1935, to June, 1936, the result is 1·4 : 1. The ratios therefore drop from 8·5 : 1 in the first few months, through 1·7 : 1 for the remainder of the first year to 1·4 : 1 in the second year, and this may probably be taken as a mean figure for all older shells also. Translating these ratios into percentage mortalities, the results are 94 per cent per annum or more for the first two months, 66 per cent for the rest of the first year, and 57 per cent thereafter. Sampling on Drake's Island was less adequate, and a figure can be obtained for the second and subsequent years only, the ratio here being 1·85 : 1, corresponding to a mortality rate of 65 per cent, which, within the limits of experimental error, may probably be taken as about the same as at Trevol. At the Yealm the results are extraordinarily different. The mean value of the ratio here for the 1935 group for the period July, 1935, to March, 1936, was 0·92 : 1, corresponding to a mortality rate of 82 per cent per annum, while for the older individuals of 15 months old and more, the mean value was 0·30 : 1, or only 23 per cent per annum.

Although these are only approximate figures, the difference between 23 per cent at the Yealm and 55–65 per cent on the other two grounds is too large not to be significant. It cannot be accounted for by collecting by fishermen, since such little collecting as there is takes place at Trevol and the Yealm, and not on Drake's Island. The only internal enemies known to have any serious effect on winkles are cercariae, and for these Rees's figures (1936, p. 358) show a total infection for all species of cercariae of only 10 per cent at Drake's Island and 2 per cent at Trevol. Even if the Trevol percentage is rather low, it is far too small to account for the observed mortality, and none of the cercariae are, according to Rees, likely to be fatal to the winkle, the only definitely fatal species, *Cercaria emasculans*, not having been found on these grounds. It must, however, be noted that among very large winkles the percentage infection by cercariae is much higher. At Aberystwyth (Rees, 1935) the total infection by all species in winter was 4–5 per cent, probably somewhat more in summer, and *C. emasculans* accounted for only about a third of this, so that there also it would be a negligible factor in the general mortality. We are forced therefore to look for either a limiting environmental factor or enemies such as birds or fish which might kill the winkles in considerable numbers, and at present the available information on these is very scanty.

Summary of Conditions on the Three Grounds.

	Trevol.	Drake's Island.	Yealm.
Level.	Mid-tide.	Mid-tide to between mean low water of neaps and springs.	Mean low water of spring tides.
Habitat.	Mud.	Stones.	Stones.
Growth-rate.	About the same as on Drake's Island.	Hts. (mm.) $\frac{1}{2}$ year . 14·0 $1\frac{1}{2}$ years . 17·4 $2\frac{1}{2}$ years . 22·4 $3\frac{1}{2}$ years . 25·4 $4\frac{1}{2}$ years . 27·3	Much less than on Drake's Island.
Yearly variation in growth-rate.	Growth-rate progressively less in 1934–35–36.	Growth-rate progressively greater in 1934–35–36.	Growth-rate approximately the same in 1934–35 (-36?).
Age at sexual maturity.	18 months.	18 months.	18 months.
Age at first considerable spawn output.	$1\frac{3}{4}$ years.	$2\frac{3}{4}$ years.	$2\frac{3}{4}$ years.
Mortality rate.	57%	65%	23%

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The Development of the Hydroid *Corymorpha nutans* M. Sars from the Egg.

By

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With 2 Figures in the Text.

DURING the summer of 1936 I obtained mature specimens of the medusa* of *Corymorpha nutans* at Plymouth. An account of the early development of the hydroid reared from the fertilized eggs of these is given below. Young polyps of this species have been figured by Allman (1871) and by Hartlaub (1907). Allman found his young polyps developing apparently from the rooting filaments of the parent hydroid which had become free. Hartlaub figures and assigns young polyps which he found in the plankton at Helgoland to this species.

A large number of medusae were captured off the Eddystone on May 18th, 1936. These were isolated overnight in a finger-bowl of sea-water. Next morning several of the medusae which were ripe had shed their sexual products. Such medusae were disintegrating, although others in the same bowl but not quite ripe were quite healthy and swimming actively. Both healthy and disintegrating medusae were removed by pipette. Left on the bottom of the bowl were a number of large opaque eggs easily visible to the naked eye. When observed they had evidently been fertilized and had a distinct yellowish pellicle around them. None had hatched on May 21st, but by May 25th a number of young had emerged and others were emerging (Fig. 1, A–D).

These liberated eggs measure from 0·26–0·28 mm. in diameter. Eggs obtained from mature medusae on May 26th exhibited activity and movement and these are figured (Fig. 2, A–F). The pellicle of the egg is very elastic and is pushed out into broad pseudopodial-like growths on the under side into contact with the substratum to which the pellicle adheres. The so-called " pseudopodia " then withdraw into the main body and the dilated pellicle shrivels up into a small tube. Several of these may be formed (Fig. 2, F) and they anchor the egg to the substratum. They may be termed anchoring filaments.

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* *Steenstrupia* (*Corymorpha*) *nutans* of the Plymouth Marine Fauna. For a description of this medusa see Browne (1896).

The young developed directly out of the eggs into young polyps instead of emerging as ciliated planulae which is the more usual way of development among hydroids. In this respect it resembles *Corymorpha palma* Torrey, 1902 (see Torrey, 1907). According to Torrey, however, the larva of *C. palma* emerges from the egg-case and wanders aimlessly about before settling down. My specimens were very inactive and the young hydroids grew out of the egg-cases and proceeded to differentiate into hydrocaulus and hydranth, the latter developing tentacles. The proximal ends of the hydrocauli were still inside the egg-cases in the majority of the specimens and would probably have remained so if the bowl had been undisturbed. The proximal ends of the young polyps, however, were not attached in any way to the egg-case.

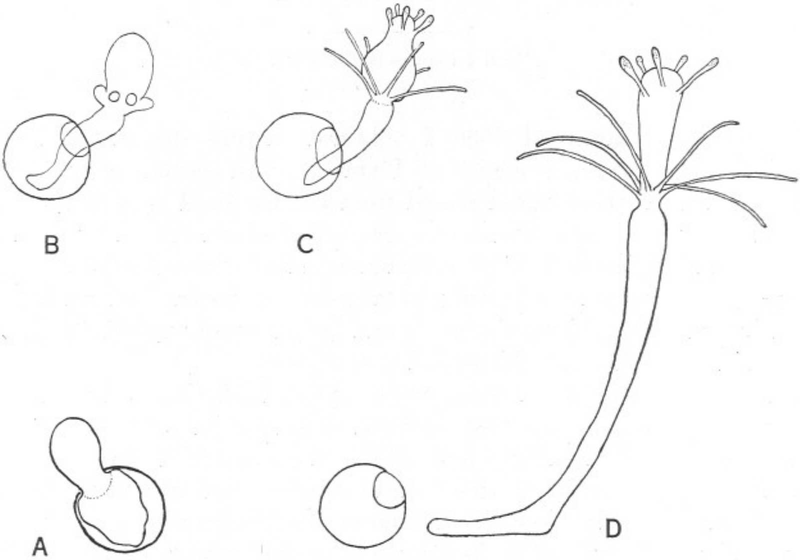

Fig. 1.—A–D, various stages of development of young polyps of *Corymorpha nutans*; Plymouth, 25.v.36.

Young polyps taken on May 26th possessed 4–6 oral tentacles and 6–8 aboral tentacles. The measurements of a typical young hydroid at this age are given below :—

Maximum length of hydrocaulus	1·6 mm.
Maximum diameter of hydrocaulus	0·14 mm.
Diameter of hydranth	0·3 mm.
Length of oral tentacles	0·12 mm.
Length of aboral tentacles	0·5 mm.

After another week one of the polyps had developed 8 oral tentacles and 15 aboral tentacles. By this time, June 3rd, the young polyps had developed rooting filaments (the " frustules " of Allman) on the proximal part of the hydrocaulus. They were always few in number and each consisted of a fine filament with a clavate tip by means of which the polyps attached themselves to the substratum. After secreting a thin perisarc around itself the protoplasmic connexion with the hydrocaulus breaks down and eventually disappears, leaving the perisarc as an empty anchoring filament. The formation of this filament and its subsequent development appears to be identical with the process described by Torrey (1907) for *C. palma*.

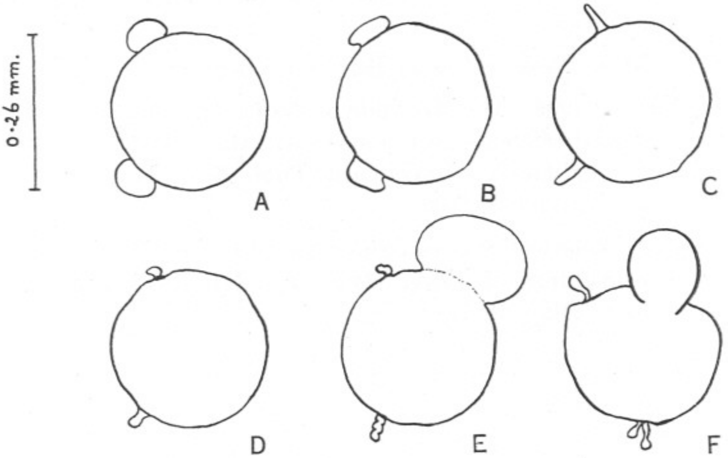

FIG. 2.—A–F, movements shown by a single fertilized egg of *Corymorpha nutans* during thirty minutes; Plymouth, 26.v.36.

