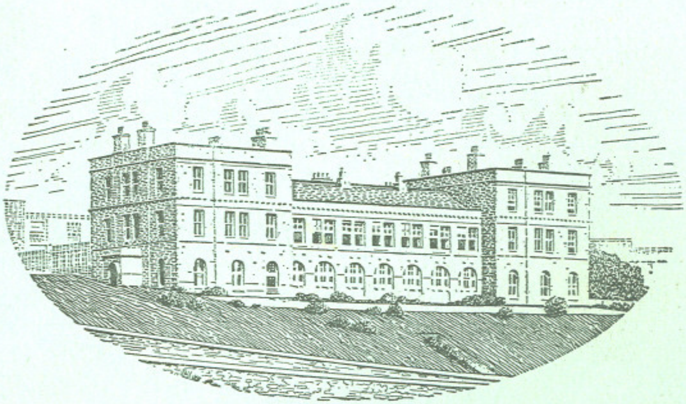
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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THE SALTASH TUCK-NET FISHERY AND THE ECOLOGY OF SOME ESTUARINE FISHES

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Student Probationer at the Plymouth Laboratory

(Text-figs. 1–17)

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INTRODUCTION

The inshore fisherman is confined by the small size of his boat to fishing grounds of very limited extent. He cannot follow one species of fish in the course of its annual wanderings, but is compelled to await the movement of his quarry into his working area. He must shoot his nets or set his lines on the same grounds, month in and month out, catching those fish which happen to come within his reach. As a result he gains a detailed knowledge of the seasonal distribution of fishes on his grounds, and of their habits during their periods of abundance: but only with those fishes which never leave his area can he form a picture of the complete life history of any species.

The mud flats which border the estuaries of the rivers Tamar and Lynher are the working grounds of a winter seine-net fishery, carried on with open boats from villages along the shores. The net used is the "Saltash Tuck Seine", a modification of the ordinary shore seine for use on very soft mud. In November 1935, at the suggestion of Dr E. J. Allen, I began an investigation of this fishery and of the fishes of the estuaries. Some weeks were spent in learning to work with a tuck-net, and then, between January 1936 and December 1937, I made just under one hundred fishing expeditions to the rivers. The professional fishermen do not use the tuck-net in summer, for salmon are then a more profitable quarry than the flatfishes and bass of the estuaries; but in the investigation of the ecology of these fishes hauls were made in every month of the year. An ordinary commercial seine belonging to a Saltash fisherman was used on some occasions; on others a tuck-net fitted with a special cod-end of fine-meshed "French netting".

I should like to thank Mr E. Ford for much assistance in the preparation of this paper. It is also a pleasure to acknowledge my gratitude to Mr J. Gould, of Saltash. Without his exact knowledge of the Tamar and Lynher, his skilled working of a tuck-net, and his constant and generous cooperation, the investigation of the fishery could never have been made.

DESCRIPTION OF THE AREA

The rivers Tamar and Lynher flow into the western end of Plymouth Sound. The estuaries are bordered by mud flats, with occasional beaches of slaty shingle. In the lower half of the tidal area the mud flats are broad, and below low-water mark slope smoothly down to the bed of the river: it is on these slopes and on the shingle beaches that the tuck-net is fished. In the upper reaches the precipitous sides of the narrow mud banks make tuck-netting impossible.

The mean tidal ranges at Devonport, Saltash and Cargreen are as follows:

	Spring tides		Neap tides	
	ft.	m.	ft.	m.
Devonport	15·5	4·74	12·0	3·67
Saltash	15·0	4·58	11·0	3·27
Cargreen	14·75	4·51	10·75	3·29

(From the *Channel Pilot*, 9th ed.)

The so-called "eddy tide" runs close inshore in the opposite direction to the main tidal flow. This eddy current is usually only a few yards in width and makes no difference to the working of the net, though it is always used by the fishermen when travelling against the tide. On the West Muds ground, however, the reversal of the current is so extensive that the net must be fished in the direction of the eddy and not with the run of the tide.

The Tamar drains the western slopes of Dartmoor, the wettest area in the west of England (mean annual rainfall at Princetown: 81·87 in. = 2079 mm.). The Lynher rises in the Cornish moors where the precipitation is almost as great (mean annual rainfall at Altarnun: 59·17 in. = 1503 mm.). Heavy rain is soon followed by a spate which, in winter, brings down masses of sodden leaves from the woods along the river valleys. These leaves are spread out on the mud banks on the inner sides of curves, and accumulate along the bottom of the river so thickly that it may be impossible to work a net where they lie. As a flood subsides it deposits a layer of fine, sticky mud called "slurry" on the flats, so that the surface level may be raised a few inches until the scouring of the next spring tides carries the deposit away to sea. A thick fall of "slurry" will sometimes so choke a net that it cannot be hauled into shallow water.

Fuller accounts of the estuaries of the Tamar and Lynher may be found in Percival (1929) and in Hartley & Spooner (1938).

Construction and Use of the Saltash Tuck Seine

The principal difference of the tuck-net from an ordinary shore seine is in the belly of the net. From a seine which can be hauled ashore no fish can escape round or under the arms once the ends of the net are on land. With the Saltash net, fished on soft mud, this beaching is not possible, and the net (as will be explained later) must be lifted into a boat anchored in 2 or 3 ft. of water. From the broad, shallow belly of a shore seine escape during the lifting would be easy. A tuck-seine is therefore fitted with a funnel-shaped cod-end, some 3 fathoms long. The mouth of this "funnel" is square in section: the two sides are continuous with the arms of the net, the top is attached to a well-corked head rope. As the net is hauled, the mouth of the funnel stands widely open and the fish swim or are swept back into the long narrow cod-end, from which escape is difficult.

A typical Saltash tuck-seine has head and foot ropes 20 fathoms long. The arms are made of 18-ply cotton netting, 32 meshes to the yard, 60 meshes deep. The net is set on the ropes by the fourth—that is, the settings are placed three mesh lengths apart with four meshes between each setting. The bunt and cod-end are made from four funnel-shaped sections of 18-ply cotton netting, 42 meshes to the yard and 80 meshes deep at the wider end. The cod-end is at least 12 ft. (3·65 m.) long and is secured by a draw string. The net is preserved in a mixture of two to three parts of oil to one part of tar. At each end the head and foot ropes are spliced together into bridles. A 4 ft. pole, weighted at the lower end, is secured across each bridle by clove-hitches in the bridle ropes. To each bridle is attached a 1-in. grass warp, 30 fathoms long, marked off into 10-fathom lengths by pieces of leather.

A Saltash tuck seine is fished from an open boat, 12–16 ft. long, with a crew of two. Work begins about 1½ hr. before low water. By that time it will be possible to work along the edges of the mud flats and shoot the net in the deep water on their slopes. The speed of the tidal stream, too, will have begun to grow less: except during the slackest neaps the current at half-tide is strong enough to lift one arm of the net and roll it round the other. The free end of one warp is made fast in the boat; this warp is referred to as the "boat warp", and the pole across the bridle to which it is made fast as the "boat pole". The warp and pole at the other end of the net are the "shore warp" and "shore pole". The boat warp is heaped in the stern of the boat and the boat pole laid across it. The upper end of the boat pole projects over the quarter, pointing against the current as the boat lies stern to the beach. The net is piled on the transom, the cod-end being looped over the projecting end of the boat pole. The shore pole is laid on the top of the net and the shore warp carried forward along the side of the boat, outside a thole-pin and into the bows. The shore warp is heaped (not coiled) in the bows, the free end on top.

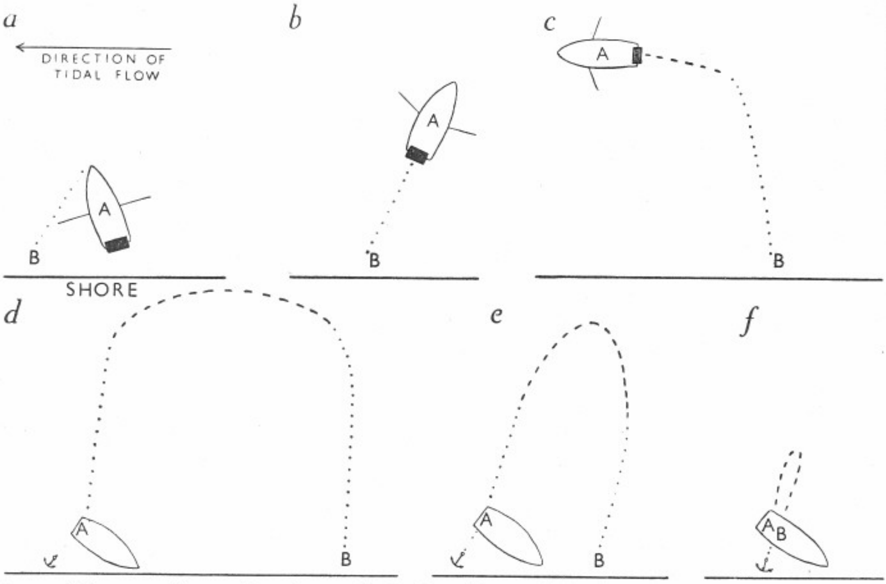

Fig. 1. Diagrams illustrating the method of working a Saltash tuck-seine; the net is represented by a broken line, and the warps by dotted lines. In figures *a*, *b* and *c* the net is piled on the stern of the boat, and is represented by a solid rectangle.

The net is now ready for shooting. One man, *B*, leaves the boat and stands in the shallows holding the free end of the shore warp (Fig. 1 *a*). The second man, *A*, rows the boat out from the shore, heading up into the tide (1 *b*). The shore warp pays out from the bows of the boat round the thole pin, tightens and pulls the shore pole overboard. *A* turns the boat parallel with the shore and rows with the tide as the net shoots itself over the stern of the boat (1 *c*). As soon as the boat pole is pulled overboard *A* turns the boat for the shore, rows inward as the boat warp pays out over the stern and anchors in the shallows some 25–50 yards below *B* (1 *d*). The anchor is made fast to a thole pin near the stern. *A* and *B* haul on their warps until *B* has 10 fathoms of warp in the water: he then moves nearer the boat and hauling is continued until the tops of the poles break the surface (1 *e*). *B* then wades to the boat dragging his end of the net with him; he climbs into the boat and goes aft to stand by *A* (1 *f*): the two men then haul the net into the boat as rapidly as possible. In a good haul a few fish are usually found tangled up in the arms of the net, but the bulk of the catch will be in the cod-end. It takes 10–15 min. to make one shot.*

A is usually the senior man; he decides how much to "head" the net into the tide. If the tide be running strongly he will shoot the net as far above *B* as he can: at slack water he will row straight offshore. Occasionally, at neap tides, a "keg-haul" is made over a submerged flat. The shore warp is made fast to an anchored buoy, and picked up after the net has been shot. Both warps are hauled into the boat. A "keg-haul" rarely yields a big catch, for the net sweeps a smaller area than is covered when a shot is made from the shore. Work continues until about one hour's flood. The rising of the tide is always felt first along the bottom of the river; a net may be rolled up by the speed of the current on the river bed, while sticks floating on the surface are scarcely moving upstream.

The number of fishermen working regularly in the estuaries has decreased and is still decreasing. The younger men willingly leave the river if they can find regular employment ashore, and the older hands all say that the fishing is finished. This is not a comparison with "good old days" remembered by occasional large catches, but a statement of fact. For example, in days gone by some of the Saltash men made a living all the year round by catching "smelts" (*Atherina presbyter*). Now this fish has become so rare that its capture excites comment: I have myself seen only nine specimens in two years' work.

The fisherman's year used to open with the oyster dredging in the Tamar: now the oyster beds are worked out. From March till August is the salmon season, when tuck-nets are put away, and the men live in house-boats in the upper reaches of the estuary, working their 100-fathom seines. It is to the salmon that the fishermen look for their living. A year with a small run of grilse, such as that of 1937 (Menzies, 1938), is a serious matter, for it may mean two bad seasons in succession—the poor 1938 season showed this only too well. In midsummer some prawns are caught in hand-nets. In the early autumn comes the herring season when light drift-nets are set at dawn and dusk. In recent years this fishery has failed within the rivers as it has in the sea outside. The small shoals of herring which did appear in the harbour in 1937 arrived in mid-October, though they had been expected a month earlier.

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* Davis (1937) has pointed out that the tuck-seine closely resembles a trawl in its action.

After the herring comes the tuck-netting season. Catches in the last few years have been so small that day after day it may not be worth while to take the fish to market. Even if a large catch be made, the estuarine fisherman will only get a good price for it if heavy weather has prevented the steam trawlers from working.

The local men attribute the decline in the fisheries to various causes—the activities of prawn trawlers in the harbour, the depredations of cormorants (*Phalacrocorax carbo carbo*) and the silting up of channels. It seems probable that the true main cause is the general disastrous decline in fish stocks which has been observed in the western end of the English Channel since 1932 (Russell, 1938).

For some years the sale of mussels (*Mytilus edulis*) from the rivers has been illegal. In December 1937 the local medical authorities banned the sale of all shellfish whatsoever from the Tamar and its tributaries, so that another possible source of income—gathering cockles (*Cardium edule*)—was lost to the fishermen. At one time several punt guns were regularly used in the winter, but professional punting is now practically extinct, although some widgeon (*Anas penelope penelope*) still come to the estuaries.

When the results of the fishing expeditions were summarized, it soon became obvious that the factors which limit the inshore fisherman in his work were also limitations upon the scientific results of the investigation. It was possible to study the changes in the composition of the estuarine fish community in detail, but the irregularity of occurrence of some fish made it very difficult to work out the changes taking place in the lives of individual species. The only estuarine species studied out of its estuarine environment was the flounder; all other fishes were studied only as they happened to appear on the fishing grounds, with the inevitable result that conclusions on the bionomics of many of them can only be put forward as a series of tentative suggestions.

METHODS OF INVESTIGATION

All fish, with the exception of clupeoids, were measured from the tip of the snout to the end of the longest caudal ray. The young clupeoids living in the estuaries of the Plymouth area often have the caudal fin considerably abraded or broken (Ford, 1928): some fish have no caudal rays at all. Clupeoids were, therefore, measured to the end of the scaled area of the caudal peduncle. Arithmetic mean lengths were calculated by dividing the fish into length groups measured to the nearest whole centimetre below, and by multiplying the divergences from the modal length by the number of fish showing each divergence, and dividing the difference between the total divergences above and below the mode by the number of fish examined. 0·5 cm. was added to the length so calculated in order to give the centre of the group.

Flounders were weighed to the nearest 1 g. below.

In the three species of pleuronectids some otolith readings were made. The narrow, opaque, white rings in the otoliths are called "winter rings", the broader, translucent zones dividing them "summer zones". That this nomenclature is justified is shown in the following table, in which the percentage of otoliths having a winter ring on the outer edge is shown for each month of autumn and winter, 1937.

Month		*Pleuronectes flesus*	*Pleuronectes limanda*	*Pleuronectes platessa*
1937	Sept.	..	4	..
	Oct.	16	7	27
	Nov.	49	5	18
	Dec.	70	37	59
1938	Jan.	93	..	..
	Feb.	84	..	..

In each species there is a marked increase in the percentage of fish showing an opaque "winter ring" as the winter fasting period comes on.

In the study of feeding habits the food organisms have been summarized on a basis of occurrence. This has been preferred to the apparently greater accuracy of numbers for two reasons:

(i) The food organisms vary considerably in size; one large shrimp obviously contains more nourishment than several mysids.

(ii) A large number of an unusual food organism in one fish would give quite undue prominence to that organism in a numerical summary.

A displacement method of assessment would perhaps be ideal, but it would be too cumbrous for use with large samples of fish.

In most species only the contents of the stomach were examined, but in the pleuronectids it was found that animal remains in the intestine were usually recognizable, being less comminuted than in other fishes. I felt it to be better, therefore, when dealing with flounders, dabs and plaice, to count the occurrence of food organisms in stomach and intestine separately, so that due prominence should be given to the commoner animals.

Observations on Estuarine Fishes

Pleuronectes flesus L., the Flounder

The flounder is caught in the tuck-nets from October until March, and is, with the bass (*Morone labrax*), the most valuable quarry of the netsmen. Very little work has been done upon this species in Great Britain; but in the Elbe and the Baltic it is the objective of important fisheries, and several investigations of its bionomics have been made. In the Tamar and Lynher the flounder is the estuarine fish *par excellence*: and on account of this, and the small knowledge of its life history in this country, it was made the special object of the investigation of the ecology of the fishes of the estuaries. The bionomics of all the fishes taken in the tuck-net were investigated as fully as possible, but, to some extent, all other species were regarded as forming part of the animate environment of the flounder.