On June 23rd the single polyp left in the bowl developed the rudiment of a gonophore stalk on the body of the hydranth on the distal side of the aboral tentacles. During the next few days the rudiment became divided but did not develop further. At this age the polyp possessed 15 oral and 17 aboral tentacles and a distinct, firm, brownish pellicle. The pellicle, however, was present on one of two polyps on June 3rd as a very thin, delicate membrane. The development was not studied further.

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On a Remarkable Process of Bud Formation in a Gymnoblastic Hydroid (*Heterostephanus* sp.).

By

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With 3 Figures in the Text.

THE process of asexual reproduction described below, is, as far as the writer is aware, unique among hydroids. In all known species of hydroids in which an asexual bud formation has been described (e.g. in *Hydra*), the mouth and oral tentacles develop at the free end of the bud and the proximal or fixed end becomes the base. The sequence of development of medusa buds is essentially similar. This method applies also to budding in other Coelenterates. In the present instance the bud instead of growing out " head first," came off " tail first "—the proximal end developing mouth and oral tentacles and the free end becoming the stalk. I can find no record of such a method having been described before.

The hydroid on which it occurred was dredged from below low-water mark near the eastern end of the Plymouth Breakwater. The polyp was found on a piece of hapteron (the so-called " root ") of *Laminaria cloustoni* on July 9th, 1936, that had been allowed to stand in sea-water for two days. When first observed the polyp was in a very contracted condition, so it was picked off the hapteron and removed to another bowl for a further period of two days.

On July 14th the hydroid was seen well expanded (Fig. 1). It consisted of a solitary polyp bearing some resemblance to a young polyp of *Corymorpha nutans* M. Sars, 1835, having oral and aboral tentacles. It differed from this hydroid in that the four oral tentacles were capitate and the eight aboral tentacles were moniliform; the latter in two closely approximated whorls of four long and four short ones. The longer tentacles carried 10–12 batteries and the shorter 6–7 batteries of nematocysts completely encircling the tentacle. Both tentacles and the stalk were very contractile, capable of expanding to five times their contracted length. The posterior end of the hydranth carried four backwardly directed papillae. The stalk was covered by a membranous hyaline perisarc. The total height of the polyp was 3 mm.

On July 17th a swelling appeared on the body of the polyp at the level of the longer whorl of tentacles carrying outwards with it one of the long tentacles. On the next day this swelling was clearly seen to be some kind of "bud." Small processes, four in number, appeared on the level of the long tentacle (Fig. 2). At this stage the number of nematocyst rings on some of the tentacles of the parent polyp had increased. One long tentacle now possessed fifteen rings and a shorter tentacle had eight.

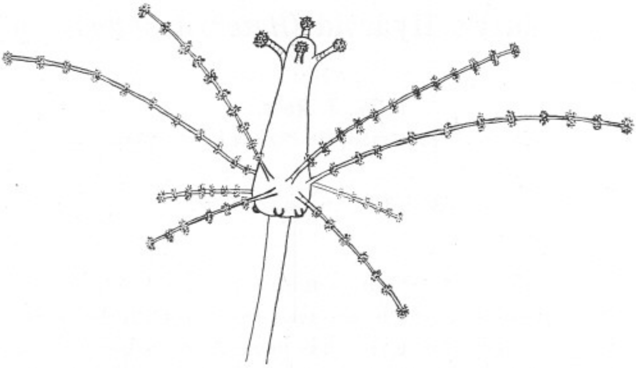

FIG. 1.—*Heterostephanus* sp., from the hapteron of *Laminaria cloustoni*, hydroid fully expanded with part only of the hydrocaulus shown; Plymouth, 9.vii.36.

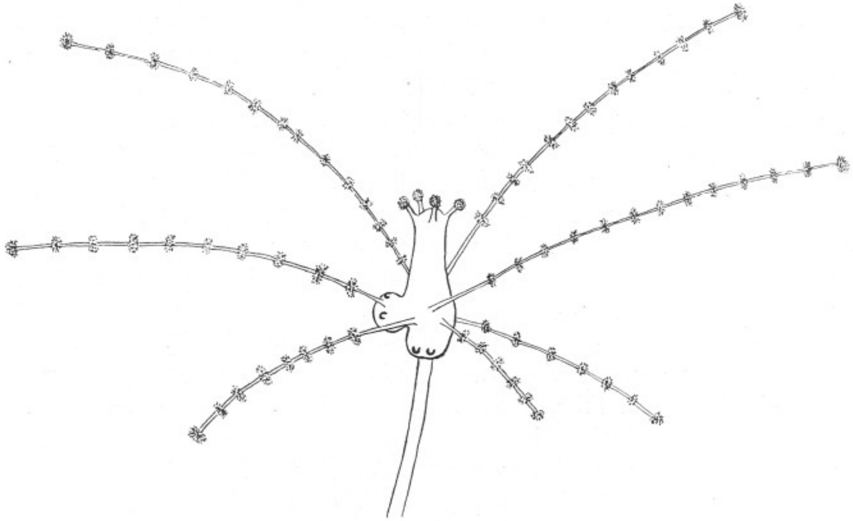

FIG. 2.—*Heterostephanus* sp., first stage of the formation of the bud (lower part of the hydrocaulus not shown); Plymouth, 18.vii.36.

Two days later the bud had grown in size and its free end had become transparent and pointed. The four processes already noted had grown

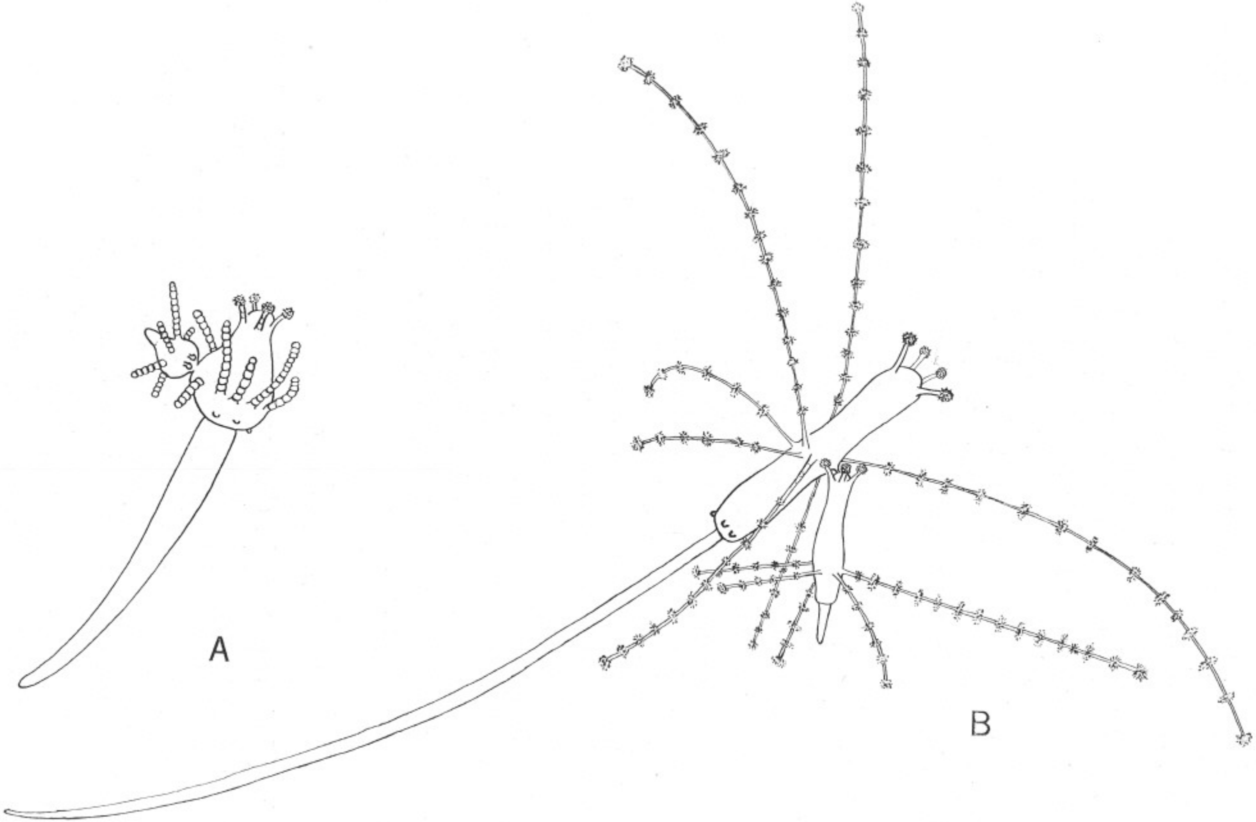

FIG. 3.—*Heterostephanus* sp.; A, hydroid contracted showing aboral tentacles and rudiments of oral tentacles; Plymouth, 20.vii.36: B, bud fully formed but still attached to parent polyp; Plymouth, 21.vii.36.

out into short annulated tentacles each with 4–6 rings. Small processes were also observed developing near the point of attachment of the bud (Fig. 3, A).

Next day (July 21st) the bud had elongated considerably. The small processes noted the previous day had developed into four capitate tentacles (Fig. 3, B). The free end had become quite distinct and resembled the stalk of the parent. On the same day the bud broke away and quickly settled down on the bottom of the bowl, attaching itself within thirty minutes of becoming free. Before nightfall, the stalk had elongated considerably (to about half the length of the stalk of the parent). Both polyps died on July 23rd, probably due to overfeeding.