Several species of flatfish enter the estuaries of the Tamar and Lynher, but the flounder is the only one of these to colonize the brackish upper reaches where salt and fresh waters mingle. The flounder has considerable powers of osmotic regulation. Von Buddenbrock (1936) found that the species had three mechanisms for maintaining the osmotic pressure of the blood when living in water of low salinity—a remarkable impermeability of the skin, a complete cessation of imbibition, and an increased secretion of urine. Flounders are numerous in the upper parts of the estuaries, where there are great salinity changes in a comparatively short time, and some of the younger fish ascend into fresh water where they "dwell and thrive to a hand's breadth and almost twice so long" (Walton, 1659). In the Tavy, a typical, acid, west-country trout stream, the flounders may be seen moving about among the brown trout (*Salmo trutta*). In the summer months flounders of all sizes are rare on most of the fishing grounds. According to the local fishermen, they wander away up the gutters which drain the saltings and creeks on either side of the rivers: and there some are certainly caught in stop-nets at low tide. Results of marking experiments begun in the autumn of 1937 suggest that there is also a spring movement of immature flounders up the main channels of the rivers, into regions where the salinities are lower than those of the winter haunts.

Growth and Age.

Several authors have emphasized the variability of the growth rate in the flounder. Cunningham (1896) found that a number of young flounders, kept in the laboratory at Plymouth and "regularly but not very liberally fed", grew from a length of 1·25 cm. in May 1890, to lengths varying between 5·0 and 19·0 cm. in May 1891. Blegvad (1932) showed a correlation between the growth rate of O-group flounders and the temperature of the sea, the length of the fish increasing with an increase of temperature; he found, too, that growth is comparatively small in areas where young fish assemble in large numbers. Lübbert and Ehrenbaum (1936) also observed that the rate of growth varied with the density of the population.

Flounders less than 7 cm. in length were never taken in the tuck-net. This was not due to the escape of the smallest fishes through the meshes of the net, for many plaice and dabs of 3 and 4 cm. were caught during the summer months. There are three possible explanations of the absence of small flounders from the tuck-net catches:

(i) That the young fish do not enter the estuaries until nearly a year old.

(ii) That the young fish usually haunt grounds where the tuck-net cannot be worked.

(iii) That the young fish have a pelagic habit and so avoid capture in a net which sweeps along the river bottom.

It is improbable that the first explanation is the true one, for Mr E. Ford tells me that he took some very small flounders in the Tamar and Lynher in a fine-meshed net used for the capture of young herring. The true reason is probably in the second or third suggestion, or in a combination of them. Be the cause what it may, O-group flounders were almost completely lacking in the material available for the study of growth.

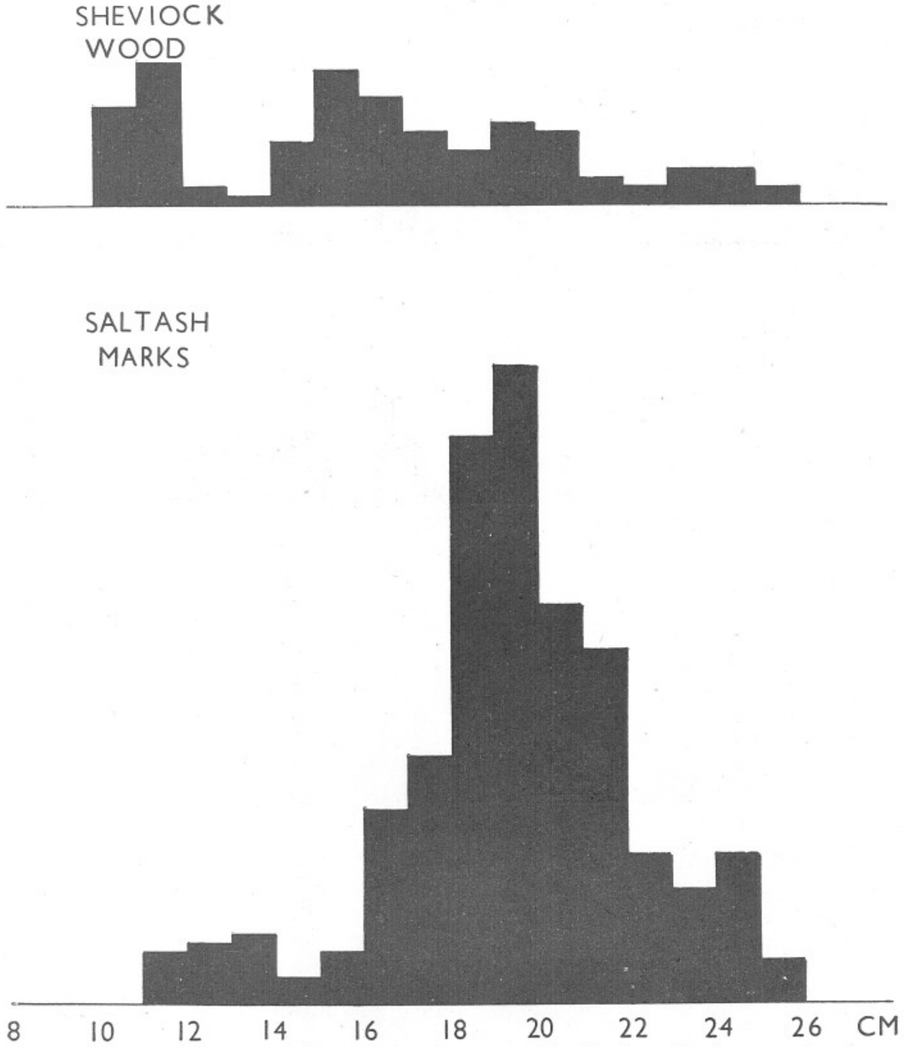

Fig. 2. *Pleuronectes flesus*; length-frequency distributions, October 1937.

There were two other sources of difficulty in the adequate sampling of the flounder population:

(i) During the summer months it was difficult to catch any flounders at all. Only on the Sheviock Wood ground were flounders numerous during the hot weather; and it proved to be impossible to arrange regular summer work there. A 16 ft. tide was needed to work at Sheviock, and the local fishermen, being much occupied with their salmon-nets, were rarely available for work with the tuck-net.

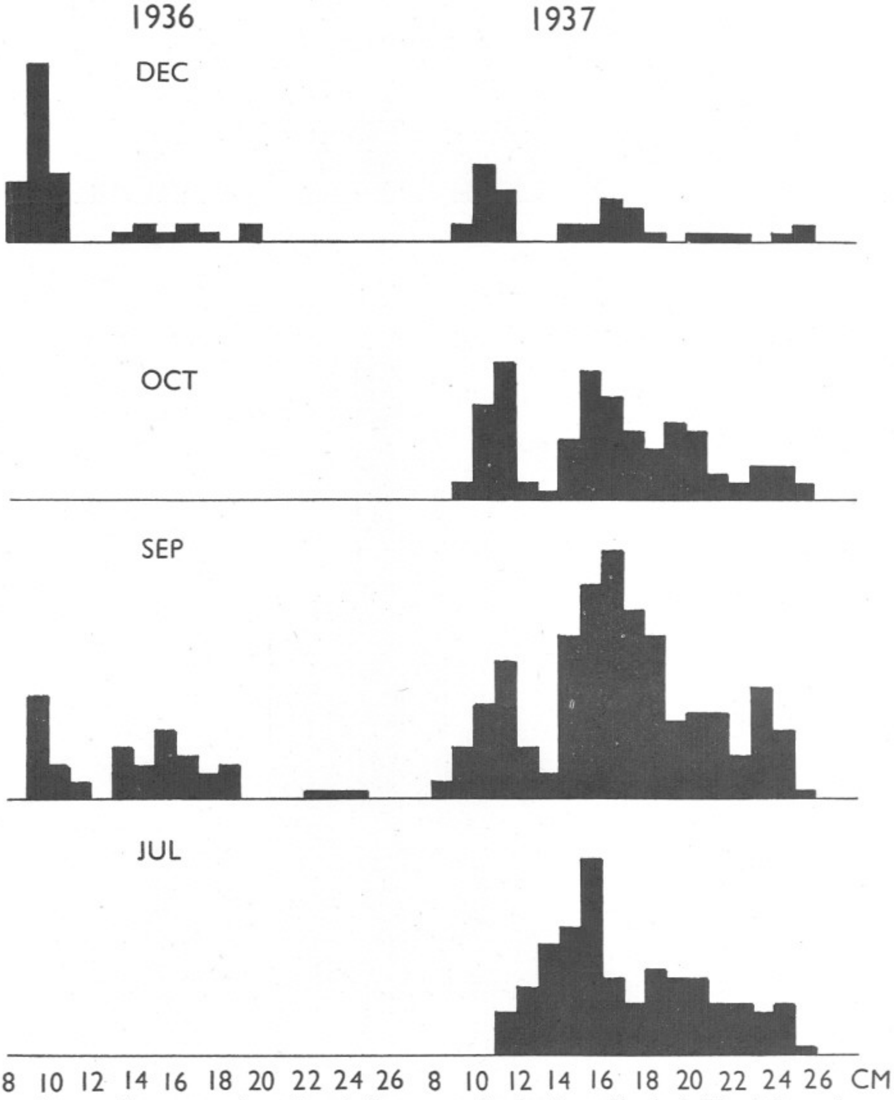

Fig. 3. *Pleuronectes flesus*; length-frequency distributions, Sheviock Wood Grounds.

(ii) The distribution of the fish was not uniform throughout the estuaries at any one time (Fig. 2) and the distribution of fish on one ground changed in the course of the year (Fig. 3). On the Saltash "marks", where the majority of the flounders were obtained, the smaller length groups were not strongly represented.

Histograms were prepared to show the length-frequency distribution of the flounders in each month of 1936 and 1937. It was found that only one modal peak consistently emerged—that of the I-group fish (Figs. 2–5). Other modes were rarely well marked so that at best the monthly histograms only suggested the possible lengths of the older year-groups. Between 14 and 24 cm. a single peak may sometimes emerge but it will be shown later that this contains at least two and perhaps three modes. Above the length of 24 cm. fish are not present in sufficient numbers to permit the deduction of year-groupings.

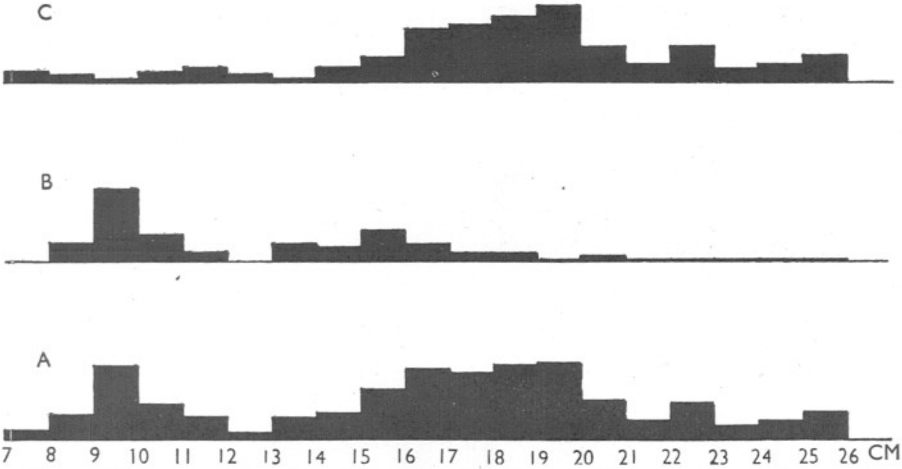

Fig. 4. *Pleuronectes flesus*; length-frequency distributions, September–December 1936

Marking experiments carried out in the autumn of 1937 showed that the Tamar flounders do not grow during the last third of the year: the length-frequency distributions for the months September, October, November and December may, therefore, be lumped together (Figs. 4, 5) in order to increase the absolute numbers of fish in one histogram. In Fig. 5 *a* "Total Fish for Autumn 1937", the modal peak of the I-group stands out clearly at approximately 11·5 cm. Above 14 cm. it would be unwise to attempt to define the position of any mode. In Fig. 5 *b*, on the other hand, "Sheviock Wood" only, there is the indication of a second modal peak at about 16 cm.: it is suggested that this mode represents the II-group. In the histogram for Saltash only (Fig. 5 *c*) this II-group mode is missing, but a modal peak is found at approximately 19 cm. Movements of marked fish exclude the possibility that there are separate populations on the two fishing grounds, growing at different speeds. It is, therefore, not unreasonable to suggest that this 19 cm. mode represents the III-group fish. Fig. 4, "Autumn, 1936", is similar to Fig. 5, though for a smaller number of fish. The I-group stands out clearly, though the flounders are nearly 2 cm. smaller than in 1937. The II-group is marked at Sheviock, the III-group at Saltash.

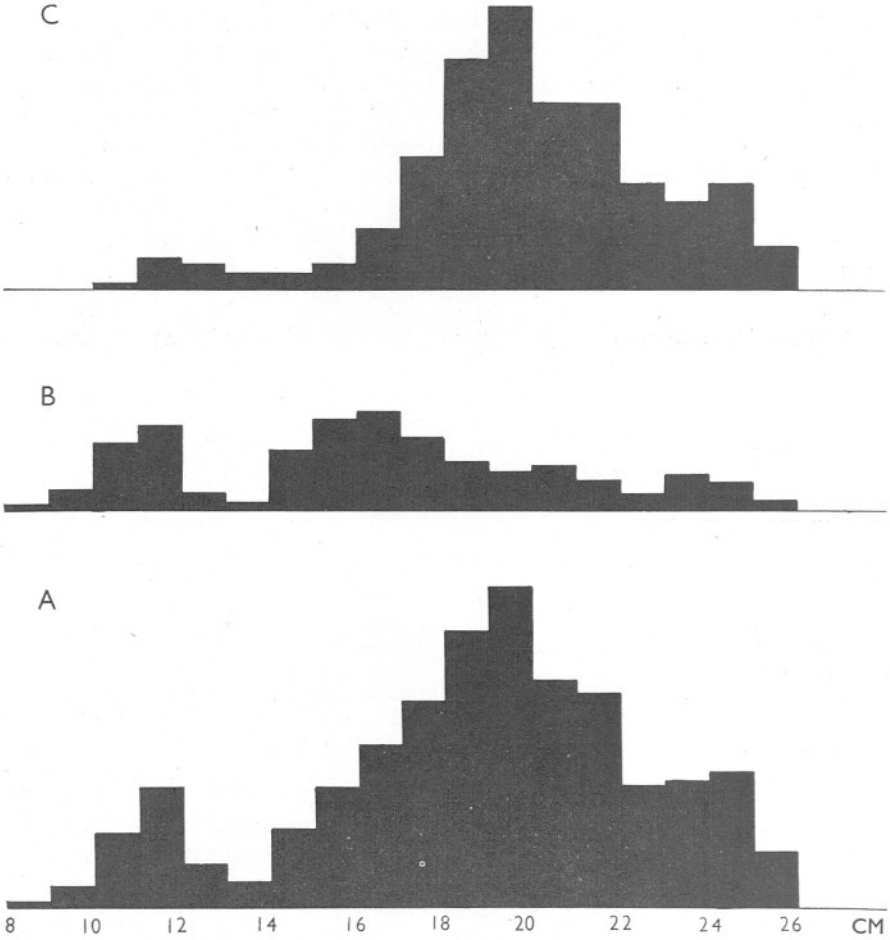

Fig. 5. *Pleuronectes flesus*; length-frequency distributions, September–December 1937.

From Figs. 4 and 5 it is impossible to tell the size or number of the year-groups above III. From the length-frequency histogram for April 1936 and April 1937 (Fig. 6) it may be suggested that those fish of the IV-group which still remain in the river are between 20 and 21 cm. in length. It must be admitted that no other monthly histogram shows this so clearly though some of them hint at it.

From the evidence of Figs. 4 and 5, coupled with such supplementary information as may be obtained from the monthly histograms, the following view of the year-grouping of the Tamar flounders is tentatively put forward:

Autumn. Period of No Growth

Year-group	Age years	Length, 1936 cm.	Length, 1937 cm.
O	½	..	..
I	1½	9·5	11·5
II	2½	15·5	16·0
III	3½	(19·0)	19·5

These figures are comparable with year-groupings of flounders on the southern coasts of Sweden (Molander, 1932):

	Plymouth Autumn		Ystad, Sweden		
Year-group	1936 cm.	1937 cm.	Sept. 1929 cm.	Oct. 1930 cm.	Nov. 1931 cm.
O	..	..	..	..	...
I	9·5	11·5	8·4	9·1	10·3
II	15·5	16·0	14·4	12·7	17·4
III	(19·0)	19·5	18·8	19·5	21·8

It is probable that the Plymouth flounders do not grow much until the summer, for the winter fast is not ended until April, and the length-frequency histograms for the earlier months of the year give no indication of an increase in length of the I-group during the first four months of 1936 or of 1937.

The approximate length groupings in April are:

Year-group	Age yr. mon.	Length cm.
O	0 11	..
I	1 11	11·5
II	2 11	15·5
III	3 11	18·0
IV	4 11	(20·5)

That the III-group has a smaller average length than in October, when the fish were some six months younger, is doubtless to be explained by the fact that the larger fish of this group have become sexually mature and gone down to the sea. The figure for the IV-group is probably low for the same reason.

These April figures are consistently smaller than those given by Lübbert & Ehrenbaum (1936) for April in the Elbe: on the other hand, they agree well with age groupings found by Kändler (1932) on the Oder Bank in the Baltic.

			Oder Bank	
Year-group	Tamar 1936 and 1937 cm.	Elbe cm.	1925 cm.	1929 cm.
O	..	8·0	4·4	4·4
I	11·5	14·0	11·0	11·1
II	15·5	19·0	15·5	16·3
III	18·0	24·0	19·35	20·1
IV	20·5	..	21·2	23·0

During 1937, many pairs of flounders otoliths were examined, in order to obtain evidence on the year grouping of the fish which would act as an independent check on the conclusions based on length frequencies. It was found that a considerable proportion of the otoliths—as much as 30% of a sample—had to be rejected as uncertain, either because it was impossible to be sure of the number of rings in the "core" or because there was a discrepancy between the two otoliths of a pair. This possibility of the absorption of one or more opaque rings in the "core" makes it necessary to use great caution in the determination of the year grouping of small numbers of fish by the examination of otoliths. The year grouping by the number of opaque rings was calculated for April 1937 and* for October–December 1937, and then compared with the lengths of the year-groups as previously determined by the study of histograms.

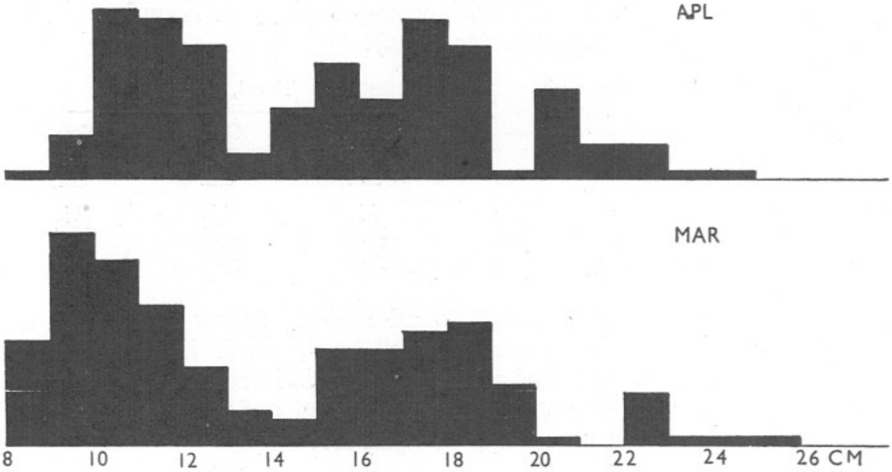

Fig. 6. *Pleuronectes flesus*; length-frequency distributions, March and April 1936 and 1937.

	April		Autumn 1937	
Year-group	Histogram 1936 and 1937 cm.	Otoliths 1937 cm.	Histogram cm.	Otoliths cm.
I	11·5	11·4	11·5	11·44
II	15·5	14·5	15·5	17·24
III	18·0	18·2	19·5	20·7
IV	20·5	..	..	..

The agreement between these two sets of figures is sufficiently close to suggest that the approximate age groupings determined from the histograms are substantially correct.

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* And by the number of summer zones.

Feeding Habits.

The digestive tracts of 1146 estuarine flounders were examined—462 in 1936 and 684 in 1937—and monthly summaries were made of the contents. These summaries are reproduced in Table I, the food organisms being enumerated on a simple basis of occurrence. The diet of the flounder is also shown graphically in Fig. 7. It will at once be seen that crustaceans form the bulk of the food: and within this principal item of diet three species are of paramount importance, contributing more than 80% of the recognizable crustaceans in each year. *Crangon vulgaris* formed 42% of the recognizable

TABLE I. *PLEURONECTES FLESUS*: MONTHLY OCCURRENCE OF FOOD ORGANISMS

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	12	23	52	26	4	1	6	7	36	43	46	48
Pleuronectes sp.	..	..	..	..	..	..	..	..	..	..	..	..
Gobius minutus and *Gobius* sp.	..	..	..	..	..	..	1	..	3	..	2	3
Clupea sp.	..	..	..	..	..	..	..	..	..	..	..	..
Teleost remains	..	..	..	..	..	..	..	..	..	..	1	1
Hydrobia ulvae	..	..	..	..	..	..	..	..	..	..	..	..
Littorina littorea	..	..	..	..	..	..	..	..	..	..	..	..
Cardium edule	..	..	..	..	..	..	..	..	..	..	..	..
Scrobicularia plana	..	..	6	..	..	..	..	..	..	..	..	..
Lamellibranch remains	..	..	..	1	..	..	..	..	..	..	..	1
Chironomid larvae	..	..	..	..	..	..	..	..	..	..	..	..
Cancer pagurus	..	..	..	..	..	..	..	..	..	..	..	..
Carcinus maenas	..	..	4	2	..	1	2	4	4	2	5	5
Leander sp.	..	..	..	..	..	..	..	..	..	..	..	..
Crangon vulgaris	7	3	6	..	..	..	3	4	20	27	44	31
Neomysis vulgaris	..	1	..	3	..	..	2	..	20	11	2	3
Macropsis slabberi	..	..	1	..	..	..	..	..	1	..	..	..
Praunus flexuosus	..	..	..	..	..	..	2	..	1	..	..	..
Schistomysis ornata	2	7	5	8	..	..	2	1	..	5	1	2
Mysid remains	2	6	6	7	..	..	..	..	30	21	..	2
Corophium volutator	1	..	4	..	..	..	..	1	..	..	..	..
Gammarus sp.	..	..	..	3	..	..	1	..	2	..	1	..
Melita palmata	..	..	1	..	..	..	..	..	..	..	..	..
Amphipod remains	..	1	3	..	..	..	..	..	..	..	..	..
Sphaeroma sp.	..	..	1	..	..	..	..	..	..	..	..	..
Gnathiid larvae	..	..	..	..	..	..	..	..	..	..	..	1
Isopod remains	..	..	..	..	..	..	..	1	..	..	..	..
Copepod remains	..	..	1	..	..	..	..	..	..	..	..	..
Crustacean remains	1	12	19	13	..	..	5	1	6	10	15	25
Oligochaete remains	..	..	..	..	..	..	..	..	..	..	..	..
Spirographis spallanzani	..	3	12	9	..	..	1	..	..	..	..	..
Melinna palmata	..	..	..	..	..	..	..	..	..	..	..	..
Sabellaria sp.	..	..	..	..	..	..	..	..	..	..	..	..
Cirratulid remains	..	..	1	..	..	..	..	..	..	..	2	..
Polydora ?hoplura	..	..	1	..	..	..	..	..	..	..	..	..
Glycera sp.	..	..	1	..	..	..	..	..	..	..	..	..
Nereis diversicolor	2	..	12	1	3	1	..	..	..	..	..	..
Polychaete remains	1	3	9	3	3	..	..	..	..	..	..	3
Zostera sp.	..	..	..	..	..	..	3	..	..	..	..	..
Fragments of vegetation	..	..	..	..	..	..	..	..	..	..	..	..

TABLE I (CONTINUED)

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	39	68	59	77	11	15	67	5	29	32	28	44
Pleuronectes sp.	..	..	..	..	..	1	..	..	..	..	..	..
Gobius minutus and *Gobius* sp.	2	..	2	1	..	1	..	2	..	1	..	7
Clupea sp.	..	..	..	..	..	..	1	..	..	..	..	..
Teleost remains	2	..	..	..	..	..	..	..	..	..	..	3
Hydrobia ulvae	..	..	..	..	2	..	..	..	..	..	..	..
Littorina littorea	..	..	..	..	..	1	..	..	..	..	..	..
Cardium edule	..	1	..	..	..	1	..	..	..	..	..	..
Scrobicularia plana	..	..	..	..	..	..	..	..	..	..	..	..
Lamellibranch remains	2	..	..	1	1	..	1	..	..	..	..	.
Chironomid larvae	..	1	..	..	..	..	..	..	..	..	..	..
Cancer pagurus	..	..	..	..	..	1	..	..	..	..	..	..
Carcinus maenas	1	2	5	1	2	7	4	1	..	..	1	4
Leander sp.	..	..	..	..	..	..	1	..	..	..	..	..
Crangon vulgaris	15	24	18	4	4	9	55	4	13	20	4	24
Neomysis vulgaris	..	2	2	..	..	3	80	..	30	1	..	1
Macropsis slabberi	..	..	..	..	..	..	..	..	4	..	..	..
Praunus flexuosus	..	2	..	2	..	..	9	..	..	..	..	..
Schistomysis ornata	10	12	8	30	2	2	..	..	1	..	4	2
Mysid remains	2	14	7	24	4	..	34	..	21	2	1	1
Corophium volutator	..	..	1	2	..	..	..	..	..	1	6	9
Gammarus sp.	..	..	5	3	..	..	17	..	1	..	2	2
Melita palmata	..	..	..	..	..	..	..	..	..	..	..	..
Amphipod remains	1	..	..	..	..	..	2	..	..	..	..	3
Sphaeroma sp.	..	4	..	..	1	..	..	..	..	..	1	..
Gnathiid larvae	..	..	..	..	..	..	..	..	..	..	..	..
Isopod remains	..	..	..	..	..	..	..	..	..	..	..	..
Copepod remains	1	2	1	..	..	..	..	..	..	..	1	..
Crustacean remains	12	28	24	33	4	5	4	1	6	14	6	14
Oligochaete remains	..	..	..	..	..	..	..	..	..	..	1	..
Spirographis spallanzani	..	4	4	11	2	..	..	..	..	..	..	..
Melinna palmata	1	..	..	..	..	..	..	..	..	..	..	..
Sabellaria sp.	..	..	..	..	..	..	..	..	..	1	1	..
Cirratulid remains	..	..	1	1	..	..	..	..	..	..	1	1
Polydora ?hoplura	..	..	..	..	..	..	..	..	..	..	..	..
Glycera sp.	..	..	..	..	..	..	..	..	..	..	..	..
Nereis diversicolor	2	5	10	2	5	5	9	5	..	..	..	1
Polychaete remains	5	7	6	6	..	2	12	1	..	2	7	2
Zostera sp.	..	..	..	..	..	..	..	..	..	..	..	..
Fragments of vegetation	2	..	..	..	..	..	..	..	..	1	..	1

species in 1936, and 32% in 1937. Mysidacea were the other important crustacean food, contributing 43% of the recognizable forms in 1936, and 52% in 1937; and in each year just over 90% of the identifiable mysids belonged to two species, *Neomysis vulgaris* and *Schistomysis ornata*. Of the polychaetes only *Nereis diversicolor* and *Spirographis spallanzani* were of much importance as articles of diet. The remains of *Scrobicularia plana* were merely the tips of the siphons neatly nipped off; one fish contained twenty-nine. *Gobius minutus* and other small teleosts and *Carcinus maenas* were eaten in numbers by the largest fish, but were too big to form a valuable supply of food for the bulk of the population.

Patterson (1904 *a*, 1906, 1907) laid emphasis on the importance of shrimps in the diet of the flounders of Breydon Water, and also mentioned molluscs, young herrings and *Ulva lactuca* as foods. Scott (1895) found that the food of flounders on the Lancashire coasts was made up of 33 % annelids and 60 % crustaceans in 1894, but entirely of annelids in 1895. Five years later, Ascroft (1900), in the same area, found that "the food of the Flounder consists principally of worms and crustacea. It is very fond of *Corophium longicorne*—it also eats a quantity of bivalve molluscs and freshwater snails." Murie (1903) in the Thames estuary found that the flounders were feeding on crustaceans and polychaetes, with some bivalves.

Of workers on the fish of continental waters, Lübbert & Ehrenbaum (1936) found that flounders in the mouth of the Elbe fed largely on crustaceans, supplemented by gastropods, mussels, larvae of aquatic insects, polychaetes and such small fishes as *Gobius*, *Ammodytes* and clupeoids. In general this dietary is very similar to that of the Tamar fish. In the fresh waters of the Elbe (Stadel, 1936) tubificid worms and sphaeriid molluscs were the food of flounders over 15 cm. in length; while the smaller fish ate tubificids, with some copepods in summer. In the Baltic, Blegvad (1932) found that the O-group flounders fed largely on crustaceans, the I-group on crustaceans and chaetopods and the II and older groups chiefly on molluscs, with some crustaceans and comparatively few annelids. In the Dybsø Fjord, Larsen (1936) showed *Cardium exiguum*, *C. edule*, *Idotea viridis* and *Gammarus locusta* to be the food organisms most commonly occurring: the flounders of this fjord ate no polychaetes.

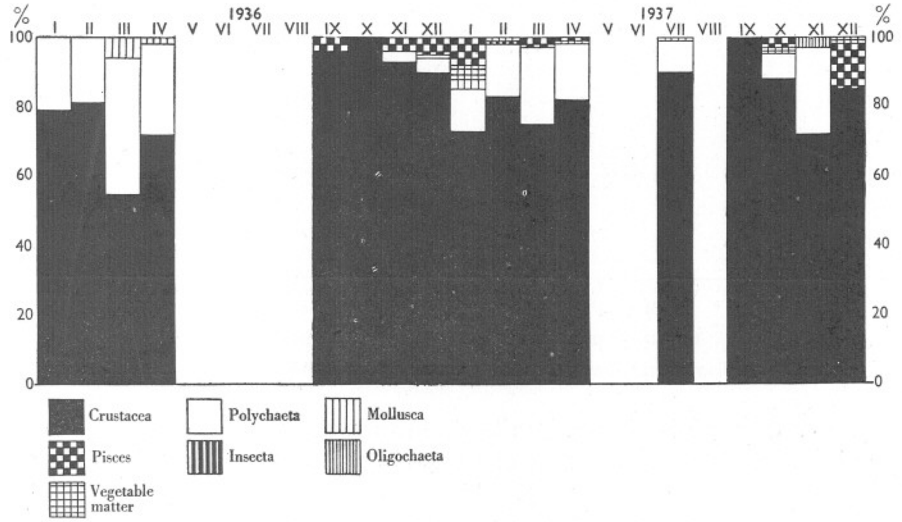

Fig. 7. *Pleuronectes flesus*; monthly variations in diet. (No figures are given for months in which less than 25 fish were examined.)

In the winter there is a marked period of fasting (Fig. 8). Feeding does not cease entirely, but the number of fish containing food drops from 90–100% in September to 30–40% in January. In the winter of 1937–8 the fast began earlier than in the preceding year, for in November 1937 only 44% of the fish contained food as compared with 78% in the same month of the previous winter. The difficulty of obtaining fish in the early summer makes it impossible to say when the fast is ended, but the fact that in April 1937 80% of a sample of ninety-nine flounders contained food, suggests that the period of full feeding must have been near at hand.

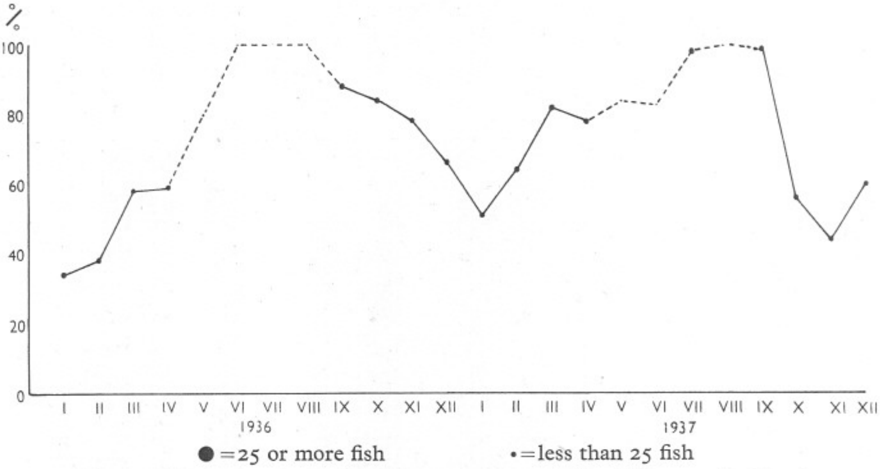

Fig. 8. *Pleuronectes flesus*; monthly percentages of fish which contained food.