On September 29th a second polyp was found among some fine gravel from the Eddystone by Dr. M. V. Lebour, who kindly gave me the polyp for examination. When found it was in a much contracted condition, but by next day it was fully expanded and could be definitely recognized as belonging to the same species as the one which I had previously found. The hydranth was brownish in colour and possessed four oral capitate tentacles and four long and two shorter aboral tentacles. The membranous perisarc was distinct and of a slightly brownish colour and better developed than in the first polyp found. At the posterior end of the hydranth there were four papillae directed backwards. The length of the hydranth expanded was 1 mm., the length of the hydrocaulus when expanded was 1·4 mm. and 0·45 mm. when contracted. The polyp lived only three days after it was found.

While the bud-formation described above may probably be the usual way of asexual reproduction in this species, the carrying away of one of the parent polyp's tentacles is perhaps not typical but depends on the point of origin of the bud.

SYSTEMATIC POSITION.

This hydroid appears to be closely related to the genera *Rhizotrichia* Stechow, 1919 (=*Trichorhiza* Russell, 1906), *Heterostephanus* Allman, 1864, *Acharadia* Wright, 1863, and *Vorticlava* Alder, 1857. It is distinguished from Acharadia and Vorticlava by its aboral tentacles being annulated with clusters of nematocysts ; from Rhizotrichia by its simple undivided hydrocaulus and by the possession of only four oral capitate tentacles. It appears, however, to be more nearly related to *Heterostephanus annulicornis* (M. Sars, 1860). It seems to differ from this last species in having only four oral tentacles, fewer aboral tentacles, in its thin perisarc, much smaller size and delicate appearance. All these differences may be due to age and growth and my specimens may possibly be young hydroids of *H. annulicornis*. Until knowledge of the gonosome of my species is obtained I do not feel justified in assigning it to *H. annulicornis* or to any other species and simply place it provisionally in the genus *Heterostephanus* Allman.

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Notes on the Culture of some Marine Plankton Organisms.

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In recent years considerable advance has been made in the methods for culturing marine organisms. We are still unable to dispense with sea-water as the main component of the culture medium, and in this respect, in spite of some notable efforts (Allen, 1914), the methods are less satisfactory than those developed for many freshwater organisms and based on synthetic media (Hartmann, 1928; Belar, 1928; Pringsheim, 1924). But the application of certain standards of purity and sterility in medium, culture dishes and instruments to culture work on marine organisms (Allen and Nelson, 1910), the enrichment of sterilized sea-water with certain nutrient salts (Allen's modification of Miquel, Schreiber), and more recently the development of the "Erdschreiber" as a culture medium (Föyn, 1934) have made possible the culture of an increasing variety of marine protozoa, algae and small invertebrates. In the last-mentioned medium Föyn cultured the algae Ulva and Cladophora, and Hämmerling (1934) two species of Acetabularia through several generations; the present author used it for Artemia, the brine shrimp (1932), and for Noctiluca (1934); Hartmann and Huth (1936) for Ophryotrocha, Shen (1936) for Dinophilus and Rühmekorf (1935) for a hypotrych ciliate, Keronopsis. Growing Ulva and Cladophora from parthenogametes of a single plant in six different media, under otherwise very similar conditions, Föyn showed that the media could be arranged in the following order of quality: pure sea-water—→Schreiber's medium—→Allen's medium—→ Killian's medium—→sea-water+soil extract—→"Erdschreiber."

Since autumn, 1935, I have been studying chiefly the life-histories of certain plankton diatoms, an account of which will be published elsewhere. In the following pages a short description is given of the culture technique developed for the centric diatoms which may be of some value for future investigators. Notes on the culture of certain other plankton organisms are included, and on attempts to rear fish larvae which failed but gave some indication of how such rearing might in future be undertaken with more success.

Culture Methods for Diatoms.

Föyn's "Erdschreiber" is a combination of Schreiber's medium (Schreiber, 1927) and soil extract, which has been used before for the culture of freshwater algae (Pringsheim, 1924). It consists of :—

$NaNO_3$	0·1	g.
Na_2HPO_4	0·02	g.
Soil extract	50	c.c.
Sea-water	1000	c.c.

The soil extract is made up by boiling for one hour 1 kg. of good garden or potting soil with 1 litre glass distilled water in an autoclave. (More recently I have been using tap water with equal success.) After 2–3 days the resulting brown and rather dirty fluid is decanted into a flask and sterilized by heating up to the boiling point. After standing for 3–4 weeks the rougher particles settle to the bottom and the fluid becomes transparent, brown or red in colour and ready for use. If mould or bacteria develop in the meantime it must be sterilized again. In any case, repeated decanting and boiling enhances the process of clarifying the fluid. Before use the soil extract is poured into another flask and boiled for a short time ; the required amounts of nitrate and phosphate are then dissolved in it and sterile sea-water added. If large quantities of culture medium are needed at short intervals one or more litres of soil extract with the nitrate and phosphate already dissolved can be kept in stock, and the culture medium quickly made up with sea-water before use. It is advisable to keep the stock solution in a refrigerator and to avoid boiling the soil extract once the salts had been added.

Throughout the work "outside" sea-water* has been used. It was first filtered through filter paper (Whatman No. 1) and then heated to boiling point. Since boiling produces some physico-chemical changes it is advisable to allow this water to stand for 3–4 weeks before use. During this period the sea-water recovers its normal O_2 and CO_2 content and the pH returns to its normal value (Schreiber, 1927). If no old sterile sea-water is available fresh sea-water should be filtered and heated only to 70° C. The flasks with soil extract, sea-water and culture medium should be closed with overlapping glass capsules. Paper bound with string round the top and neck of the flasks is useful for keeping the dust off the glass capsules.

Small watch glasses, 5 cm. in diameter, with ground edges, containing about 2 c.c. of fluid and covered with round glass plates, and Petri-dishes

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* At Plymouth the water from the Sound or in the Aquarium circulation is too contaminated for delicate organisms and water is therefore collected in the open sea well outside the Breakwater ; this is called "outside" sea-water.

about 10 cm. in diameter, were used as culture dishes. These as well as the flasks for sea-water and culture medium, the glass capsules and pipette tubes—in short, all glass ware for culture purposes—were first cleaned by being either put into or filled with a mixture of sulphuric acid–bichromate for several hours. Then they were thoroughly rinsed with tap water and finally the smaller glass ware was boiled in a porcelain dish with glass distilled water, and the flasks filled with a small amount of distilled water and boiled over the gas burner.

The greatest difficulty confronting the culturing of marine unicellular algae is to start the culture free from flagellates and bacteria. Allen and Nelson (1910) often succeeded by diluting a small quantity of a plankton sample containing diatoms, or colonies of a species developed in a raw culture, in a large quantity of culture fluid and subdividing it into a number of culture flasks. Schreiber used a special apparatus, the "plankton purifier."

In my own experience the direct method, that is the isolation of a few or single cells from a plankton sample, gave quick and satisfactory results. The diatoms were isolated under a low-power binocular dissecting microscope from catches with a very fine silk tow-net. This dissecting microscope is the most important piece of apparatus for culture work. Even for the smallest plankton diatoms the combination of the eye-pieces ×8 and the objectives ×3, ×4 and ×8 gives a range of magnifications sufficient not only for isolation, washing and subculturing of the cells, but also for the study of the division rate, and control of the general health of the diatoms, of the appearance of resting-spores or auxospores, and even of the presence of infections by very small flagellates. It is only for ensuring purity from bacteria that one has to use the high-power microscope.

The diatoms were picked out singly with fine pipettes. It is important to take the cells out with as little fluid as possible to avoid contamination. For this purpose the fine end of the pipette should be long (about 5 cm.) and of a more or less uniform diameter with an opening not exceeding twice or three times the diameter of the cell to be isolated. The cell drawn into the pipette is then squirted sharply* into a watch glass with 1–2 c.c. of sterile culture medium. If left in this watch glass for a few days the cell might divide and give rise to a colony, but small flagellates would almost invariably develop and eventually overgrow the diatoms completely. It is therefore essential to wash the isolated cells by passing them through a further 2 or 3 sterile water samples in watch glasses. Working with the lowest possible magnification it does not take long to find a single diatom cell in a volume of 1–2 c.c. of water. Next day if the

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* In my experience only *Rhizosolenia robusta* is liable to be caught by the surface film and has therefore to be transferred very gently.

diatoms are in a healthy state they have either divided or grown in size or are suspended in the water, in short, they show a definite improvement as compared with their usually lethargic state in the overcrowded townettings. The washing is repeated once or twice and the cells left for a few days in a watch glass, well covered with a glass plate. If they reproduce satisfactorily a sample may be washed after a week or so and transferred into a Petri-dish. In spite of a good initial growth of the diatoms the subsequent cultures must be carefully watched for the presence of small flagellates. The reproduction of these may at the beginning be inhibited by the growth of the diatoms, particularly if the light and temperature conditions are very favourable for the diatoms. However, after some weeks or even months the growth of the diatoms may stop and on careful examination one may find enormous numbers of flagellates of a size of 2–6μ.

Before every operation involving the transference of diatoms from one culture dish into another—isolation, washing, subculturing—the pipette should be sterilized by dipping it into boiling glass-distilled water in a beaker and afterwards cooled in sterile culture medium. This is necessary in order to avoid contamination and to clean the pipette.

The cultures were kept at room temperature and placed near a window facing north. During the winter months a 100-w. lamp hanging at a distance of about 1 m. was used to increase the illumination during the day. In summer the cultures of *Coscinodiscus Granii* grew better in a dim light at a distance of 2–3 m. from the north window.