The smaller fish are the first to begin fasting. In the winter of 1936–7 the arithmetic means of the lengths of the empty fish and of the whole sample were:

	Empty fish cm.	Whole sample cm.
Nov. 1936	15·7	19·3
Dec. 1936	15·5	16·7
Jan. 1937	18·1	17·9
Feb. 1937	17·0	16·8

The maturing fish continue to feed during the fast of the immature flounders which will remain in the estuary; the fast of the spawners will come later, when they have gone down to the sea to breed. In December 1937 and January 1938 ten out of thirteen ripening males and fourteen out of sixteen ripening females had fed, while only 59% in December and 44% in January of the whole population contained food. Stadel (1936) concluded that there was no pause in the feeding of the flounders living in the fresh waters of the Elbe, but he had examined no fish in January or February: moreover, he mentions that Ladiges had obtained evidence that there was a winter fast in flounders of 11–115 mm.

The fast of the spawning flounders in the sea is prolonged, and the cessation of feeding is more complete than within the estuaries. Of 140 mature flounders trawled off Plymouth between January and April, only three contained food: these were two females and a male caught in February 1937 with remains of crustaceans in their stomachs.

During the fast the gut may become tightly contracted and stained green with bile. In many fish, on the other hand, the intestine is filled with gritty, black mud, containing no remains of animal or fresh vegetable matter. This mud is not found in the stomach in any quantity, suggesting that it is not deliberately swallowed: it may be that particles of mud engulfed in the process of respiration tend to accumulate in the gut owing to a slowing down of peristalsis during the fasting period.

Breeding Habits.

Flounders are typical catadromous fish: they feed and grow in fresh and brackish waters until the onset of sexual maturity, when they go down to the sea to breed. In the Tamar and Lynher the gonads begin to develop in November; most of the ripening fish leave the estuaries in January, and all have gone before the end of February. Off Plymouth they are caught at sea from the latter half of January until the end of April, being trawled in 20–30 fathoms of water on the "Rame Mud", "Corner" and "Looe-Eddystone" grounds. Cunningham (1896) has remarked that flounders are rarely found in more than 30 fathoms of water. Some spent females return to brackish water, but no spent males have been taken within the estuaries. Fish which remain in the sea after breeding feed and grow and come again to the spawning grounds, but it has proved impossible to trace their distribution during the period of recovery and growth. Captain Lord of s.s. *Salpa* tells me that flounders are rarely trawled out of the breeding season, except for an occasional fish taken after heavy autumn floods. It may be that the sea fish move close inshore after spawning, for a long-line fisherman in Whitesand Bay told me that he caught some flounders on the sandy shallows there. Ehrenbaum (1911) found a migration of spent flounders from the Bornholm deeps towards the Pomeranian coast.

The arithmetic mean length of the sea-caught female flounders in 1937 was 34·6 cm., that of the mature females caught in the estuaries in the winter of 1936–7 only 27·9 cm. If all the spent female flounders returned to brackish water after each breeding season, it might reasonably be expected that the arithmetic mean lengths of the ripening fish within the river in any winter, and of the mature fish in the sea outside in the following spring, would be approximately the same. The actual difference of 6·9 cm. suggests that only a small proportion of the spent females do, in fact, return to the estuaries: this is in accordance with the findings of Schnackenbeck (1926) and Ehrenbaum (1929). The smallest mature female taken measured 21·2 cm. So far as otolith readings may be trusted, the female flounders of the Tamar and Lynher become mature in their fifth winter.

The spawning period is apparently a long one. The walls of the ovary often represent a speckled appearance, for little knots of clear, ripened eggs lie in the opaque mass of less developed ova. A similar state has already been described by Steven (1938) in the mackerel, *Scomber scombrus*. As the number of the ripe eggs increases they collect in the anterior part of the gonad, which projects into and almost fills the body cavity, pressing the empty flaccid gut against the septum transversum. At this stage the anterior, lower part of the ovary is uniformly translucent, the posterior part uniformly opaque. The capture of half-empty females also suggests that there is not a single, continuous oviposition, but rather a succession of spawnings as batches of ripe eggs are accumulated. A completely spent female has been caught in the middle of February and a fish still very full of eggs in mid-April. Russell (1930, 1937) has found post-larval flounders off Plymouth in March, April, May and June.

Male flounders mature in their fourth and fifth winters, the two age groups contributing more or less equally to the recruitment of the spawning stock. The Plymouth fish not only grow more slowly than those of the Elbe, but mature later, for Ehrenbaum (1929) found that most of the males in German waters became sexually mature at the end of their third year. The arithmetic mean length of the mature male river fish in the winter of 1936–7 was 23·5 cm., the smallest measuring 18·2 cm. and the largest 27·4. The mean length of the sea-caught males in the spring of 1937 was 28·05 cm. No spent males were caught in the estuaries; and the difference in the mean lengths of the sea-caught and river-caught fishes suggests that there is no extensive return to brackish waters after spawning.

The otoliths of sea-caught flounders seem to be even more unreliable than those of river fish in the determination of the age of individuals. It may be that the strain of spawning, and the change from an estuarine to a marine life so alters the metabolism of some fish that the regular laying down of summer and winter rings ceases or is at least interrupted. The largest number of winter rings found in any fish is seven.

Changes in Condition through the Year.

During 1937 the condition factor, k, was calculated for each flounder from the formula

$$k=\frac{W\times 1000}{l^3},$$

where W = weight in g., l = length in cm.

The variation in condition from month to month is shown in Figs. 9 and 10,

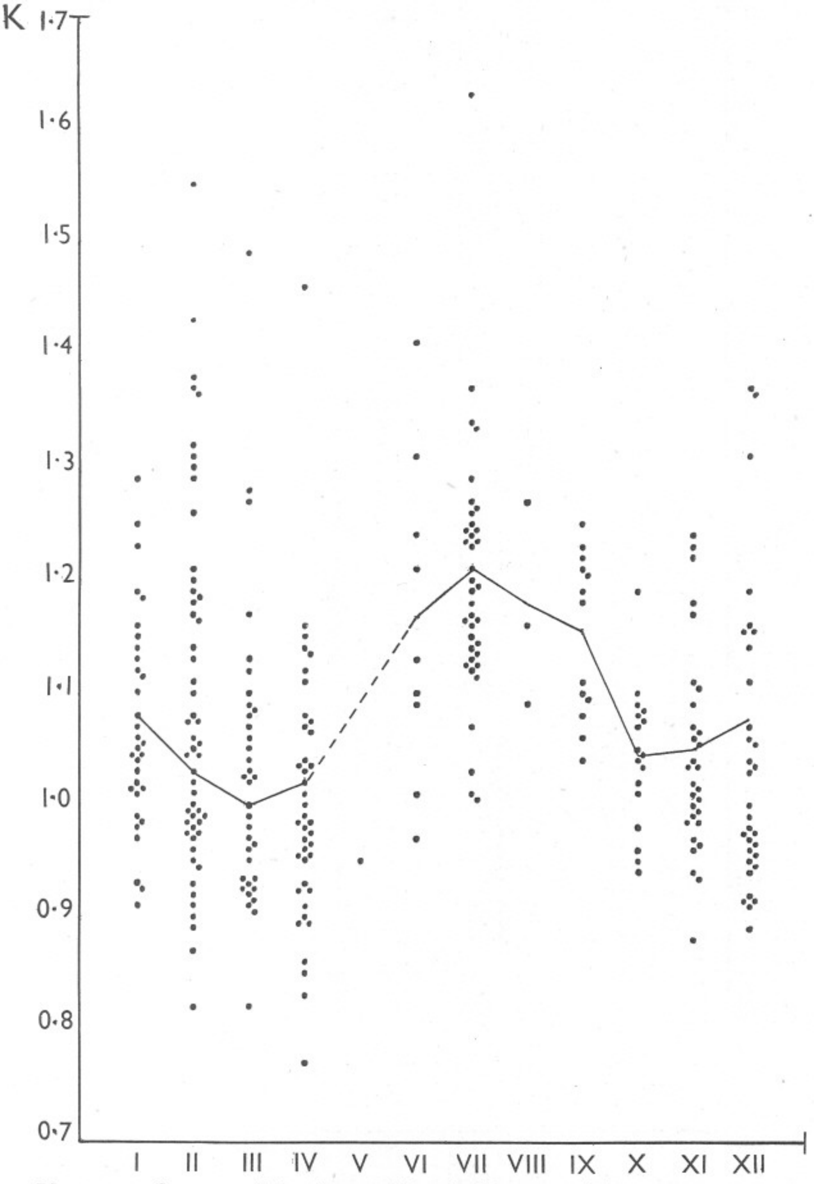

Fig. 9. *Pleuronectes flesus*; condition factors of female fish, 1937. (The mean condition factors for each month are joined by a line.)

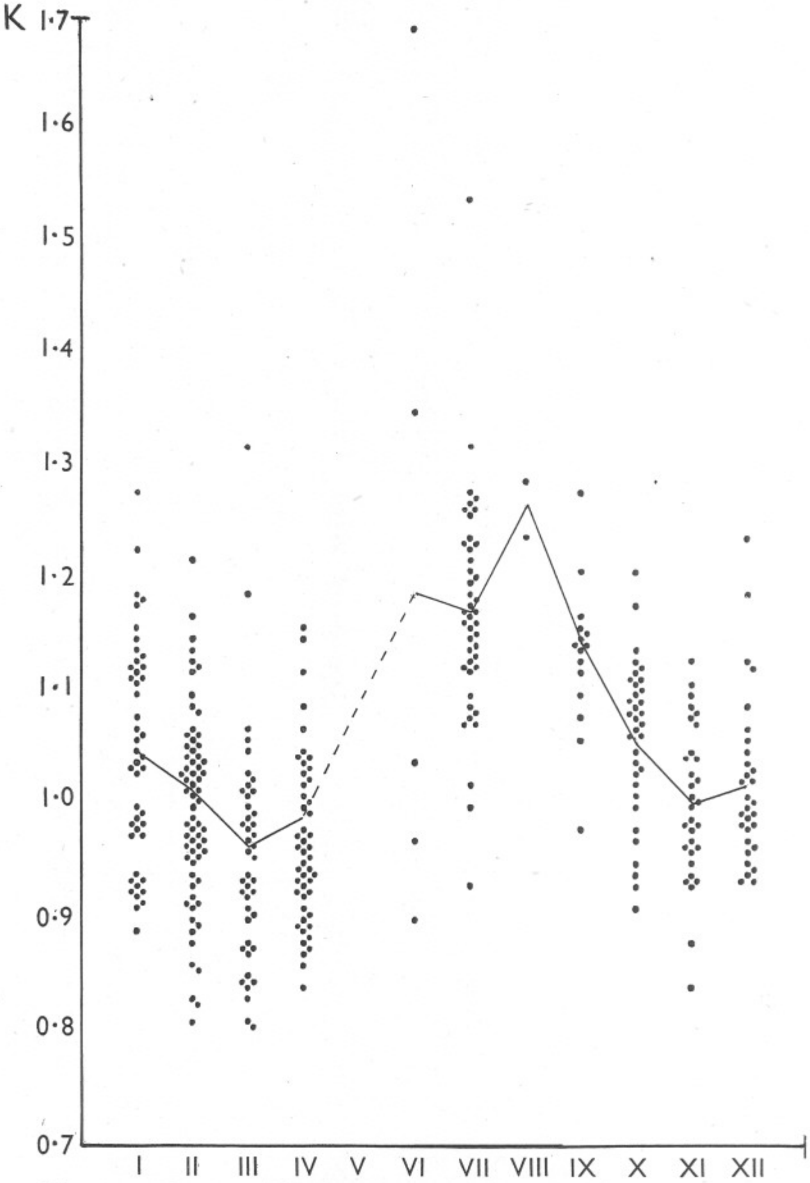

Fig. 10. *Pleuronectes flesus*; condition factors of male fish, 1937. (The mean condition factors for each month are joined by a line.)

while the following table shows the mean monthly condition factors for each sex.

Month	*k*, females		*k*, males	
1937	River	Sea	River	Sea
Jan.	10·88	..	10·46	..
Feb.	10·28	13·33	10·15	10·45
Mar.	9·93	12·05	9·63	9·58
Apr.	10·02	10·58	9·91	9·25
May	(9·57)	..	..	..
June	(11·7)	..	(11·95)	..
July	12·03	..	11·77	..
Aug.	(11·75)	..	(12·75)	..
Sept.	11·56	..	11·45	..
Oct.	10·45	..	10·68	..
Nov.	10·54	..	10·05	..
Dec.	10·76	..	10·23	..

Flounders of both sexes were poorest in condition in March, towards the end of the winter fast: there was a rapid improvement in the early summer and both sexes were at their best about July. In September they had begun to go back, although all were still feeding. With the beginning of the fast in October the decline in condition became more rapid. The continued feeding of the ripening fish through the last months of the year tends to raise the mean condition factor until the time comes for the spawners to go down to the sea. This is especially marked in the females, whose weight increases enormously with the development of the ova. The difference in *k* of sea-caught and river-caught fish in February and March clearly illustrates this. As the spawning proceeds the weight of the females rapidly decreases, until by midsummer the poorest of the river flounders are the light-weight fish which have returned from the sea.

Ripening males do not show so great an increase in weight in comparison with the immature fish. The strain of spawning seems to tell heavily upon them, for spent fish caught at sea are among the worst conditioned fish examined. It may be that spawning is a greater strain on the males than on the females, with the result that they die younger. It has already been shown that the larger breeding fish are females.

Daily Movements.

It is not possible to make equally good catches of flounders at all hours of the day. On some grounds several shots may be made in the morning or at midday, and only a dozen fish will be captured. In the late afternoon the fishing will be no better, until the time comes when the daylight begins to fade. A shot made then will sweep up three or four score of fish. On the Butterfly ground, just above Saltash, I have made hauls over the same area, separated by only a quarter of an hour: the first yielded no flounders at all; the next, made at the "change of light", contained seventy fish, and one made immediately after about fifty. There must have been a sudden and rapid inshore movement of the flounders. There is great competition among the fishermen for the right of making the first haul at "change of light" on a good dusk ground; the first boat may arrive half an hour before sunset. When more than one boat is working on a ground of limited extent, shots are made in turn, and the later arrivals must not start work until the first crew have hauled their net. The flounders do not stay along the tide edge all night: the fishing at midnight on the best of the dusk grounds is little better than at midday. When surface drift nets are set for the herring at dusk, flounders are frequently taken in them. In October 1937 a marked fish was caught by its mark in a surface net, some 50 ft. (15 m.) above the bottom. The flounder does not at any time limit itself to the bottom in its search for food—Patterson (1904*a*) has remarked on its activity in shrimp hunting, often near the surface; but this evening movement of so many fish up the slopes of the mud-banks and towards the surface, with the subsequent scattering during hours of darkness, is very reminiscent of the following of an optimum of illumination by planktonic organisms (Russell, 1926). It may be that the fish are moving under the influence of the same stimulus, or combination of stimuli, that orders the daily movements of so many small invertebrates.

"*Left-Sided*" *Fish.*

The flounder is peculiar among pleuronectids in the regular occurrence of left-sided fish, or "flukes", that is, fish in which the eyes have moved to the left side on metamorphosis instead of to the right, and in which the left side is pigmented and the right side colourless. Of 2363 flounders examined in 1936–7, 126 fish (5·33%) were left-sided. Duncker (1899) investigated 1120 fish from the Tamar and found the proportion of left-sided specimens to be 5·36%. The close agreement of these two figures, separated by an interval of nearly 40 years, is striking and suggests that the proportion of "flukes" may be a racial character of a population of flounders. Lübbert & Ehrenbaum (1936) state that in the Baltic about 35% of the flounders are "flukes" and that the proportion in the Black Sea is scarcely half that figure. They put forward the suggestion that the proportion of left-sided fish increases from the south to the north of the species' range; but the consistently low percentage of "flukes" in the west of England seems to be against this view.

Pleuronectes limanda L., the Dab

On the fishing grounds nearest to the sea, dabs are the most numerous of the flatfishes: and they are entirely confined to these seaward grounds. Flounders will press upstream into fresh water, young plaice, brill and soles are regularly found in the brackish conditions of the Sheviock Wood ground, but the dabs remain in the essentially marine environment of the Hamoaze and the neighbourhood of Saltash. (Professor de Beaufort, of Amsterdam, informs me that in the Zuyder Zee, before the construction of the enclosing dykes, dabs showed a similar distribution, being found in the marine conditions near the open sea, and never venturing so far into brackish waters as the plaice were wont to do.)

Growth and age.

The growth of the dab during its estuarine life was studied by means of length-frequency histograms, by the calculation of arithmetic mean lengths of discrete length-groups and by some examination of otoliths.

In the winter of 1935–6, the dabs showed a group of small fish with a modal length of about 6 cm., and a second, less compact, group with a modal length of 13 cm., and a length dispersion from 8·0 to 23 cm. (Fig. 11 *a*). In March 1936 the larger group was suddenly very much reduced in numbers, so that the smaller fish, with a modal length of 6–7 cm. came to dominate the catches (Fig. 11 *b*). Through the spring and early summer this one length-group was caught; the average length increased. At the same time the dispersal of the lengths became greater. In July 1936 a new length-group appeared (Fig. 11 *c*), with an arithmetic mean length of 3·86 cm. By October 1936 this length had increased to 5·7 cm., while the fish in the preceding group were mostly between 12 and 17 cm. in length (Fig. 11 *d*). Neither the "small" nor "large" groups showed marked increase in length through the winter of 1936–7 (Fig. 11 *e*). In March 1937 the reduction of the larger group was again seen (Fig. 11 *f*), and the story of the recruitment in summer, and increase in length and length-dispersal of the preceding group was repeated. In 1937 the recruitment took place in June, and was on a much smaller scale than in the previous year; the small fish were only well represented in June and December (Figs. 11 *g*, *h*).

The study of the growth of the dab was made easier by the fact that it was possible to catch the juvenile fish while they were still very small, and to follow their development until they were about a year old. To some extent the difficulty of fixing modes in length-frequency histograms was encountered, but the comparatively short period spent by most dabs in the estuaries made this source of uncertainty of considerably less importance than in the flounder.

Examination of Fig. 11, with its repeated story of the sudden reduction of the larger of two size groups, suggests the possibility that the majority of the Tamar dabs remain for a little under two years in the estuaries and then go down to the sea.

The development of a year-group can best be traced in the growth of the recruitment of 1936. In that year post-larval dabs were most numerous off Plymouth in May (Russell, 1937), so that the young fish caught in the estuaries in July were about two to three months old; the arithmetic mean length of the year-class was then 3·86 cm. This length group was quite

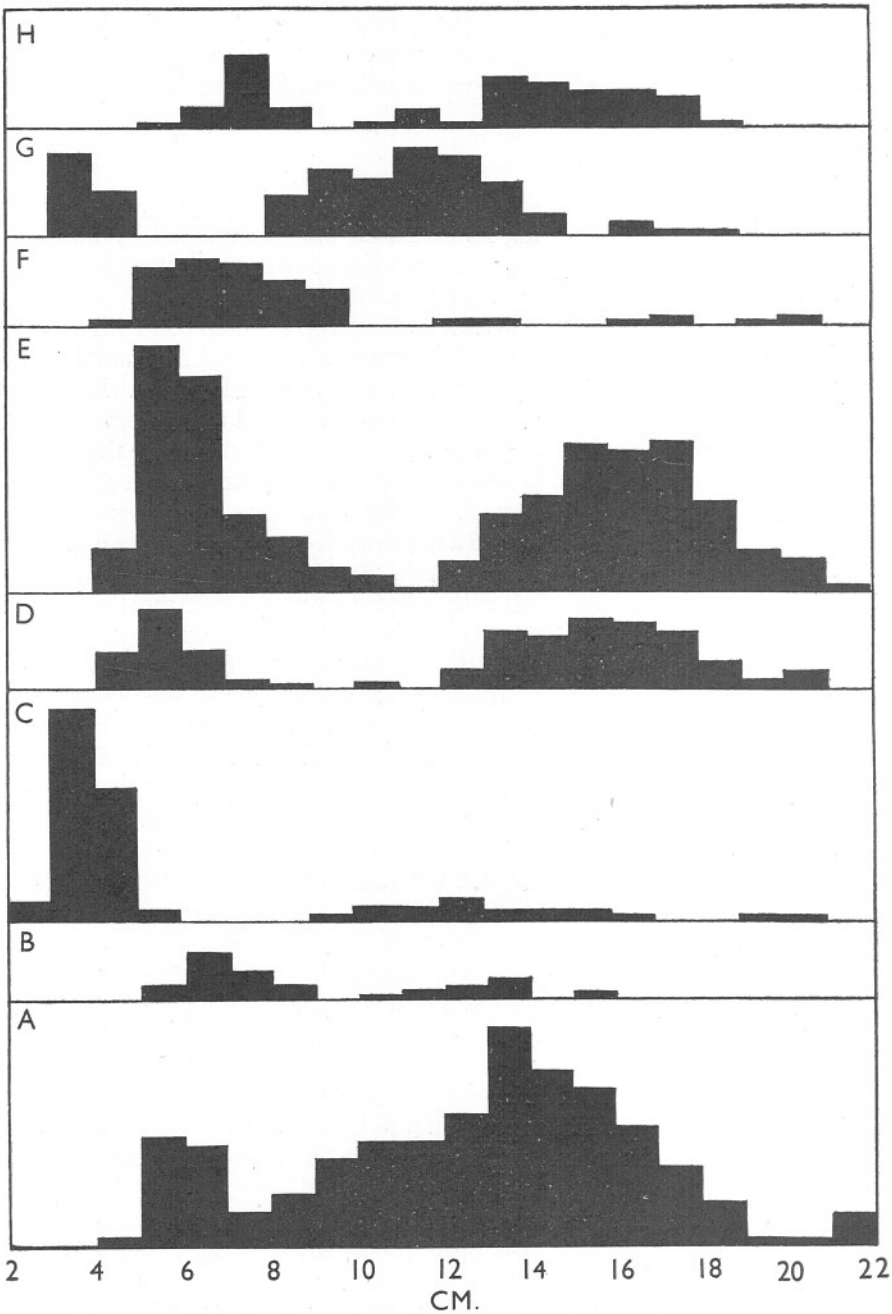

Fig. 11. *Pleuronectes limanda*; length-frequency distributions. *A*, November 1935–February 1936; *B*, March 1936; *C*, July 1936; *D*, October 1936; *E*, November 1936–February 1937; *F*, March 1937; *G*, June and July 1937; *H*, December 1937.

distinct from that of the preceding classes until April 1937. The growth of these O-group fish in their first year can, therefore, be shown below:

	1936						1937		
Month ...	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Arithmetic mean length in cm.	3·86	4·02	5·0	5·7	6·2	6·41	6·24	7·14	7·2

It will be seen that there is little increase in length in midwinter.

The 1937 class fish were scarcer than those of 1936; only twice during the first nine months of their O-group year were adequate samples obtained, in late June, and in December 1937 (Figs. 11 *g*, *h*). In June they had an arithmetic mean length of 3·82 cm.; by December they had grown to 7·43 cm. This was just 1 cm. longer than the preceding O-group in that month, and also larger than the O-group fish of the 1935 class, which in December had a mean length of 6·5 cm.

It will be seen (Figs. 11 *b*, *f*) that all the fish of the larger year-group do not go down to the sea in spring. After the summer growth period has begun it is no longer possible to distinguish I-group fish from the laggards of the II-group. It is of course probable that the larger fish of the "big" length-group will belong to the II-group—there is some evidence for this from examination of otoliths—but the distinction can no longer be made from length groupings. On the other hand, a large year-class will, as I-group fish, strongly dominate the "big" length-group, although they do not entirely compose it. In June and July 1937, the mean length of the "big" group was 11·65 cm.; by December it had increased to 14·4 cm. These figures are, at least, rough approximations to the growth of the I-group fish during their second year of estuarine life.

In the autumn of 1937 some dab otoliths were examined. They proved to be more legible than those of flounders, showing the broad, well-marked summer zones. Samples of 3-zone fish were always small, but in general they were longer than the 2-zone class. The arithmetic mean length of all 3-zone fish examined between September and December 1937, was 19·94 cm. The arithmetic mean lengths of the 2-zone, which usually formed the bulk of the samples, were:

Month	Arithmetic mean length cm.
Sept.	13·93
Oct.	14·83
Nov.	14·97
Dec.	15·0

The very slight length increment in the winter months suggests that growth ceases during the fasting period.

Only one good sample of 1-zone dabs was obtained: this was in December 1937 the only month after June in which the O-group, as determined by length frequencies, was well represented. The arithmetic mean length of these 1-zone fish was 7·7 cm. A single 4-zone dab was examined—a male of 26·9 cm., with testes showing no sign of ripening—on December 8.

The close correspondence between the average mean length of the O-group fish as determined by length frequencies (7·43 cm.) and by examination of the otoliths (7·7 cm.) and the agreement between the mean lengths of the 2-zone or I-group fish (15·0 cm.) and the approximation reached on the basis of the dominance of I-group fish in the "big" group (14·4 cm.) allow the following summary of the growth of estuarine dabs to be put forward:

In their first year dabs grow to a length of 6–7 cm.: there is a slowing down of growth in the winter months. In their second year the fish reach a length of 14–15 cm., and growth again ceases in the fasting period. In this second year some males begin to mature (in December 1937 68% of the I-group males were ripening). Most dabs go down to the sea when just under two years old, but a few remain in the estuaries for a third summer, and grow to a length of 20–21 cm.

The growth of the dab in the Plymouth area is considerably greater than that found by Poulsen (1933) in Danish waters:

Length in cm.

		Danish Waters				
Year	Plymouth area	Horn's Reef	West Limfjord	Kattegatt	Belt Sea	Baltic
1	6–7	4	5	5·5	5	3·8
2	14–15	8·4	11	12·3	11·8	8
3	20–21	15·2	17	19·3	17·5	15

Poulsen found that the Danish dabs were "keen competitors" with plaice for their food. In the Tamar and Lynher, as described below, the dabs live largely on organisms exploited by no other fish: it may be that a greater abundance of available food accounts for swifter growth in these rivers.

At the run to the sea, the majority of the two-year-old males are sexually adult. In December 1937 68% of the I-group males had ripening gonads, a figure which corresponds closely with Poulsen's finding that in the Baltic 70% of the two-year-old males were mature. No I-group females were sexually mature: Wheeler (1924) states that female dabs off Plymouth become adult at the end of the third year, and Poulsen found first maturity at the same age in Danish waters.

Feeding Habits.

During their estuarine life dabs change their feeding habits as they grow. The small fish of the O-group feed almost entirely on crustaceans, juvenile mysids and copepods, but when they reach a length of 7 cm. (that is, when about 9 months old) small polychaetes begin to enter into their diet, and by the time they reach a length of 9 cm. marine worms form the bulk of their food.

Change in Diet of Dab with growth: 1936

Polychaetes and crustaceans, expressed as percentages of total occurrence of polychaetes + total occurrence of crustaceans.

Length cm.	Polychaetes %	Crustaceans %
19–24	69	31
18	80	20
17	68	32
16	75	25
15	69	31
14	65	35
13	85	15
12	72	28
11	57	43
10	57	43
9	58	42
8	40	60
7	43	57
6	22·3	77·7
5	20	80
4	..	100
3	..	100
2	..	100

For the rest of their life in the river mouths, a sabellid worm, *Spirographis spallanzani*, is the most important food organism. A dab which has been feeding on this polychaete is often distended with the crowns and pieces of the body. It seems that the worm is either extracted from its muddy flexible tube, or else the crown of tentacles and the anterior segments are bitten off short: pieces of the tube are uncommon in the gut. Steven (1930) found that the dab was in the habit of making a sudden snap at tubicolous polychaetes, its "pounce" being horizontal, rather than vertical as in the lemon sole (*Pleuronectes microcephalus*). Even when too small to take a whole crown, a 5 cm. dab will nip off a few spirographid tentacles. Some crustaceans are taken by the larger fish. In general, dabs eat a greater variety of food organisms than any other estuarine fish. Fig. 12 and Table II show the changes in the food of the dab from month to month. The predominance of crustaceans in the diet in July and August 1936 and August 1937, is due only in part to the exclusively crustacean food of the small O-group fish. The larger fish show a change in feeding habits during the summer, eating more shrimps and mysids, and fewer worms. The dab is the only fish in the estuary which feeds regularly on hydroids; when this food could be identified it was always *Gonothyrea loveni*. At times, small spawn masses were found in the guts of dabs: these could not be identified with any certainty, but seemed to belong to some mollusc, perhaps *Archidoris*, which is common in the lower tidal reaches. Dabs took some food which had fallen or been washed into the river from the land, a large slug, a spider, a hawthorn berry and seeds of grasses and an umbellifer were found in different fish.

In the Thames estuary, Murie (1903) found that "the dab's food is quite varied in character, depending somewhat on the time of year, and much on the locality where fished". He listed young shrimps, mysids, amphipods, crabs, worms, young mussels, *Sertularia*, echinoderms and fish as food organisms. Scott (1895) found that on the Lancashire coast, annelids and a smaller quantity of crustaceans were the most important foods of dabs less than 3 in., and that molluscs occurred in 20 % of the larger fish in 1894, and 34 % in 1895. He found that dabs took some echinoderms, but that plaice and flounder did not. Poulsen (1933) regarded the dabs of Danish waters to be "keen competitors" of the plaice, and on calculations based on the work of Blegvad estimated that molluscs made up 37 % of the food, annelids 21 %, crustaceans 12 % and "other groups" 30 %. He found that these "other groups" made up only 0·1 % of the food of the plaice, a fact which suggests a more varied diet for the dab.

The estuarine dabs fast to some extent in winter (Fig. 13): this fasting period is less regular than in the flounder and plaice. In 1936 there were two months, October and December, in which less than 60 % of the dabs examined contained food; but in November 79 % of the fish had been feeding. In 1937 only

TABLE II. *PLEURONECTES LIMANDA*: MONTHLY OCCURRENCE OF FOOD ORGANISMS.

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	19	51	31	42	47	4	52	27	34	23	30	22
Hydrobia ulvae	..	..	..	..	1	..	1	..	..	..	1	..
Carcinus maenas	..	1	..	..	2	..	2	..	..	..	..	..
Eupagurus bernhardus	..	..	..	..	1	..	4	..	..	1	..	..
Crangon vulgaris	..	1	..	..	3	1	5	1	2	8	15	1
Decapod larvae	..	..	..	..	..	..	..	3	..	..	..	..
Schistomysis ornata	..	1	1	4	7	..	3	3	1	1	..	1
Neomysis vulgaris	1	2	..	4	..	..	22	1	3	5	2	3
Mysid fragments	1	2	3	4	14	1	11	5	6	6	2	2
Pariambus typicus	..	..	..	..	..	..	..	2	..	..	..	..
Caprellid fragments	..	..	1	..	..	..	..	4	1	..	..	..
Gammarus locusta and *Gammarus* sp.	1	..	..	4	1	..	1	6	..	..	5	2
Corophium volutator	..	2	3	2	2	1	1	..	..	..	1	1
Amphipod fragments	..	2	1	2	6	..	2	3	..	2	3	2
Copepod fragments	1	4	15	11	..	..	5	14	1	1	2	4
Crustacean fragments	1	2	3	10	15	2	18	6	6	2	7	6
Spirographis spallanzani	14	56	24	40	61	2	26	..	34	14	13	15
Cirratulid fragments	..	..	1	..	..	..	..	..	..	..	..	..
Polydora sp.	..	1	1	..	..	..	..	..	..	..	..	..
Polychaete fragments	7	14	..	4	4	..	3	1	2	1	5	2
Oligochaeta indet.	..	..	1	1	..	..	..	..	..	..	..	..
Gonothyrea loveni	..	..	..	..	..	..	..	..	..	..	..	..
Hydroid remains	..	..	1	5	..	..	..	..	..	..	..	..
"Spawn"	..	..	..	..	2	..	1	..	..	..	..	..
Vegetable matter	..	..	1	..	..	..	1	1	..	..	..	2

TABLE II (CONTINUED)

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	28	59	53	35	61	75	21	34	30	37	29	48
Hydrobia ulvae	..	..	..	..	..	..	..	..	1	1	..	..
Carcinus maenas	1	..	..	..	..	1	2	3	..	..	2	..
Eupagurus bernhardus	..	..	..	..	..	..	..	1	..	..	..	..
Crangon vulgaris	..	1	..	..	2	6	6	14	2	1	1	..
Decapod larvae	..	..	..	3	5	3	..	1	..	..	..	..
Schistomysis ornata	..	..	1	3	2	..	1	..	..	..	1	1
Neomysis vulgaris	..	1	3	1	..	..	..	1	5	..	..	..
Mysid fragments	..	..	2	1	2	..	1	5	..	..	..	..
Pariambus typicus	..	..	..	..	..	..	..	1	..	..	..	20
Caprellid fragments	..	..	..	..	..	..	..	2	..	..	1	..
Gammarus locusta and *Gammarus* sp.	..	1	..	..	..	2	..	1	..	..	..	4
Corophium volutator	..	..	1	1	1	..	..	2	2	10	5	16
Amphipod fragments	..	2	..	..	1	..	..	2	1	5	1	4
Copepod fragments	2	2	5	11	2	7	1	3	..	..	1	..
Crustacean fragments	3	3	4	2	7	10	..	9	10	9	4	11
Spirographis spallanzani	37	101	77	39	86	51	13	4	21	11	15	14
Cirratulid fragments	..	3	1	1	..	1	..	..	..	1	1	2
Polydora sp.	..	..	..	..	..	..	..	..	..	1	..	12
Polychaete fragments	1	9	..	..	..	4	3	1	..	7	5	20
Oligochaeta indet.	..	1	..	..	1	..	..	..	..	..	..	..
Gonothyrea loveni	..	..	..	..	..	4	..	3	1	..	2	..
Hydroid remains	..	..	1	2	2	11	2	6	1	3	1	..
"Spawn"	..	..	..	..	..	2	4	3	1	..	..	2
Vegetable matter	..	..	..	..	..	1	..	..	..	..	1	..