Subcultures were made every two to three weeks and inoculated mostly with 10–100 cells. In spring and summer subcultures of rapidly growing forms like Ditylium, Chaetoceros, Skeletonema and Melosira had to be made at shorter intervals. It is advisable to keep the old cultures for some time because, for reasons mostly unknown, not all subcultures are equally successful. I had several times to return to 4- to 6-weeks old cultures, and then a sample of these old cells was passed at intervals of 1–2 days through a number of watch glasses before inoculating a Petri-dish. Washing the cells to be transferred is also necessary when cultures contain bacteria.

Bacteria-free cultures were not aimed at and no special bacteria tests made. They correspond to Allen's " persistent " cultures, or what are generally called " pure cultures," containing only harmless bacteria besides the one cultured species of protozoa, in contrast to " absolutely pure " or bacteria-free cultures. Since the cultures were frequently examined and a large surface of the watch glasses and Petri-dishes was thus exposed to the air, the occasional appearance of mostly harmless bacteria was to be expected. However, from my experience it seems very probable that with the same methods, but using culture flasks or test tubes instead of Petri-dishes, one could easily get continuous cultures of absolute purity.

It may be mentioned that in January and February, 1936, after having grown extremely well for three months, the cultures of Ditylium gave some trouble by producing numerous cells with slightly contracted and highly refractive protoplasts. The division rate was also very much reduced and it became difficult to make new subcultures. Eventually the difficulties were overcome by adding traces of $CuSO_4$ to the culture medium. The pipette was dipped into a m./10,000 solution of $CuSO_4$ and washed off in the Petri-dish prepared for the subculture. Previously similar traces of Cu were introduced by using for the sterilization of pipettes porcelain-distilled (instead of glass-distilled) water which according to tests made by Dr. L. H. N. Cooper contained definite traces of copper. This might be interpreted as showing that in winter, and probably also in autumn, sea-water contains too little copper, or none at all, which must therefore be added to the culture medium, while in spring there is a sufficient supply of it in sea-water. However, although from January until March many cultures without the addition of $CuSO_4$ were not successful, whereas those supplied with traces of it showed excellent growth, I would hesitate to regard copper as an essential part of the culture medium without more elaborate and controlled experiments. There might have been small numbers of bacteria present the effect of which was checked by $CuSO_4$.

The following diatom species were obtained in pure cultures.*

Biddulphia mobiliensis (Bail.) Grun.
Chaetoceros didymus Ehr.
  ,, *pseudocrinitus* Ostenfeld
Coscinodiscus excentricus Ehr.
  ,, *Granii* Gough
  ,, *radiatus* Ehr.
  ,, *sub-bulliens* Jörgensen
  ,, *obscurus* (?)
  ,, spec.
Ditylium Brightwelli (West)
Melosira Borreri Greville
Rhizosolenia alata Brightw. form *indica* (Péragello)
Skeletonema costatum Greville
Streptotheca thamensis Shrubs.
Thalassiosira spec.

This list includes only those species which were cultured for at least three months through several subcultures—some are now 16 months old.

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* Most of the diatoms cultured were kindly identified by Dr. Marie V. Lebour.

Some others have been cultured for shorter periods and abandoned because there were too many cultures to be cared for. It was, however, reasonably certain that under the conditions given they could have been kept for much longer periods. These species were :

Chaetoceros borealis.
,, *gracilis*.
Eucampia zoodiacum.
Lauderia borealis.
Rhizosolenia Shrubsolei (?).

Cultures of *Biddulphia regia* and *B. sinensis* were not very successful. For short periods of about 4 weeks they divided quite actively. But after that the growth stopped, their shape becoming slightly abnormal and their chromatophores dark brown.

The methods described above were definitely inadequate for *Corethron criophilum* and *Hyalodiscus stelliger*. Although I tried repeatedly, not more than one division took place in isolated Corethron cells and none in Hyalodiscus. The cells of the first species looked extremely healthy the first few days after isolation into " Erdschreiber," being freely suspended in the water, but afterwards the protoplast disintegrated.

THE CULTURING OF OTHER ORGANISMS.

Dinoflagellates.

The culture methods described above were tried out on some plankton dinoflagellates. Only the culture of *Prorocentrum micans* was successful. Two cells were isolated from a plankton sample on September 27th, 1935, and treated in a similar way to the diatoms. They reproduced very quickly and the culture is still in good condition (February, 1937).

Certain other autotroph dinoflagellates, *Ceratium tripos*, *C. fusus*, *C. furca* and *Dinophysis tripos* behaved similarly to Corethron among the diatoms. At first they were much healthier and moved about more actively than in the original plankton sample. One or two divisions took place, with the subsequent separation and restitution of the daughter cells, but no persistent culture could be established although some cells remained alive for longer than a month. One typical example may be given. On October 4th, 1935, several *Ceratium tripos* were isolated and carefully washed, on the 17th one cell was isolated and washed again. By the 24th it had divided and the two cells were then transferred into fresh medium. On November 5th there were seven cells ; these were washed twice. On the 8th there were only six alive ; they were washed three times. On the 12th six were transferred and of these on the 18th four were alive, which were washed once. On the 22nd only one was alive and very active. This Ceratium was alive on the 23rd and 24th and was transferred each day but by the 30th it had died.

Whatever the reason for the inhibition of their division may have been, it was certainly not caused by the presence of any contaminating organisms, flagellates or bacteria.

Some colourless and probably saprophytic species could be kept alive for some time, *Peridinium depressum* for nearly 4 weeks, and two specimens of *Peridiniopsis* spec. for six weeks. The latter " moulted " after about five weeks, abandoning the old shells and forming new ones, a process which also occurs often in overcrowded cultures of Prorocentrum.

Nannoplankton flagellates.

My attempts to obtain pure cultures of diatoms and dinoflagellates drew my attention to a big and varied group of autotroph nannoplankton flagellates, most of them probably unknown systematically.

If a diatom or a dinoflagellate is picked out from a plankton sample with only a tiny drop of the original medium and transferred into a watch glass with " Erdschreiber," one will almost regularly obtain the growth of one or more species of flagellates rather than that of the diatom or dinoflagellate. If these are passed through one or two watch glasses with sterile medium whereby the original drop of plankton fluid is diluted to 2–4 c.c. one may still obtain a flagellate culture, but it is more likely that it will be a pure culture of one species only. From their presence in diatom cultures started in the way just described it may be concluded that almost every drop of plankton fluid contains one or more flagellates.

By that very indirect method I obtained within several weeks cultures of about a dozen flagellates which were—and some are still—kept in 100 c.c. culture flasks with about 50 c.c. of " Erdschreiber " and subcultured every 3–5 weeks. No special study has been made of them so far. In size they range from less than 2μ to 10μ. The colour of the chromatophores and of the cultures respectively is opaque-green, green, brown and yellow-brown. The movement is characteristic in some species. In one flagellate the periods of movement and of rest, i.e. free suspension in the water, follow each other at varying intervals, the movement starting and stopping with extreme suddenness. Most of the flagellates probably belong to the Chrysophyceae and Cryptophyceae, and a few to the Volvocales.

Once I had gained some experience with regard to their size, shape and movement these tiny flagellates could be found in every sample of townettings examined. Under the binocular, eyepiece ×8, objective ×8, one can see them distinctly down to a size of about 4μ, and under favourable light conditions even those 2μ in size. By the use of the dissecting microscope with its wide field one gets a better, if only a very general, idea of their number and variety than by isolating drops of plankton fluid and examining them under a high power. They appear to be more numerous in spring, summer and autumn than during winter. They were often present in fair numbers in tow-nettings which were extremely poor in diatoms and other phytoplankton. During the autumn and winter of 1935–6 single drops of plankton fluid were occasionally placed in watch glasses with culture medium and invariably gave growth to mostly mixed cultures of flagellates.

The technique of isolating and washing single cells of diatoms cannot be applied to these organisms. It is very difficult to handle objects less than 12μ in size in that way. The isolation is possible, but not the washing in watch glasses because of the difficulty of finding the isolated object again. The dilution method as used by Allen (1910) seemed to be the appropriate one and was tried out with success. One picks out under the binocular what one believes to be a single flagellate—in fact there will probably be two or more specimens in the drop of water drawn into the pipette—and places the drop in 1 c.c. of medium. This is distributed over 5–10 culture flasks and if successful one or the other flask may give a pure culture of a flagellate. If a culture contains two species of flagellates they sometimes will not reproduce at the same rate, but one will have its flowering period after the other. The culture may, for instance, take a more and more intensive golden-yellow colour owing to the growth of one type, then this colour may fade away in a day or two and give way to the green tint of the second flagellate. By repeated subculturing at the right time one can sometimes succeed in gradually separating the two species or eliminating one. The use of solid media would probably give better and quicker results (see Ålvik, 1934).

Some of the flagellates cultured were tried out as food for various larvae. A harpacticid copepod has been cultured for three generations. The adults, about 1 mm. in length, could be fed on flagellates 12μ in size. Newly hatched nauplii died on this diet but lived very well on flagellates of $5–7\mu$. Several polychaete larvae could be observed taking them in, as could plankton copepods. The latter could not be kept longer than 3–4 weeks, but the cause of their death was probably not lack of or inadequacy of food (see p. 765).