Note. The "Occurrence" basis of presentation of food analyses is less suited to the dab than to other estuarine fishes. Fishes which had been eating crustaceans were rarely so distended with food as those which had taken *Spirographis*. For the sake of uniformity, the occurrence basis has been used, but it should be noted that this table and Fig. 11 do not sufficiently emphasize the importance of *Spirographis spallanzani* as a food of the dab.

*Other Organisms**

Ascidian fragments 1 (X). Ophiuroid fragments 1 (X), 1 (XI).
Polyzoan fragments *1 (XII)*. Cephalopod indet. 1 (VII).
Pulmonate mollusc (? *Arion* sp.) *1 (X)*. *Littorina rudis 1 (V)*.
Cardium edule 1 (II), 1 (VIII), 1 (X). *Mytilus edulis 1 (IV)*.
Chlamys opercularis and *Chlamys* sp. *1 (VII)*, 1 (VII).
Molluscs (fragments of shell) *3 (VII)*, 1 (VI), 1 (IX).
Dipteran larvae *1 (III)*, *1 (IV)*. Arachnida, Araneid indet. 1 (III).
Cancer pagurus 2 (II). *Praunus flexuosus* 1 (VIII), 1 (XII).
Caprella aequilibra 5 (IX). *Apherusa* sp. *1 (VII)*.
Sphaeroma sp. *1 (XII)*, 1 (VIII), 1 (XI).
Gnathiid larvae *1 (II)*, 1 (III). *Pseudocuma cercaria 1 (III)*.
Cumacean fragments 3 (VI). Cyprids of *Balanus* sp. *3 (VIII)*, *1 (X)*.
Pseudocalanus elongatus 9 (X). Ostracoda indet. *1 (XII)*.
Amphitrite sp. 1 (VII). *Ampharete grubei 2 (VIII)*.
Melinna palmata 1 (VI). Ampharetid fragments 1 (VI).
Capitellid fragments 1 (II). Spionid fragments *1 (III)*, 1 (II), 1 (XII).
Nephthys hombergi 1 (VII), 2 (XII). *Nereis cultrifera 1 (V)*.
Nereis diversicolor 2 (VI).

* Figures in italics are for 1936: those in ordinary type for 1937.

49 % of the November fish contained food, but in the following month 75 % had fed. In December 1935 84 % of the fish opened showed traces of food; in January 1936, only 50 %. The fast appears to end earlier than that of the flounder.

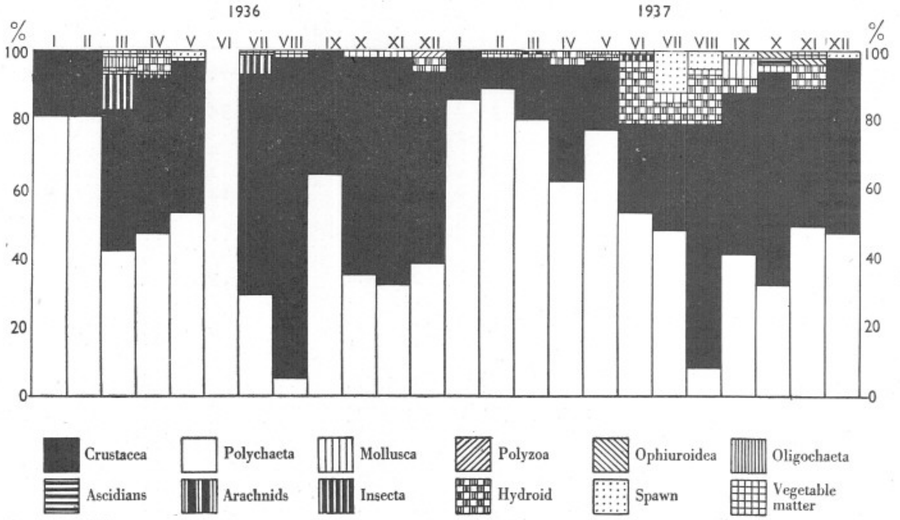

Fig. 12. *Pleuronectes limanda*; monthly variations in diet. (No figures are given for months in which less than 25 fish were examined.)

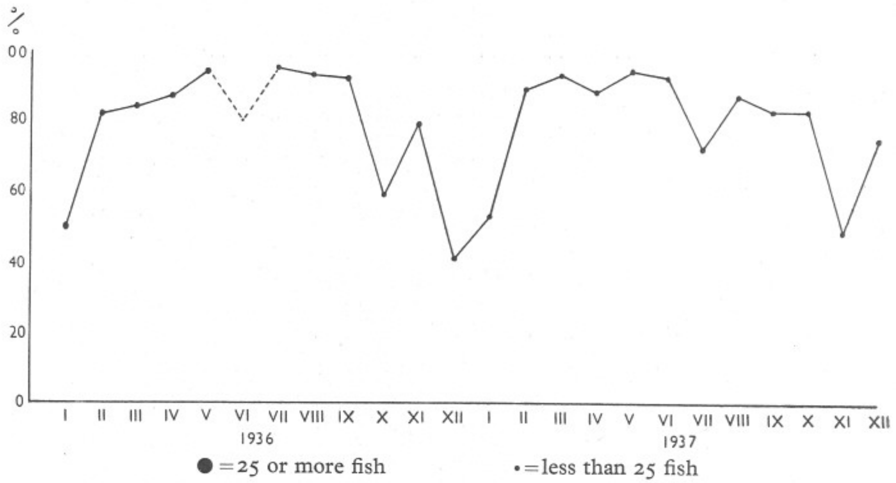

Fig. 13. *Pleuronectes limanda*; monthly percentages of fish which contained food.

The dab occupies a special place in the ecological relationships of the estuarine fishes. During its first growth period it competes directly with other carnivorous species, but in its second year of life it relies on food organisms which are not largely taken by any other fish.

Pleuronectes platessa L., the Plaice

The estuaries are a nursery ground for many plaice during the first year or two of their lives: the young fish travel some distance up the rivers, being regularly caught at Sheviock Wood and in the mouth of the Tavy, where they must endure considerable changes in osmotic pressure with the ebb and flow of the tides. At Sheviock Wood on September 21, 1937, the salinity 1 ft. below the surface decreased from 25 °/₀₀ 2 hr. before low water to 14 °/₀₀ at low tide. Von Buddenbrock (1936) found that plaice were capable of enduring salinities as low as 10 °/₀₀, but that below that limit their powers of osmotic regulation broke down. The young fish at Sheviock were, therefore, living in water of a salinity near the lower limit of toleration of their species, suggesting that salinity is, as would be expected, the factor which limits the upstream migration of young plaice. Maturing fish are rare in the estuaries; the "run" to the sea takes place under some other urge than that of reproduction.

In most tuck-net catches the large majority of the plaice are under 25 cm. in length, with an occasional big fish up to 40 cm. long. Only very extensive marking experiments would show whether these fish have wandered in from the sea, as the fishermen believe, or had remained for several years in brackish water.

Growth and Period of Estuarine Life.

The length-frequency distributions of the plaice examined during the investigation are not here reproduced. During the winter of 1935–6 fish of 6–17 cm. were caught; in February 1936 there came a sudden reduction in the proportion of the larger of these fish so that the average size of the plaice in the catches decreased. In May a new length-group appeared, of small fish 2–4 cm. long. At the same time the fish of the length-group which had been caught between February and April (the smaller fish of the population of the previous winter) were caught less frequently. During the summer of 1936 the recruiting stock dominated the catches, but in September larger fish became numerous once more. The length-frequency distribution in the winter of 1936–7 was essentially similar to that of the previous year, and in February 1937 the sudden reduction of the proportion of larger fish was repeated. The recruitment of 1937 was much smaller than that of 1936 and was not clearly seen until July. In September the larger fish became numerous again, and in the winter the widely dispersed length distribution was found once more. In the winter of 1937, a year of small recruitment, there was a higher proportion of the larger fish than in the winter populations of the two previous years.

The general similarity of these changes in length-frequency distribution to those shown by the dab will at once be remarked. It is probable that they tell a similar story of two years of estuarine life with a descent to the sea at the end of the second year. The main difference from the dab is in the virtual absence of I-group fish from the catches in the summer months. There are two possible explanations of this. One is that I-group plaice, possessing considerable powers of osmotic resistance, ascend in summer to the creeks and upper tidal reaches. The other explanation is that most of the estuarine plaice go down to the sea when some 12 months old, and return at the age of 16 months, only to descend once more at the end of their second year. The first explanation seems to be the more probable, for in the "old days" big plaice used to be taken in the salmon seines working in the upper parts of the estuary in summer. The mesh of a salmon net would allow all but the largest of the estuarine plaice to escape. Such an up-river movement would be similar to that made by flounders at the same season.

The results obtained from the measurement of plaice do not permit much accurate estimation of their growth during the period of estuarine life. In 1936 the O-group was distinct from fish which may have belonged to the I-group for only three months. In May, the arithmetic mean length of the O-group was 3·5 cm., in June 4·5 cm. (this was a sample of only nine fish, caught on June 6, 1936), and in the middle of July 7·1 cm.; during the summer months the growth of the recruiting stock appears, therefore, to be very rapid. In August a "small" group was present, but there were fish in it of lengths up to 13 cm., which may have been members of the I-group. In 1937, the O-group was clearly defined only in July: the fish had a mean length of 5·8 cm., that is, they were 1·3 cm. shorter than the recruiting stock in the same month of the previous year.

Some indication of the size of the estuarine plaice at the end of the first year may be obtained, if it be assumed that the O-group fish will dominate the population after the run to the sea of the I-group at the end of January. In February 1936 the mean length of the fish remaining in the estuary was 9·0 cm.; in February 1937 it was 8·5 cm. A few individuals of the I-group may still be in the rivers, and allowance must be made for them. The rough approximation may be made that the estuarine plaice do not reach a length of more than 8 cm. in their first year. Since a length of 6–7 cm. is reached in July of the first summer, there must be a great slowing down of growth during the winter fast.

In the autumn of 1937, the otoliths of all plaice were examined. It proved to be impossible to read a large proportion of them (33 % in November, 61 % in December) with certainty. Otoliths showing only one summer zone were so uncommon in this year of small recruitment, that no deductions could be made from them. Arithmetic mean lengths of age-groups, as determined by the number of summer zones, were:

	I-group 2 summer zones cm.	II-group 3 summer zones cm.
Oct.	19·7	24·83
Nov.	16·0	22·5
Dec.	13·5	17·5

The presence of 3-zone fish suggests that, as in the dab, a few plaice spend three growth periods in brackish water, instead of the more usual two. The reduction in the mean length of both year-groups in successive months is puzzling; the histograms for this period show a reduction in the numbers of bigger fish to have taken place by the end of October. It may be that the larger members of each year-group go down to the sea first, but it must be admitted that there is no independent evidence for this view. As a generalization it may be said that the estuarine plaice have a mean length of about 16 cm. at the end of their second growth period. This was the length of the two-year-old fish used for feeding experiments at Plymouth by Dawes (1930).

Feeding Habits.

In the estuaries the plaice feeds largely on polychaetes and crustaceans (Table III and Fig. 14). It takes more molluscs than most of the fish living on the same grounds, but this food is of less importance than in most localities. Small plaice take more crustaceans than polychaetes, large fish more polychaetes; but the change of diet is less striking than in the dab, and crustaceans remain a more important food of big fish.

TABLE III. *PLEURONECTES PLATESSA*: MONTHLY OCCURRENCE OF FOOD ORGANISMS.

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	22	28	37	5	33	9	44	35	38	23	25	16
Paphia pullastra	..	..	7	..	2	2	..	..	..	..	..	1
Cardium edule	..	..	..	..	1	..	3	2	..	1	..	..
Lamellibranch remains	..	..	1	..	1	..	2	1	1	..	1	..
Crangon vulgaris	..	..	..	..	..	..	5	1	1	2	2	..
Schistomysis ornata	..	1	3	..	..	2	5	5	..	3	1	4
Neomysis vulgaris	..	1	..	..	..	..	20	1	1	6	2	..
Mysidacean fragments	..	1	1	1	3	3	18	4	3	3	3	1
Corophium volutator	2	5	15	2	2	..	6	2	1	3	1	1
Gammarus sp.	1	..	1	..	1	..	..	..	..	..	..	..
Amphipod fragments	1	2	3	..	2	..	..	..	..	2	7	2
Copepod fragments	..	..	..	..	18	1	1	..	..	..	..	..
Crustacean fragments	2	3	14	1	5	5	30	10	7	6	8	..
Spirographis spallanzani	..	7	3	1	1	..	..	..	8	4	2	..
Ampharete grubei	..	..	..	..	..	..	3	12	..	..	..	..
Melinna palmata	..	..	..	..	..	..	1	6	..	1	..	1
Ampharetid remains	..	..	..	..	..	..	..	2	..	3	..	..
Cirratulids indet.*	1	2	9	3	..	..	5	12	2	..	2	3
Polydora ciliata	5	6	2	..	..	..	..	..	..	..	..	..
Polydora hoplura	2	2	..	..	1	..	..	..	2	..	2	..
Polydora sp.	3	7	3	..	..	..	4	..	..	1	2	..
Spionids indet.	6	7	3	1	3	1	..	..	..	..	..	..
Nephthys hombergi	2	4	13	..	5	1	3	..	1	..	1	..
Nereis diversicolor	..	..	4	..	3	2	2	..	1	..	..	1
Eulalia viridis	..	1	..	..	1	..	..	..	..	..	..	..
Phyllodoce sp.	1	1	..	..	..	..	..	..	..	..	1	..
Polychaete remains	22	9	17	3	14	2	17	19	15	9	10	10

TABLE III (CONTINUED)

The figures give the number of stomachs and intestines containing the specified category of food organism for each month.

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	20	40	39	10	32	20	38	28	29	24	28	30
Paphia pullastra	..	..	2	..	3	..	1	1	..	..	..	..
Cardium edule	..	1	1	..	..	..	6	4	2	1	..	..
Lamellibranch remains	..	..	2	1	1	..	2	1	1	..	..	..
Crangon vulgaris	..	..	..	..	7	2	5	1	2	1	1	..
Schistomysis ornata	2	1	..	..	3	..	2	1	1	..	..	..
Neomysis vulgaris	2	1	4	..	..	..	1	1	10	1	..	..
Mysidacean fragments	1	..	1	..	3	..	1	3	..	..	..	..
Corophium volutator	1	3	3	1	..	..	..	..	2	20	19	12
Gammarus sp.	..	..	2	..	..	..	..	..	..	..	..	..
Amphipod fragments	4	2	5	1	1	..	1	1	..	1	2	1
Copepod fragments	1	..	..	..	..	..	2	..	..	..	..	1
Crustacean fragments	6	8	6	1	3	5	5	8	7	1	8	5
Spirographis spallanzani	..	4	3	2	5	1	..	..	13	6	3	1
Ampharete grubei	..	..	..	..	..	2	..	..	..	..	..	..
Melinna palmata	..	..	4	..	2	1	2	5	7	..	1	..
Ampharetid remains	..	..	..	..	..	..	..	..	1	..	..	1
Cirratulids indet.*	4	12	7	3	..	..	4	..	..	1	2	2
Polydora ciliata	..	..	..	..	..	..	..	..	..	..	..	..
Polydora hoplura	..	1	..	..	..	..	..	..	..	1	2	6
Polydora sp.	1	1	..	..	..	..	1	..	1	..	3	..
Spionids indet.	1	1	1	..	1	..	1	..	..	..	..	..
Nephthys hombergi	..	5	13	3	20	5	3	4	..	..	1	1
Nereis diversicolor	..	..	3	..	4	1	7	5	3	..	..	..
Eulalia viridis	..	..	..	..	..	..	..	..	..	..	..	3
Phyllodoce sp.	..	..	1	..	..	..	..	..	..	..	..	..
Polychaete remains	10	23	26	4	17	16	23	22	4	1	6	9

* Many of these cirratulids appeared to be *Heterocirrus zetlandicus*; but owing to the close similarity of juvenile *Audouinia tentaculata* to this species (Wilson, 1936) it was felt that it would be better to list them simply as "Cirratulids".

*Other Organisms**

Gobius sp. *2 (VIII)*. Teleost remains *1 (VII)*. *Abra* sp. *1 (IX)*.
Scrobicularia plana 6 (VII). *Mytilus edulis* *1 (VII)*.
Dipteran larvae *4 (III)*. *Carcinus maenas* *1 (VIII)*, 1 (VII).
Decapod larvae *1 (V)*. *Praunus flexuosus* *1 (IX)*.
Macropsis slabberi 1 (IX). *Pariambus typicus* 1 (IX).
Sphaeroma serratum and *Sphaeroma* sp. *1 (III)*, 3 (III), 1 (XII).
Cyathura carinata 1 (V). Gnathiid larvae *1 (III)*.
Isopod fragments 1 (III). *Temora longicornis* *11 (V)*.
Eurytemora affinis *11 (V)*. Oligochaete fragments *2 (III)*, *4 (V)*, 1 (V).
Sabellaria sp. 1 (X). Hydroid fragments 1 (VI), 1 (VII), 1 (XI).
"Spawn" *2 (III)*, *1 (V)*. Diatoms 3 (VII). Vegetable matter *1 (VIII)*.

* Figures in italics are for 1936, those in ordinary type are for 1937.

Percentage of Polychaetes and Crustaceans

cm.	Polychaetes	Crustaceans
20–25 and over	77	23
18	67	33
16	67	33
14	62	38
12	70	30
10	70	30
8	59	41
6	49	51
4	32	68
2	32	68

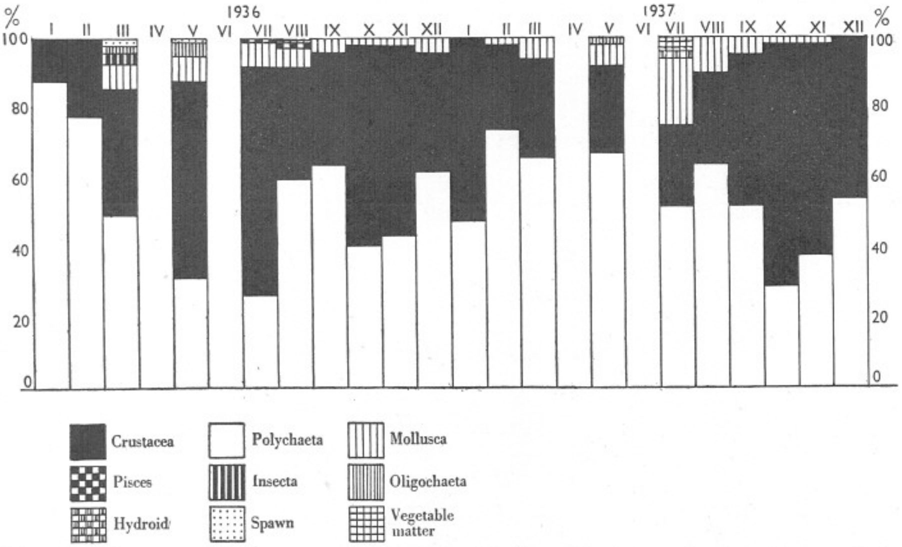

Fig. 14. *Pleuronectes platessa*; monthly variations in diet. (No figures are given for months in which less than 25 fish were examined.)

Scott (1895) found a decrease in consumption of crustaceans in fish over 3 in. (7·6 cm.) in length and Murie (1903) found that plaice in the Thames estuary took more "lob-worms" and fewer crustaceans as they grew larger. Both these authors and Todd (1915) found molluscs to be the most important food of the larger immature fish.

Plaice consume fewer tubicolous polychaetes than do dabs; Steven (1930) attributes this to the fact that the plaice moves horizontally towards its food, a method more suitable for the capture of free-swimming polychaetes than the tubicolous forms with their powers of swift retraction. *Paphia pullastra* is one of the most frequently occurring molluscan foods. The whole animal is not eaten; only the tips of the pallial siphons are neatly nipped off.

There is a winter fasting period (Fig. 15). Todd (1915) found that in the North Sea 100% of the plaice less than 20 cm. in length were empty in

November, 53% in December, and 92% in February. The largest percentage of empty stomachs in the estuaries was 72% in December 1936. In the winter of 1937–8 the fast began very late—67% of the fish still contained food in December 1937.

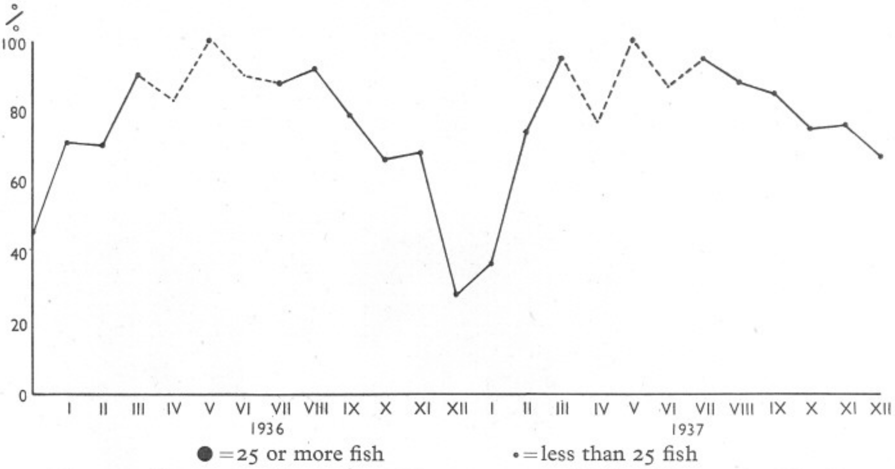

Fig. 15. *Pleuronectes platessa*; monthly percentages of fish which contained food.

Rhombus laevis (Rond.), the Brill

Small brill, ranging in size from 7 to 26 cm., were caught at intervals by the tuck-net. The modal length of thirty-one fish measured between November 1935 and December 1937 was 18 cm.; the mean length was 17·76 cm. All were immature.

The chief food of the brill was *Gobius minutus*, with other small teleosts and *Crangon vulgaris* next in importance as shown below. In their feeding habits, brill were, therefore, outside the competition for the smaller organisms which were eaten by most of the estuarine fishes; they occupied a special place in the food relationships of the estuarine predators.

Food of *Rhombus laevis*

	Total occurrences		Total occurrences
Gobius minutus	14	*Crangon vulgaris*	8
Gobius sp.	2	*Neomysis vulgaris*	1
Clupea sp.	1	Mysid fragments	3
Teleost indet.	3	Crustacean fragments	1

Solea vulgaris Quensel, the Sole

Immature soles were sometimes caught in the tuck-net: the largest was 19 cm. long, the smallest 6 cm. In the winter months, when most of the fish were taken, the length-frequency distributions showed two distinct groups:

one 6–12 cm. long, with an arithmetic mean length of 9·9 cm., and the other of 15–16 cm., with a mean length of 15·7 cm. Of fifty-nine soles measured between October and March, only five were in this larger group, but it is suggested that there are, in fact, fish of two year-groups living in the rivers in winter. Some of these soles were caught at Sheviock Wood. In the "old days" big soles were caught in the salmon nets in summer, but none of these fish have been seen for some years.

Food found in the stomachs of soles is shown below. In diet, the sole seems closely to resemble plaice.

Solea lascaris (Risso), the Sand Sole

In July and August 1937, thirteen sand soles were taken in the rivers, ranging in size from 11 to 18 cm. Their stomach contents are shown below.

Food of *Solea vulgaris* and *S. lascaris*

	Solea vulgaris	*Solea lascaris*
Lamellibranch fragments	1	..
Carcinus maenas	1	..
Crangon vulgaris	6	8
Mysid fragments	3	..
Corophium volutator	3	..
Crustacean fragments	7	1
Polydora sp.	3	..
Nereis diversicolor	2	3
Polychaete fragments	12	2

Clupea harengus L., the Herring

In the winter months hauls of adult herrings are sometimes made with the tuck-net. In January and February 1936 two catches of mature fish were made, ninety-six fish on January 22 and seventy-nine on February 7. Scale readings showed that these fish belonged to the II- and III-groups:

Scale readings of adult herrings: R. Tamar

	January 1936	February 1936
Total catch	96	79
II-group fish	84	63
III-group fish	12	16

Vertebral counts of the fish of these two samples gave the arithmetic mean numbers of vertebrae as 55·82 in January and 55·80 in February: the difference between these two means, 0·021, is much less than the standard error of the difference, so the fish may be presumed to belong to the same "race".

None the less, there was a conspicuous difference between those in the two hauls. In the first the II-group fish had a length dispersal of 16–21 cm., and a mean length of 19·4 cm.; the mean of the III-group was 20·8 cm. In the second haul, the mean length of the II-group fish was 20·77 cm., with a length dispersal of 19–22 cm., and the mean of the III-group fish was 22·5 cm. The January shoal, therefore, consisted of smaller fish of each year-group than the February shoal. Since Ford (1933) found that between 1924 and 1928 the average length of three-zoned, three-ringed fish varied from 24·2 to 25·9 cm., it seems that in both hauls the III-group fish were some of the smallest of their year class.

There was a marked difference in the sexual condition of the females in these two shoals. In January the mean length of the II-group females was 19·4 cm., and only one fish out of fifty-one was spent: six of the eight III-group females were virgin fish. In the February shoal, the mean length of the II-group females was 20·84 cm.; twenty-eight out of thirty-seven fish were spent and so were all the six III-group females. In both shoals none of the II-group males, and only three out of a combined total of fifteen III-group males were spent. The contrast between the female fish of these two samples suggests that both size and sexual condition may be among the factors influencing the organization of herring shoals.

Occasional specimens of third and fourth year herring were taken on other dates.

The majority of the herrings caught in the estuaries belonged to the O-group. These young fish are, at times, extremely numerous: but the appearance of the shoals is irregular, and during the period of the investigation it was not possible consistently to sample the population. During 1927 Ford (1928 *a*) fished for young clupeoids in the estuaries with a fine-meshed tuck-net; he found, as has already been noted, that the practice of measuring fish to the longest caudal ray could not be followed with O-group herring on account of the battered and broken state of the tails of so many of the fish. This abrasion of the tail was observed again in 1936–7: consequently, for O-group fish only, the length used is the "body length" from the tip of the snout to the end of the scaled area of the caudal peduncle. The fish of the older year-groups do not show this reduced condition of the tail: it may be that the fin-rays are regenerated, but perhaps the fish with battered tails die off.

Between November 1935 and March 1936, the O-group herrings taken in the tuck-net belonged to a single length-group, of fish 6–10 cm. long. Few herrings were caught during the summer of 1936, but in September of that year fish of two length-groups were caught, one of 3–5 cm., the other of 8·5–12·5 cm. The smaller group was not met again during the winter, but some fish of the larger group were taken until March 1937. In May 1937 a new group of fish was found, 3·5–5 cm. long. In June the young herring were 4–7·5 cm. in length, and by August the length distribution was 7–9·5 cm. In September the length distribution was 9–11·5 cm. and by December 1937 was 10–12·5 cm. The most complete series of observations was made in 1937, when adequate samples of fish were obtained in May, June, August, September, October and December: the growth during this period was from a mean length of 4·72 cm. in May to 11·5 cm. in December. These figures correspond closely with the growth found by Ford in 1927: from a mean length of 4·76 cm. on May 26 to one of 10·92 cm. on December 5.

I am told by Mr Ford that the herring population of the estuaries at any time is made up of numerous shoals, in which the length distributions of the fish vary considerably, and that the distribution of these shoals is constantly changing. In view of these facts it was thought best not to attempt to draw a series of detailed conclusions from the data collected while tuck-netting, but simply to produce summaries of measurements as evidence of the youth of the major part of the herring population.

No young herring were caught during the month of April, for the population is reduced by the departure of the I-group fish to the sea some time before the arrival of the O-group of the succeeding year class. For the herring, as for so many other species, the estuaries are a nursery ground. Most species, having once left brackish water, do not return in any strength: the herring, however, is of a different habit, for there is a second visit of part of the population (not necessarily of the individuals which were reared in the river mouths) in the autumn months. I-group herring are uncommon; some caught at West Muds on August 8 1936 were named by the fisherman "little summer herring". A few fish showing one winter zone and two summer rings were taken in 1937.

There is a drift-net fishery for herring in the river mouths from mid-September until mid-November: light drift-nets (a typical net would be 8 fathoms long, 46 meshes to the yard and 120 meshes deep) are worked from the open tuck-boats with a crew of one or two men. The nets are shot across the tide and float before it, the thickly corked head-rope at the surface. The boat is not kept fastened to the net; the men row along the line of the floating corks, and at times lift a few feet at one end of the net to see how the fish are "striking". Each of these shots is called a "drive" and may last from 10 min. to half an hour, the time varying with the area of water unobstructed by piers and buoys and with the speed of the current. Series of drives are made at dawn and dusk, and sometimes at the change of the night tide: change of light and of tide are mentioned by Graham (1931) among the factors believed to cause a "swim" of herring in the North Sea. The fishermen find that the herring become meshed equally on both sides of the net, and from this believe that the fish, when caught, are rising directly from the bottom rather that moving up or down the harbour.

Only once did I have the opportunity of examining drift-net fish. These were eight fish of the III- and IV-groups, and were the whole catch from 3 hr. work on October 20 1936. Seven were empty, the eighth contained the remains of a small teleost. In both 1936 and 1937 bad fisheries in the rivers preceded very poor seasons for the steam and motor drifters working off Plymouth.

Feeding Habits.

Herring in the estuaries feed almost entirely on crustaceans. The food analyses are set forth in Table IV, and call for little comment. Copepods are the most important food in winter, mysids in the summer months. Ford (1928 *a*) mentions mysids and copepods as the principal foods of young herring in the Tamar and Lynher. The O-group fish have no winter fast.

Clupea sprattus L., the Sprat

In the old days, sprats were caught in big seines worked by a crew of six men; but in the last few years there has been little sprat fishing in the harbour, for the shoals of well-grown fish have not been there to catch. In November 1935, some sixty small sprats, 3–4·5 cm. long were caught in the tuck-net. After that month, sprats were uncommon until August 1936: from then until September 1937, large samples of sprats were obtained in all months except October and November. In August 1936 the length-frequency distribution was from 3 to 5·5 cm.; by December it had increased to 3·5–7·5 cm., and by May 1937 had reached 4·5–8·5 cm. In May 1937 a new length-group appeared, 2·5–3·5 cm. long; by September, this group had a length-frequency distribution of 3–4·5 cm., while the previous length-group was now 5·5–8 cm. long. Irregularity of sampling makes it impossible to do more than make suggestions of possible interpretations of the data. It seems that one year-group, first met in August 1936, grew from a length of a little under 5 cm. in that month to a length of about 7·7 cm. in the following June. A second length-group, presumably the succeeding year class, first appeared in May 1937, when the mean length of the fish was 3 cm.: during the first 5 months of estuarine life they increased their length by only 0·6 cm.

These small sprats make excellent "whitebait", but the local fishermen are unable to obtain any sale for them.

The sprat is a direct competitor with the herring for its food, in which copepods bulk largely. Stomach content analyses are shown in Table V. There was no winter fasting period.

Clupea pilchardus Walb., the Pilchard

In September 1936 I had the opportunity of measuring a sample of pilchards caught in a tuck-net at Kiln Bay. There were fifty-five fish with a length distribution from 21 to 26·5 cm. and an arithmetic mean length of 24·3 cm. On October 20 of the same year twenty-seven were caught in a herring drift-net off Saltash. They had a length distribution of 20–25·5 cm., and a mean length of 23·64 cm. The fishermen tell me that pilchards are never common in the estuaries, and that there is practically no sale for them.