All these experiments led me to the conclusion that the autotroph nannoplankton flagellates are of great importance in the food economy of the sea. The bulk of living matter provided by them is probably much smaller than that of diatoms and dinoflagellates, although the proportion in which they appear in tow-nettings certainly is misleading, since flagellates of $2–10\mu$ are not retained in the net to the same extent as the bigger phytoplankton. But their reproduction is more rapid and they are of the right size to be taken in by the filter-feeding organisms, and are far more numerous and more often present in the plankton than small pennate diatoms of the type of *Nitzschia closterium* var. *minutissima*, cultured by Dr. E. J. Allen and successfully used by him and his collaborators in rearing various marine larvae.

Some of the minute algae mentioned above are probably related to or identical with those found in Norwegian oyster pools and investigated by Ålvik (1934). This author obtained pure cultures of six algae which he described as new species. Previous to this work it has been shown by Gaarder (1933) that oysters and their larvae need green algae of 2–3μ as food.

From studies of the plankton of tanks at Conway with enriched sea-water where a good settlement of oyster larvae took place, and of tanks with untreated sea-water where few larvae or none settled, Mr. H. A. Cole (private communication) arrived at a similar conclusion to the Norwegian author (Gaarder, 1933), namely, that nanno-plankton flagellates of a size of 7μ and less are suitable food for oyster larvae.

The whole group of nannoplankton flagellates certainly deserves further investigation along the same lines as those for larger plankton organisms, i.e. systematics, life-history, distribution in the sea, abundance in different seasons, requirements with regard to nutrients, light and other factors governing the life in the sea. An important start has been made by Gaarder (1932), Gaarder and Spärck (1932) and Ålvik (1934) with their studies on Norwegian oyster pools.

Larvae.

To get an idea of the efficiency of " Erdschreiber " as a culture medium larvae were picked out occasionally from the plankton and attempts made to rear them. A Pilidium larva (of a nemertine) was isolated on October 17th, 1935, and transferred every few days into a watch glass with fresh medium and *Chlamydomonas* spec.* as food. This was taken in readily and on November 1st metamorphosis took place. It was very interesting to note that after the release of the young worm the " larva," not much changed in its external appearance, continued swimming about very actively, with the apical sensory hair in slight motion as before. It was alive and active on the 7th but reduced in size and irregular in shape. On the 13th it had disappeared.

On October 1st, 1935, Dr. Allen kindly gave me a Phoronis larva which he had found in a plankton sample. It was placed in " Erdschreiber " with Chlamydomonas as food. The larva started feeding immediately

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* This has been used before as food for *Artemia salina* and *Noctiluca miliaris* (Gross, 1932, 34).

and the algae were driven into the oesophagus and after some time passed into the gut. Here they were kept moving round, towards the oesophagus on the dorsal side, posteriorly on the ventral. After half an hour there were a great number of Chlamydomonas in the gut and its fluid was green. However, the next and the following days very few were taken in and the larva, particularly its tentacles, became gradually reduced in size. The larva remained alive until the 26th.

Oikopleura larvae were isolated several times and provided with flagellates of various sizes but always died within 24 hours.

Herring.

The larvae were reared from eggs which had been artificially fertilized* on January 21st, 1936. They hatched on the 31st and on February 1st respectively and 120 larvae were kept in groups of 4—10 in finger-bowls at conditions varied with regard to medium, food and temperature. The following media were tried : " outside " sea-water unsterilized, sterilized by heating to 60°, 70° and 100° C., Allen's modification of Miquel, and " Erdschreiber " with varying amounts of soil-extract. As food were offered : *Chlamydomonas* spec., *Prorocentrum micans*, *Thalassiosira* spec., *Coscinodiscus radiatus* and *Skeletonema costatum*. The cultures were kept at room temperature (reaching 17° C. during the day, dropping to 8–11° at night), on a window-sill on a landing (with a lower day-maximum of about 12–13°) and in containers with running tap water (9–12°).

The yolk sac was absorbed after 6–8 days in all larvae except in those kept under running tap water where most larvae retained it as long as 13 days. Until the yolk sac had gone the mortality was negligible, after that it increased considerably. The majority of the larvae were alive 10 days after the yolk sac had been exhausted, some survived until the 19th–24th at room temperature, and until the 27th in cultures kept under running tap water.

There was no obvious difference in the viability of the larvae kept in different media. Chlamydomonas and Prorocentrum could be seen inside the gut in many larvae soon after the yolk sac had been absorbed, but Thalassiosira only in one larva. The other diatoms were probably too big. Chlamydomonas was sometimes taken in in large masses, so that the gut could be seen as a green line with the naked eye. Some larvae were watched extruding faecal pellets consisting of remnants of Chlamydomonas and to a far lesser extent Prorocentrum.

Lack of food can therefore not have been the cause of their death. That the food offered was inadequate is not likely since Prorocentrum represents an important item of the diet of young herrings (7–12 mm.) in

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* I am indebted to Mr. E. Ford who performed the artificial fertilization.

nature (Hardy, 1924). What else could be the reason for the failure in rearing herring larvae ?

Some incidental experiments may be recorded which throw some light on this problem. The larvae—following the ordinary routine in culturing—were transferred to finger-bowls with fresh medium and food every 5–7 days, sometimes at shorter intervals so as to avoid any harmful effects of accumulating metabolic products. However, a very puzzling result was often obtained, the larvae dying a few hours after the transference. At first I thought that they had been damaged by handling them with too narrow pipettes. I then used bigger ones and finally small finger bowls as a kind of spoon with which I transferred the larvae. But the effect remained the same. One instance may be given with more details. A culture of 15 larvae was kept from January 8th till the 13th on the laboratory landing in pure sea-water and all the animals were very healthy during that period. On the 13th seven larvae were taken out with a broad pipette and placed in fresh sea-water from the same bottle as on the 8th. Half an hour later six larvae were lying at the bottom of the bowl, opaque in colour and very weak. Three hours later three larvae were dead, the next day three more, while the last larva fed on Chlamydomonas and survived until the 20th. The herrings which had been left in the old sea-water on the 13th remained very healthy until the 19th when they were cautiously transferred into fresh sea-water+food. Fifteen minutes later four animals were dead, lying at the surface of the water with the body bent abnormally, the brain opaque and the fins broken. A further two larvae died the following day. Similarly several larvae kept under running tap water were killed when transferred into fresh medium.

The explanation may be found in the fact that the stock of sea-water kept in the room was of a temperature several degrees higher than the old medium kept on the landing and under running tap water, and that the sudden change of temperature proved fatal even in such a short time.

Angler-fish.

On March 25th, 1936, a piece of spawn of Lophius was brought in by S.S. *Salpa*. Most of the larvae were hatched and were moving about in the capsules. They were liberated by deliberate cutting with a pair of scissors through the gelatinous ribbon in which they were embedded* and placed in small tanks and finger bowls with the same media as the herrings. Some cultures were kept in an unheated cellar where the temperature varied from 12 to 14·5°, i.e. much less than in the laboratory-rooms, others in a bath with running tap water of a temperature varying between 10·5

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* If left in it most larvae will hatch out into the water, but an enormous growth of bacteria takes place.

and 12°. The yolk sac was absorbed between April 10th and 14th. Prorocentrum, small copepods and cladocera from the plankton and newly hatched nauplii of *Artemia salina* were offered as food. I have only noticed that Artemia nauplii were taken in by the young anglers. On the 15th only three larvae out of 200 kept in the cellar had survived, but 45 out of 150 kept under running water. Of the latter 12 were alive and very lively on the 20th, and 5 on the 21st. They died on the 23rd.

Pilchard.

Larvae of *Sardina pilchardus* were obtained from eggs brought in by S.S. *Salpa* from Station E2 on May 12th. Sixty larvae hatched on the 14th and were kept in the cellar in finger bowls standing in a tank with running tap water. The temperature of the tank water varied from 13·5 to 14·5° C. The media used were sterile sea-water and "Erdschreiber." On the 19th almost all larvae had their yolk sac absorbed ; on the 22nd they were seen feeding actively and their guts contained masses of Chlamydomonas and smaller numbers of Prorocentrum. Five larvae were placed in another finger bowl and taken to the main laboratory to show them to some colleagues. They were brought back after about 10 minutes and 20 minutes later 3 were dead and 2 very weak. As the rest of the Pilchards in the original dish were in perfect health the cause for their sudden death could only have been the increase of temperature for 10 minutes.

DISCUSSION.

The preceding account affords an opportunity for discussing the problem why some plankton organisms can be cultured or reared and others not. The methods adopted for culturing diatoms were adequate for quite a number of them. Adding to the list given on pp. 757–58 some more which had been cultured by Allen and Nelson—*Asterionella japonica*, *Chaetoceros densum*, *C. decipiens*, *C. constrictum*, *Cocconeis scutellum*, *Nitzschia closterium*, *N. seriata*, *Rhizosolenia stolterfothi*, to mention only those species not represented on my list—one obtains a very representative selection of most diatom groups present in the plankton off Plymouth. It is all the more peculiar that two species, *Corethron criophilum* and *Hyalodiscus stelliger*, have resisted every attempt to culture them. It appears to me unlikely that these two species should require a medium fundamentally different from that in which there was an excellent growth of the other diatoms all the year round, or that species of Ceratium should need a medium different from that suitable for Prorocentrum and Noctiluca, or an Oikopleura larva a medium different from that of a Pilidium larva. It seems more probable that the temperature of the

Laboratory rooms, being much more variable and altogether higher than that in the sea, is only tolerated by a limited group of species.

The experiments with fish larvae produced good evidence for the assumption that the weakest point of the culture technique used was the lack of controlled and sufficiently low temperature. It has been shown by Lebour (1925) that the critical stage in the life-history of the Angler was not, as might have been expected, directly the yolk sac was absorbed, but a few days afterwards, because for three days the fishes were catching food fast and eating it. In my experiments the Anglers and Herrings survived about 14 days after the yolk sac was absorbed, and the Pilchards 10 days, during which they fed and undoubtedly grew in size. But as the Herrings died 15 minutes after having been transferred into fresh medium of a temperature 1–3° higher than the original medium it cannot be surprising that the rest of them died within 2 weeks or so if exposed to slower but even bigger changes of room temperature. Both Herrings and Anglers kept under running tap water lived a few days longer than at room temperature, although when kept in the cellar the room temperature was considerably steadier than the temperature of the laboratory. The conclusion which may be drawn from these preliminary experiments is that fish-larvae need not only a steady but low temperature. Garstang (1900) concluded from experiments on the rearing of the "Butterfly Blenny" (*Blennius ocellaris*) "that the conditions which are most important for the healthy development of sea-fish larvae, and for the survival of a high percentage of fry through the critical stages of metamorphosis, are the following: (1) A liberal supply of pure water; (2) Mechanical, but moderate, agitation of the water . . . ; (3) Provision of suitable food prior to the absorption of the yolk; and (4) A fairly constant, but not excessive supply of food each day. . . ." Point (4) appears to me of minor importance and low temperature should be included. Under controlled temperature conditions, with supply of the right food for the different stages, one would, I think, stand a fairly good chance of rearing fish larvae. It is one of the improvements of the culture technique which might also lead to a successful breeding of plankton copepods. Crawshay (1915) in experiments on the rearing of plankton copepods showed that temperature is a factor of the greatest importance and that "the daily fluctuations of air temperature to which uncovered vessels are exposed are liable to produce conditions that must sooner or later prove fatal to animals so sensitive to such changes." The best success—rearing of nauplii to the adult stage, with *Nitzschia closterium* as food—he obtained by keeping the culture vessels at a temperature with a varying range of no more than 1·6°, a maximum daily variation of 1°, and an average temperature of 12·3°. Clarke and Gellis (1935) kept copepods at different carefully controlled temperatures with *Nitzschia* *closterium* (from Dr. Allen's culture), Dunaliella, Carteria and Chlamydomonas as food. Under these conditions the majority of the copepods died after about two weeks. But it is possible that those forms were too large since certain experiments " indicate that bacteria and other constituents of the nannoplankton may be an important food for copepods in the sea."

I am grateful to Mr. F. S. Russell, Dr. S. Kemp, F.R.S., and Dr. E. J. Allen, F.R.S., for kindly reading and correcting the manuscript of this paper and giving much helpful advice.

SUMMARY.

The methods are described which made possible the establishment of pure cultures of a number of centric plankton diatoms and of the dinoflagellate *Prorocentrum micans*.

By means of a modified technique cultures were obtained of some nannoplankton autotroph flagellates varying in size from 2 to 10μ. Attention is drawn to their great number in the plankton and to their importance as food in the sea.

Herring, Angler and Pilchard larvae were reared for respectively 27, 29 and 15 days after hatching. The young Herrings and Pilchards fed on *Chlamydomonas* sp. and *Prorocentrum*, the Anglers on nauplii of *Artemia salina*. Some evidence is given for the conclusion that the ultimate failure in rearing these species was caused by too high and variable temperatures.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs. Part I: Some New Observations on Sorting Mechanisms in Certain Lamellibranchs.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. 79, 1936, *pp.* 181–308.

Accounts are given of the ciliary feeding mechanisms in *Nuculana minuta* (Müller); *Glycymeris glycymeris* (L.) and *Arca tetragona* Poli; *Heteranomia squamula* (L.), *Monia squama* (Gmelin), and *M. patelliformis* (L.); *Pteria hirundo* (L.); and *Solen marginatus* Montagu, *Ensis siliqua* (L.), *E. arcuatus* (Jeffreys), and *Cultellus pellucidus* (Pennant). These Lamellibranchs agree in possessing a certain ciliary sorting mechanism on the gills themselves, namely, adjoining tracts of frontal cilia beating in opposite directions on the same gill filament or leaflet. This occurs in Nuculana on the inner leaflets only; in the Arcidae and Anomiidae (with flat gills) on all filaments; in Pteria, Solen and Ensis (with plicate and heterorhabdic gills) on the ordinary and apical filaments only, and complicated by a difference in the direction of the frontal currents in the plical grooves and on the crests; in Cultellus (with flat gills) on both lamellae of the inner demibranch, but on the ascending lamella only of the outer demibranch.

Tracts of fine frontal cilia, beating continuously, convey particles intended for consumption, while tracts of coarse cilia, fully active only when stimulated, transport material intended to be rejected. In all, except the Protobranch Nuculana, unwanted material is carried to the ventral edges of the demibranchs, which are generally ungrooved or slightly grooved, rarely deeply grooved. In the Arcidae and Anomiidae the current along the edge is posterior in direction, so that such unwanted material as does not fall on the mantle is transported directly to the exterior. In Pteria, Solen, Ensis, and Cultellus the marginal current is oralward, but if the load be heavy much falls on the mantle, and is conveyed posteriorly by its recurrent tracts and finally rejected on sudden closure of the valves.

In the Anomiidae the sorting mechanism on the gills was not observed functioning satisfactorily under experimental conditions, in that there was no appreciable transportation of intended food particles dorsally, and it would seem that members of this family mainly feed on particles brought directly to the broad dorsal food grooves by the water current set up by the lateral cilia.

In Nuculana the highly specialized method of sorting on the small gills seems to have been inherited from a form in which the gills played a considerably greater part in nutrition than they do in this Protobranch, which feeds largely by means of extrusible palp appendages. In *N. minuta* the strength of the inhalent and exhalent currents is augmented at intervals by dorsal contraction of the gills, in which there are striated muscle fibres.

In the Arcidae and Anomiidae the ciliary currents of the visceral mass and mantle are described in detail. In the section on the Anomiidae an Appendix is added on the hypobranchial gland of the genus Monia.

D. A.

Nouvelles Observations sur l'Acétylcholine et la Choline-Estérase chez les Invertébrés.

By Z. M. Bacq.

Arch. Internat. Physiol., Vol. XLIV, 1937, *pp*. 174–189.

The muscles of worms, sipunculi, molluscs and echinoderms are made to contract by acetylcholine. The muscles of sea anemones and crustaceans are insensitive to acetylcholine. Choline-estérase is present in the tissues and fluids of worms, sipunculi, molluscs and echinoderms. It exists in the muscles of the crustaceans, but it does not exist in the blood of the crustaceans or in the muscles of the sea anemones. It is absent from the blood of Arenicola. So far, experiments undertaken in order to demonstrate the existence of cholinergic nerves in Cephalopods have been unsuccessful. Acetylcholine and eserine are without action on the stellate ganglion of Cephalopods.

Z. M. B.

L'"Amphiporine" et la "Némertine" Poisons des Vers Némertiens.

By Z. M. Bacq.

Arch. Internat. Physiol., Vol. XLIV, 1937, *pp*. 190–204.

In the tissues of the nemertean worms Amphiporus and Drepanophorus, there exists an alkaloid "amphiporine" which according to its pharmacological and chemical properties may be classified in the nicotine group.

Amphiporine is not localized in the proboscis of the nemertine and is not, strictly speaking, a venom.

The tissues of most nemertines (particularly in the species Lineus) contain another substance deprived of nicotine-like action, but active at low concentration on the neuro-muscular preparation of the crab.

Z. M. B.

The Development of Isolated Blastomeres of the Ascidian Egg.

By Arthur Cohen and N. J. Berrill.

Journ. Exp. Zool., Vol. LXXIV, 1936, *pp.* 91–117.

Isolated half-blastomeres of *Ascidiella aspersa* produce small tadpoles which possess 0 to 3 papillae, 0 to 2 sense organs, 20 to 22 notochord cells and 19 to 21 muscle cells. The normal tadpole developing from a whole egg possesses 3 papillae, 2 sense organs, 40 to 44 notochord cells and 38 to 40 muscle cells. The first three cleavages of the half-blastomere are strictly partial, but the sliding of the cells as their free surfaces are reduced to a minimum soon masks the characteristic pattern. Explanations are offered to account for the presence of as many as the full complement of papillae and sense organs which would fit both a determinate and regulative conception of the ascidian egg. The presence of partial cleavage and only half the normal number of notochord and muscle cells can only be accounted for on the basis of rigid determination. It is concluded that the eggs of this species should be considered as belonging to the determinate class, although regulation of a type dependent on the action of surface forces occurs.

A. C.

Heterogonic Growth in the Abdomen of *Carcinus maenas*.

By J. H. Day.

Report of the Dove Marine Laboratory (*Third Series, No.* 3), 1935, pp. 49–59.

From measurements of 560 specimens of *Carcinus maenas*, growth-ratios of individual abdominal segments were determined. These in turn were used to show the growth-gradients along the whole abdomen. While it is realized that these gradients in the abdomen are merely parts of a more general gradient permeating the whole body, it is evident that there is a growth-centre in the third abdominal segment of young individuals of both sexes. Mature crabs have a growth-centre in the sixth segment. The balance of evidence is in favour of the separate origin of the two growth-centres, rather than a gradual movement along the abdomen.

There is also evidence that the appearance and increasing influence of the growth-centre in the sixth segment is correlated with sexual development and in this connexion it is interesting to note that at the onset of sexual maturity there is a rise in growth-potential in the female and a fall in the male.

It is believed that this is the first recorded case of an organ, the abdomen, passing from the influence of one growth-gradient to another, the second of which is correlated with sexual development.

J. H. D.

Observations on the Sporozoa Inhabiting the Gut of the Polychaete Worm *Polydora flava* Claparède.

By R. Ralph Fowell.

Parasitology, Vol. XXVIII, 1936, *pp.* 414–430.

Polychaete worms harbour some very characteristic Sporozoa; and *Polydora flava* is certainly no exception to the rule. A Coccidian—which is clearly an Eimeriid—is, perhaps, the most interesting parasite of Polydora owing to its striking resemblance to the Coccidia of higher animals; and it is also remarkable in being an intranuclear parasite. Unfortunately, the fate of the undivided contents of the oocyst is unknown.

The other parasites of *Polydora flava* include a dicystid gregarine, *Polyrhabdina polydorae*, and a schizogregarine, *Selenidium axiferens* n. sp.; this organism possesses a remarkable axial tube which extends from one end of the body to the other and completely encloses the nucleus. The axial tube forms an integral part of the fibrillar complex, being connected, by whorls of radial fibrils spaced at regular intervals along the body, with a superficial system of longitudinal myonemes underlying the pellicular grooves. Schizogony and stages in sporogony, up to the formation of isogametes, are described; and association in *Polyrhabdina polydorae* is recorded for the first time.

R. R. F.

Neuro-muscular Transmission in Crabs.

By Bernhard Katz.

Journal of Physiology, 1936, *Vol.* 86, *pp.* 45–46 P. *and Vol.* 87, *pp.* 199–221.

The electric excitability and the effect of different pharmacological agents on the neuro-muscular system of *Carcinus maenas* were investigated. The mechanical response of the flexor muscle of the dactylopodite in isolated walking legs, and the electric response of nerve and muscle were recorded. Visible muscle contraction, during indirect stimulation, results from repetitive nerve excitation only. The majority of muscle fibres come into action at frequencies of 60–120 per sec. (20° C.). The gradation of the muscle response is controlled by the number of " facilitated " nerve endings, increasing statistically with frequency. The time constant k (Hill) in nerve excitation, determined from strength-duration curves (repetitive condenser discharges) for electric response of the nerve, or for threshold contraction of the muscle, is about 1 msec. at 20° C. The limb nerve gives prolonged multiple response to constant current both at make and break, due to its very slow accommodation process. The frequency of impulses varies with intensity of applied current up to an upper limit (about 300 per sec. at 20° C.), determined by the absolute refractory period. Calcium, in about fifteen times normal blood concentration, quickening the accommodation process, abolishes reversibly the multiple response. The nature of neuro-muscular transmission is investigated. Curare, acetylcholine and eserine have little or no effect on the neuro-muscular junction. Potassium applied to the neuromuscular junction causes contracture, even in three times normal concentration. The initial part of the contracture is of a tetanic nature, being accompanied by rhythmic electric response. Magnesium, even in 2·5 times normal blood concentration, has a reversible curare-like blocking effect on the myoneural junction, and acts as an antagonist to potassium in respect of contracture. The electric response of the nerve is abolished by potassium, increased by magnesium, in about the same concentrations as those effective on the nerve endings.

B. K.

Observations and Experiments on Sex-change in the European Oyster. V. A Simultaneous Study of Spawning in 1927 in Two Distinct Geographical Localities.

By J. H. Orton.

Mélanges Paul Pelseneer, Mémoires Mus. Roy. Hist. Nat. Belg., Ser. 2, *Fasc.* 3, *pp.* 997–1056.

In this study some 10,000 oysters from the Fal Estuary and some 5,000 from the River Blackwater were examined during and about the spawning season in 1927, giving mostly large weekly samples. An analysis for sex-proportions and spawning confirms and establishes the fact that on English beds at least 50% of the population above the age of three years mature annually as ripe females, mostly near the beginning of the spawning season, and become gradually expended as they spawn during the season. Spawning began at different dates on both beds when the sea-temperature attained about 15° C.; a correlated study of seasonal

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variation in sea-temperature is given. Fluctuation in weekly percentage of premature and normal whitesick, greysick and blacksick are noted with their bearing on oyster-culture, and periods of development of larvae *in situ* in the parent in the sea are adduced from the results. The factors contributing to the spawning stimulus, the effect of temperature and salinity fluctuation on spawning, the theory of the time-calorie period of development in relation to spawning and other problems are discussed.

The female population on the Blackwater was exhausted to a minimum of 3% in August, whereas 20% of the population on the Fal were unexpended at the same time and failed to spawn effectively. A discussion of the phenomena and probable controlling factors is given. A study of the gross proportion of the population acquiring femaleness (including assumptions of the hermaphrodite phase) during the season, and of other problems, is being continued from the data obtained.

J. H. O.

The Photo-electric Measurement of Submarine Illumination in Off-shore Waters.

By H. H. Poole.

Rapp. and Proc. Verb. Cons. Internat. p. l'Explor. de la Mer., CI, 2e *Partie,* 12 *pp.*

Photo-electric cells of the selenium rectifier type appear to be the most suitable at present available for the measurement of submarine daylight.

As a low-resistance circuit is essential for measurements in bright light, and it is difficult to combine this with adequate sensitivity in a galvanometer suitable for use at sea, the modified Campbell Freeth potentiometer circuit has been made use of. This combines zero effective resistance with a sensitivity extending to 10^{-9} ampère, and is virtually unaffected by the rolling of the ship.

A brief description is given of the marine equipment which has been found to be suitable.

The optical conditions affecting a submerged photometer are considered, and the need is pointed out for a suitable opal diffusing window in contact with the water. Notes are given of the colour filters used for isolating different parts of the spectrum.

Depth errors due to the drift of the ship must be guarded against, and the error due to shading reduced as far as possible by suspending the photometer from a spar projecting over the stern. The length of the spar is generally limited by motives of convenience, and by the extent of the ship's pitching motion.

The accuracy obtainable under water varies greatly according to the weather. As, however, the illumination generally falls by from 10 to 20 per cent per metre (or much more for red light) depth errors are likely to be as important as photometric errors.

The vertical extinction co-efficient found from the ratio of the illuminations at two different depths is a convenient index of the opacity of the water, although Pettersson's direct method of comparison of the opacities of different waters possesses some important advantages. H. H. P.

The Effect of Parasitism by Larval Trematodes on the Tissues of *Littorina littorea* (Linné).

By W. J. Rees.

Proc. Zool. Soc., London, 1936, *pp.* 357–368, *Plates I–IV.*

The effects produced by the following larval trematodes were studied : *Cercaria Himasthla secunda* (Nicoll), *C. littorinae* Rees, *C. lophocerca* Lebour, *C. emasculans* Pelseneer and an ubiquitous cercaria (near *C. ubiquitoides* Stunkard). The total percentage infestation varied considerably depending on local conditions, including the distribution and habits of the final hosts of these larvae.

Differences in the parasitization of the digestive gland and gonad by the different parthenitae were found to be due to three factors which are interdependent : 1. The nature of the parthenita, whether sporocyst or redia. 2. The size of the individual parthenitae. 3. The presence of a " blocking layer " formed by inactive sporocysts. W. J. R.

An Investigation of the Post-Larval Development of the Shore Crab, *Carcinus maenas,* with Special Reference to the External Secondary Sexual Characters.

By C. J. Shen.

Proc. Zool. Soc., London, 1935, *pp.* 1–33, 28 *figs.*

The male and female crabs can be distinguished not only in the adult stage, but also in early post-larval stages, by means of the following three external sexual characters : (*a*) the pleopods, (*b*) the abdomen, and (*c*) the carapace.

The first character alone is diagnostic for all crabs ; the second and third ones are applicable only within limits.

(*a*) *The pleopods* of the megalopa and first young crab stages do not show any remarkable sexual characters except a slight difference in size, but the sexes can be readily distinguished by means of the pleopods at the second young crab stage.

(*b*) *The abdomen:* The form of abdomen can be distinguished between the two sexes at about the fifth young crab stage.

(*c*) *The carapace:* The form of carapace in early post-larval stages exhibits no significant sexual differences. The growth-rate, however, is rather higher in the female as compared with the male from the fifth young crab stage onwards.

C. J. S.

New Species of Zostera from Britain.

By T. G. Tutin.

Journ. Bot., Aug., 1936, *pp.* 227–230.

A new species of Zostera belonging to section Alega was noticed during an investigation into the causes of the disease of *Z. marina* L. and named *Z. Hornemanniana*. It differs from *Z. marina* which is its closest ally in the narrow leaves, rounded or emarginate at the apex, with three primary and two marginal nerves, much smaller flowers and inflorescences, and in having the style twice as long as the stigmas and seeds only 2·5 mm. long. It appears to be fairly common round the coasts of the British Isles and Western Europe and occupies a distinct ecological niche. It usually occurs on soft mud in estuaries at rather high levels, though in one locality it grows permanently submerged. It keeps its distinctive characters in cultivation and is readily recognizable in the field, though herbarium specimens often present difficulties to the systematist. The chromosome number is twelve, the same as in the other two British species, the chromosomes closely resembling in size those of *Z. marina*. The plant is quite fertile and shows no evidence of hybrid origin.

T. G. T.

The Development of the Sabellid *Branchiomma vesiculosum*.

By Douglas P. Wilson.

Quart. Jour. Micro. Sci., Vol. 78, 1936, *pp.* 543–603.

The Sabellidae are a large and widely distributed family of Polychaetes whose mode of development is almost entirely unknown. In this paper the embryology of the well-known species *Branchiomma vesiculosum* Montagu is described in detail and illustrated for the first time. The larvae were obtained from artificial fertilizations and were reared through metamorphosis and for some time afterwards. The larvae are well provided with yolk and do not feed during their pelagic life, which lasts only eight or nine days. They have a prototroch, but no telotroch. In the last swimming stages the primary buds of the branchial apparatus arise on the head in front of the prototroch; the collar buds appear behind the prototroch. During metamorphosis tissues of the prototroch and larval parts of the head clump together to form a snout-like structure that gradually breaks up into pieces which are discarded. The young worm secretes a tube of mucus for itself on the bottom and later builds one with sand grains.

At metamorphosis there are generally three or four chaetigers of thoracic type already formed; afterwards thoracic chaetigers are added in front of the pygidium until the adult number of eight has been attained. Succeeding segments are all abdominal in type. There is no change over from abdominal to thoracic constitution during normal development as has been reported for Serpulids, or as occurs in adult Sabellids during certain types of regeneration.

The early larvae of *Sabella pavonina* (Savigny) are shown to resemble closely those of Branchiomma.

D. P. W.

Observations on Pigmentary Co-ordination in Elasmobranchs.

By U. M. Wykes.

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 460–466.

Hogben's recent study of the pigmentary system of English Elasmobranchs showed that the colour responses of these fishes are under the control of two pituitary hormones. The experiments of Parker on Mustelus, however, have led him to conclude that in this fish melanophore contraction is brought about by nervous impulses.

The possibility of nervous control of pigmentary responses was investigated in *Raia brachyura*, *R. maculata*, *Rhina squatina*, and *Scyllium canicula*. No melanophore changes could be observed either macro- or microscopically after section of four consecutive spinal nerves in black or white adapted specimens, nor after electrical stimulation of spinal nerves, the haemal canal, or skin. Adrenalin, while having no effect on excised skin, was found to cause slight general pallor on subcutaneous injection. Possibly adrenalin injections affect the colour indirectly as a result of vaso-constrictor action. When the circulation in the tail and pelvic fins was impeded by an aortal ligature, melanophore changes were temporarily eliminated in these regions, though they could still be induced in the rest of the body.

These experiments suggest that, in the species investigated, the nerves play no part whatever in the control of background responses, which are under the exclusive influence of circulatory hormones.

U. M. W.

The Structure of Nerve Fibres in Sepia.

By J. Z. Young.

Journ. Physiol., Vol. LXXXIII, 1934, *pp.* 27–28 *P.*

The peripheral nerves of Decapod Cephalopods contain very large axons, those of Loligo approaching 1 mm. in diameter. These, as well as the smaller axons, are surrounded by nucleated sheaths. The substance of the axon is semi-fluid, and when the larger axons are cut their contents pour out from the end of the tube. A faint longitudinal striation is visible in the axon of the living nerve fibres, but there are no neurofibrils which can be followed for long distances.

J. Z. Y.

The Giant Nerve Fibres and Epistellar Body of Cephalopods.

By J. Z. Young.

Quart. Journ. Micr. Sci., Vol. LXXVIII, 1936, *pp.* 367–386.

In Decapod Cephalopods there is a system of giant nerve fibres which probably serve to produce rapid contractions of the muscles of the mantle. In Loligo the giant fibres in the stellar nerves arise in a special giant fibre lobe of the stellate ganglion, and they are syncytia, each being formed by fusion of the processes of a large number of nerve cells.

In Octopods there are no giant fibres, but in the position of the giant fibre lobe there is a small closed vesicle, coloured yellow in some species, to which the name "epistellar body" is given. The walls of this vesicle contain curious cells, the neurosecretory cells, whose general structure resembles that of neurons, but whose processes (axons) end blindly embedded in a homogeneous non-cellular matrix which fills the cavity of the epistellar body.

After removal of both epistellar bodies from *Eledone moschata* the animal shows general muscular weakness, which lasts for some days. It is suggested that the epistellar body has arisen in phylogeny from the giant fibre lobe and that the neurosecretory cells produce at their inner ends a hormone which passes into the blood stream.

J. Z. Y.

The Innervation and Reactions to Drugs of the Viscera of Teleostean Fish.

By J. Z. Young.

Proc. Roy. Soc., London, B., Vol. 120, 1936, *pp.* 303–318.

Faradic stimulation of the vagus nerve of Lophius or Uranoscopus is followed by movements of the stomach, whereas stimulation of the splanchnic nerve causes movements of the pyloric caeca and intestine.

There are no other motor nerves to the intestine other than those contained in the single pair of splanchnic nerves. Acetylcholine was found to cause a rise of tonus and initiation of rhythmic contractions in the muscles of the stomach, intestine, rectum and gall bladder, whereas adrenaline produced the reverse effects.

The walls of the ovary and urinary bladder receive motor fibres from the abdominal sympathetic ganglia, and these muscles are also usually caused to contract by acetylcholine and are inhibited by adrenaline. These results make it very difficult to draw any clear line between sympathetic and parasympathetic systems in fishes, and in particular they show that there is nothing corresponding to the sacral parasympathetic system of Mammals.

J. Z. Y.

The Structure of Nerve Fibres in Cephalopods and Crustacea.

By J. Z. Young.

Proc. Roy. Soc., London, B, Vol. 121, 1936, *pp.* 319–336.

The sheaths around the axons of Cephalopods are nucleated throughout, and the tissue of which they are composed resembles collagenous connective tissue. The axons may be nearly 1 mm. in diameter and each consists of a rather viscous fluid apt to flow out of the sheath if the latter be damaged. No definite neurofibrils traceable for long distances are present in the axoplasm, but there is a faint longitudinal striation which is visible during life and becomes much more definite if the axon be damaged in any way, presumably on account of the coagulation of longitudinally orientated micelles. It is estimated that 65–70% of the cross-sectional area of Cephalopod nerves is occupied by the axoplasm.

In the leg nerves of Maia each axon is surrounded by a continuous sheath, whose nuclei extend even to the innermost layers. There is some fat present, especially in the inner layers. The sheaths around the larger axons of Maia are very thick, consisting of many concentric layers. 60–70% of the cross-sectional area of the leg nerves of Maia is occupied by axoplasm.

J. Z. Y.

Book Notice.

Color Changes of Animals in Relation to Nervous Activity. By G. H. Parker. University of Pennsylvania Press, 1936. London: Humphrey Milford: Oxford University Press, IX+74 p. 7/-.

The apparent paradox that the colour changes of teleostean fishes and reptiles are controlled by nerves, while those of amphibia are controlled by hormones has long been a barrier to the formulation of a consistent theory of colour response in vertebrates. Professor G. H. Parker has arrived, on the basis of numerous experimental investigations by himself and his collaborators, at a new interpretation which claims to overcome this difficulty. The interpretation is presented in the Leidy Memorial Lectures which are published in the book under review.

That the activation of melanophores is effected through the mediation of a chemical substance, a neurohumour, which is liberated at the chromatophoral nerve endings, is a conception which gains strong support from recent discoveries of chemical agents in nervous transmission. But the interpretation of the experimental data in terms of a neurohumoral mechanism has led Professor Parker to postulate a principle which many physiologists will find it hard to accept, especially as it is supported, at best, by indirect evidence. This principle is that when chromatophoral nerves are cut "they are not at once paralysed, as was formerly thought, but they are by the very act of cutting thrown into a state of superactivity which may last in *Fundulus* for two, three, or more days."

The whole of Professor Parker's theory of the control of pigmentary activity must stand or fall by the validity of this new conception. That it is unorthodox does not mean that it is untrue, but, since physiological methods exist to-day which are capable of subjecting it to a conclusive test, Professor Parker's case must remain *sub judice* until such tests have been applied.

At the same time it has to be admitted that no other interpretation has ever been put forward to account for some of the phenomena, like the paling of dark bands after nerve section, with which Professor Parker deals. A working hypothesis is far better than no hypothesis at all, and Professor Parker has made a contribution of first importance to the subject by drawing attention to many new phenomena that have hitherto been overlooked, and by advancing a theory that will undoubtedly stimulate much further work and discussion.

A. Sand.

The Journal of
Experimental Biology

(Late *The British Journal of Experimental Biology*)

EDITED BY
J. GRAY
ASSISTED BY
G. P. WELLS and E. ASHBY
Hon. Secs Society for Experimental Biology

Vol. XIV, No. 1 *Price* 15*s. net* January, 1937
Subscription per volume 42*s. net*

Contents

Published for The Company of Biologists Limited
by THE CAMBRIDGE UNIVERSITY PRESS
London: *Fetter Lane*, E.C. 4.

THE
QUARTERLY JOURNAL
OF
MICROSCOPICAL SCIENCE

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CONTENTS OF No. 314—*New Series*

Volume 79, Part II, December, 1936

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OXFORD UNIVERSITY PRESS
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OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor Huxley, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of Argyll, Sir Lyon Playfair, Lord Avebury, Sir Joseph Hooker, Dr. Carpenter, Dr. Günther, Lord Dalhousie, Professor Moseley, Mr. Romanes, and Sir E. Ray Lankester.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000, and from that time until 1933 a sum of over £16,000 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

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All correspondence should be addressed to the Director, The Laboratory, Plymouth.

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NOTICE.