TABLE IV. *CLUPEA HARENGUS*: MONTHLY OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism in each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	15	27	43	..	10	3	10	2	27	11	5	1
Gobius sp.	..	..	..	..	..	..	..	1	..	..	..	..
Teleost remains	..	..	..	..	..	..	..	..	..	1	..	..
Crangon vulgaris	..	..	..	..	..	..	..	..	..	..	..	..
Decapod larvae	..	1	3	..	6	..	1	..	..	..	..	..
Neomysis vulgaris	1	2	4	..	..	..	3	1	13	4	2	..
Macropsis slabberi	1	1	..	..	..	..	..	..	5	..	..	1
Schistomysis ornata	..	..	3	..	..	..	1	..	1	2	..	..
Praunus flexuosus	..	..	..	..	1	..	1	..	1	5	..	..
Mysidacean fragments	2	2	1	..	..	2	4	1	10	4	1	..
Corophium crassicorne	..	..	..	..	1	..	..	..	..	..	..	..
Corophium volutator	..	..	..	..	..	..	..	..	..	..	..	..
Corophium sp.	..	..	..	..	1	..	1	..	..	..	..	..
Gammarus sp.	..	1	1	..	..	..	..	..	..	..	..	..
Amphipod fragments	..	1	1	..	2	..	..	..	1	..	..	..
Gnathiid larvae	..	1	7	..	..	..	3	..	1	..	..	..
Cirripede cyprids	..	..	5	..	..	1	..	..	..	..	..	..
Harpacticoid copepods	9	11	23	..	..	1	..	..	..	..	..	..
Corycaeus anglicus	1	..	..	..	..	..	..	..	..	..	..	..
Cyclopoid copepods	..	..	1	..	..	..	..	..	..	..	..	..
Eurytemora affinis	9	9	8	..	..	..	..	..	..	..	..	..
Temora longicornis	4	..	..	..	..	..	..	..	..	..	..	..
Paracalanus parvus	..	..	1	..	..	..	..	..	..	..	..	..
Calanoid copepods	..	1	..	..	..	..	..	..	2	..	..	..
Copepod nauplii	..	1	..	..	..	..	..	..	..	..	..	..
Copepod ova, spermatophores and fragments	19	18	28	..	..	..	2	..	5	1	..	..
Ostracoda	..	..	1	..	..	..	..	..	..	..	..	..
Crustacean fragments	2	9	10	..	7	1	4	..	3	5	2	1
Nereis diversicolor	..	4	7	..	..	..	..	..	..	..	..	..
Polychaete fragments	..	..	1	..	..	..	..	..	..	..	..	..

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	7	7	4	..	16	21	2	17	14	..	2	12
Gobius sp.	..	..	..	..	..	..	..	..	..	..	..	..
Teleost remains	..	..	..	..	1	1	1	..	..	..	..	..
Crangon vulgaris	..	..	..	..	..	1	..	2	..	..	..	2
Decapod larvae	..	..	..	..	..	1	..	..	..	..	..	..
Neomysis vulgaris	2	2	1	..	3	5	..	9	10	..	..	1
Macropsis slabberi	..	..	2	..	..	..	..	..	9	..	..	..
Schistomysis ornata	..	1	..	..	..	4	..	..	..	..	..	2
Praunus flexuosus	4	..	..	..	..	4	..	5	1	..	1	..
Mysidacean fragments	..	1	1	..	1	4	..	3	3	..	2	3
Corophium crassicorne	..	..	..	..	..	..	..	..	..	..	..	..
Corophium volutator	..	..	..	..	..	..	..	..	..	..	..	..
Corophium sp.	..	..	..	..	..	..	..	..	..	..	..	..
Gammarus sp.	..	..	..	..	..	..	..	4	..	..	1	3
Amphipod fragments	..	..	..	..	..	..	1	..	..	..	..	2
Gnathiid larvae	..	..	..	..	..	1	..	..	..	..	..	..
Cirripede cyprids	..	..	..	..	..	..	..	..	..	..	..	..
Harpacticoid copepods	..	..	..	..	1	2	..	..	..	..	..	..
Corycaeus anglicus	..	..	..	..	..	..	..	..	..	..	..	..
Cyclopoid copepods	..	..	..	..	..	..	..	..	..	..	..	..
Eurytemora affinis	..	1	..	..	3	..	..	..	..	..	..	..
Temora longicornis	..	..	..	..	4	..	..	..	..	..	..	..
Paracalanus parvus	..	..	..	..	..	..	..	..	..	..	..	..
Calanoid copepods	..	..	..	..	1	2	..	..	..	..	..	..
Copepod nauplii	..	..	..	..	..	..	..	..	..	..	..	..
Copepod ova, spermatophores and fragments	..	..	..	..	16	5	..	..	..	..	..	2
Ostracoda	..	..	..	..	..	..	..	..	..	..	..	..
Crustacean fragments	3	4	1	..	..	7	1	3	1	..	1	2
Nereis diversicolor	..	..	..	..	..	..	..	..	..	..	..	..
Polychaete fragments	..	..	..	..	..	..	..	..	..	..	..	..

TABLE V. *CLUPEA SPRATTUS*: MONTHLY OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism in each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	6	4	4	..	3	..	..	9	19	..	7	5
Lamellibranch sp.	..	..	..	..	..	..	..	..	..	..	..	..
Decapod larvae	..	..	..	..	..	..	..	..	..	..	..	..
Neomysis vulgaris	..	..	..	..	..	..	..	..	1	..	..	..
Macropsis slabberi	..	..	..	..	..	..	..	..	3	..	..	..
Mysidacean fragments	1	..	..	..	..	..	..	1	4	..	..	..
Corophium volutator	..	..	..	..	..	..	..	..	..	..	..	..
Amphipod fragments	..	1	..	..	..	..	..	..	..	..	..	..
Gnathiid larvae	..	..	..	..	..	..	..	..	1	..	..	..
Cirripede cyprids	..	..	..	..	..	..	..	..	..	..	..	..
Harpacticoid copepods	3	3	2	..	3	..	..	1	..	..	..	6
Corycaeus anglicus	..	..	..	..	..	..	..	..	..	..	..	..
Cyclopoid copepoids	..	..	..	..	..	..	..	..	..	..	..	..
Acartia clausi and *Acartia* sp.	..	..	..	..	1	..	..	2	1	..	..	..
Eurytemora affinis	5	3	2	..	..	..	..	..	3	..	..	6
Temora longicornis	5	..	..	..	2	..	..	..	1	..	..	1
Pseudocalanus elongatus	..	..	..	..	..	..	..	..	..	..	..	..
Calanus finmarchicus	..	..	..	..	..	..	..	..	1	..	..	..
Calanoid copepods	..	..	..	..	2	..	..	2	10	..	..	2
Copepod nauplii	..	..	..	..	..	..	..	..	..	..	..	..
Copepod ova, spermatophores and fragments	12	5	6	..	4	..	..	7	7	..	..	9
Podon intermedius	..	..	..	..	..	..	..	..	..	..	..	..
Crustacean fragments	..	1	..	..	1	..	..	..	5	..	..	..
Polychaete fragments	..	..	2	..	..	..	..	..	..	..	..	..
Peridinium sp.	..	..	..	..	..	..	..	..	..	..	..	..

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	24	12	22	11	32	5	3	12	21	..	..	1
Lamellibranch sp.	1	..	..	..	1	..	..	7	..	..	..	..
Decapod larvae	..	4	2	1	1	..	..	..	1	..	..	..
Neomysis vulgaris	..	..	..	..	..	..	..	..	8	..	..	..
Macropsis slabberi	..	..	..	..	..	..	..	..	4	..	..	..
Mysidacean fragments	..	..	..	..	..	..	..	..	..	..	..	..
Corophium volutator	..	..	..	..	..	..	..	..	1	..	..	..
Amphipod fragments	..	..	..	..	..	..	..	..	..	..	..	1
Gnathiid larvae	..	..	..	..	..	..	..	..	..	..	..	..
Cirripede cyprids	..	..	..	..	6	..	..	..	..	..	..	..
Harpacticoid copepods	6	3	5	3	3	..	..	..	3	..	..	..
Corycaeus anglicus	..	..	..	..	..	..	..	..	3	..	..	..
Cyclopoid copepods	1	1	..	..	..	..	..	..	..	..	..	..
Acartia clausi and *Acartia* sp.	..	..	1	..	1	..	..	..	..	..	..	..
Eurytemora affinis	2	6	16	..	3	1	..	..	3	..	..	..
Temora longicornis	..	..	..	..	2	..	..	..	..	..	..	..
Pseudocalanus elongatus	..	3	7	..	4	..	..	..	1	..	..	..
Calanus finmarchicus	..	1	..	..	..	..	..	..	..	..	..	..
Calanoid copepods	3	3	..	2	1	..	..	..	1	..	..	..
Copepod nauplii	2	..	..	..	..	..	1	..	..	..	..	..
Copepod ova, spermatophores and fragments	17	7	16	14	40	4	3	8	11	..	..	..
Podon intermedius	..	..	..	..	..	..	..	..	1	..	..	..
Crustacean fragments	2	1	1	1	1	2	..	..	..	..	..	..
Polychaete fragments	..	..	..	..	..	..	..	..	..	..	..	..
Peridinium sp.	..	..	..	..	..	..	..	1	..	..	..	..

Salmo trutta L., the Sea Trout

Small sea-trout—called "Peal" by the west countryman—were occasionally taken in the tuck-net: a few of these were killed in the cod-end, or gilled, and these were opened for stomach contents.

Length cm.	Date	Place of capture	Food	Notes
16·7	7. ii. 36	Pier Ground, Saltash	..	..
35·4	21. x. 36	Off Saltash	*Clupea* sp., small, 4 or 5	Gilled in a herring drift-net, set near the surface
17·7	8. xii. 37	Saltash	*Clupea sprattus*, 6 cm., 1; *Clupea* sp. 8 cm., 1	..
38·5	17. xii. 37	Sheviock Wood	*Clupea* sp., *ca.* 10 cm., 1; *Crangon vulgaris*, 1	♀ Kelt: weight 437 g.
22·0	17. xii. 37	Sheviock Wood	*Gobius minutus*, 3 of *ca.* 7, 5 and 5 cm.	♀ Imm.
17·5	17. xii. 37	Sheviock Wood	*Gobius minutus*, 6 cm., 1; small Teleost, 1; *Crangon vulgaris*, 1	♀ Imm.

O'Donoghue & Boyd (1930) found that sea-trout caught in Scottish waters fed much in marine conditions off the river mouths, and less in the upper estuaries and in fresh water; they found that a large proportion of fish was eaten, especially clupeoids and *Ammodytes*.* Nall (1930), after a survey of the food of the sea-trout in salt water, wrote: "The inference, therefore, is that where herring and sprats are present, the Sea-trout prefer them to other forms of food."

It is curious that no sea-trout smolts were seen during the run to the sea in the early summer, for the Tavy is a famous sea-trout water. The slower Tamar does not rank so high as a sporting river for these fish (Nall, 1930).

Salmo salar L., the Salmon

Salmon pass through the estuaries on their way to the fresh waters of the Tamar and Lynher. The "run" begins at the end of February.

Anguilla vulgaris Turton, the Eel

Eels from 40 to 60 cm. in length were sometimes taken in the tuck-net. They fed upon crustaceans, especially *Carcinus maenas*. Many small eels, 10–20 cm. long, lived under stones at Neal Point and Henn Point.

Syngnathus acus L., the Pipe-fish

Occasional specimens of the pipe-fish were netted: most of them were brought in alive to the laboratory aquarium. A pipe-fish of 40·4 cm. on August 13 1937 contained fragments of *Neomysis vulgaris*.

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* No trace of *Ammodytes* was found in any fish caught in the estuaries, nor were living sand-eels seen or captured.

Atherina presbyter Jenyns, the Smelt

In late October 1936 a Saltash fisherman showed me nine smelts which had been caught in a sprat seine on West Mud; their length distribution was:

Length, cm.	12	13	14	15	16
Number	1	2	3	2	1

Three fish of 17·5, 17·0 and 15·8 cm. were taken at West Mud on June 25 1937; all had empty stomachs.

These were the only smelts seen during the investigation. In the "old days", smelts were so numerous that some of the Saltash men made a living by fishing for them; now the capture of half a dozen excites comment among the estuarine fishermen.

Mugil chelo Cuv. and Mugil auratus Risso, the Grey Mullets

Grey mullet are common in the Tamar and Lynher, but very difficult to catch. The fishermen say that mullet are the most cunning fish in the rivers, and that they lie among stones, or in depressions in the mud, and allow a net to be dragged over them. Even if a shoal be enclosed, and the foot-rope of the net be lying on smooth mud, the capture of the fish is not certain, for they will leap over the head-rope and so escape: on May 29 1937, about twenty fish from one shoal jumped out of the net, and only five were landed. The number of fish obtained was too small to allow any study of growth rates. Of the ten fish examined, nine were *Mugil chelo*, the largest 27·8 cm. long, the smallest 9·8 cm.: the tenth was *Mugil auratus*, of 16·8 cm. The gut was always found to be full of dark, grey-green mud, containing finely divided plant remains. I am told by the fishermen that at high spring tides mullet move up to the saltings and browse on the "sedge-weed" (*Obione*) growing on the edges of the creeks.

In the warm, summer weather, shoals of mullet swim in the shallows along the edge of the mudflats, moving so close to the surface that their progress may be traced by the rippling of the water above them; this rippling the fishermen call "reaming". About 2.0 a.m. on October 7 1937 the grey mullet at West Muds were observed to be jumping wildly: a fish 20 cm. long would leap a foot or more into the air and fall into the water a yard away. I was told that this nocturnal jumping was not unusual; Patterson (1904 *b*) records an instance of it on Breydon Water.

GADIDAE

The gadoids were the outstanding example of the type of estuarine fishes which were, by reason of the irregularity of their occurrence, difficult to study in detail. Five species were taken in the estuaries: *Gadus merlangus* was the most numerous, except during the winter of 1936–7, when *G. luscus* outnumbered it as shown below:

Season ...	Winter 1935–6	Summer 1936	Winter 1936–7	Summer 1937	Winter 1937
Months ...	Nov.–Mar.	Apr.–Sept.	Oct.–Mar.	Apr.–Sept.	Oct.–Dec.
Numbers of:					
G. merlangus	143	139	26	369	77
G. luscus	8	27	152	48	60

G. pollachius was caught regularly, in small numbers; *G. morrhua* was occasionally, *G. minutus* very rarely, found in the catches.

Gadus merlangus L., the Whiting

The length-frequency distributions of the whiting caught in the estuaries always showed a single, unimodal curve, suggesting that a single age-group was being dealt with in each month. The length-frequency histograms are not here reproduced; the length distributions, and arithmetic mean lengths are given in Table VI.

The appearance of a small group in the summer months, with rapid growth during the autumn and winter, and a disappearance of the stock in spring, suggests a single year of estuarine life. The recruitment in 1936 and the stock of whiting in the winter of 1936–7 were both small; the young fish grew from a mean length of 8·0 cm. in May to one of 12·05 cm. in August; in the

TABLE VI. *GADUS MERLANGUS*: MONTHLY LENGTH DISTRIBUTION

Length in cm.	1935		1936											
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
4	..	..	..	..	..	..	..	1	..	..	..	..	..	..
5	..	..	..	..	..	..	2	1	4	..	..	..	..	..
6	..	..	..	..	..	..	7	2	4	..	..	..	..	..
7	..	..	..	..	..	..	7	..	2	..	..	..	..	..
8	..	..	..	..	..	..	4	1	..	3	..	..	..	..
9	..	..	..	..	..	..	2	..	4	3	..	..	..	..
10	..	..	..	..	..	..	4	..	4	12	..	..	..	..
11	..	..	..	..	..	..	..	..	3	13	..	..	..	..
12	..	..	..	..	1	..	..	..	..	18	3	1	1	..
13	1	..	..	..	..	..	..	..	..	11	2	1	..	..
14	1	1	..	..	..	..	..	..	..	5	3	1	1	..
15	1	..	1	..	..	1	..	..	..	3	3	3	1	2
16	1	..	2	2	2	..	..	..	1	..	1	1	1	..
17	2	1	..	2	..	..	..	..	..	..	..	..	2	2
18	1	1	6	5	3	..	..	..	..	..	..	1	1	..
19	1	..	10	9	4	..	..	..	..	..	..	..	..	..
20	5	..	10	9	1	..	1	..	..	..	..	..	..	..
21	5	..	8	8	2	2	..	..	1	..	..	1	..	..
22	10	..	2	7	2	1	..	..	..	..	..	..	..	..
23	3	..	..	4	1	..	..	..	..	..	..	..	..	..
24	1	..	2	1	..	..	..	..	..	..	..	..	..	..
25	1	..	..	..	..	..	..	..	..	..	..	..	..	..
26	..	..	..	1	..	..	..	..	..	..	..	..	..	..
No. of fish caught	33	3	41	48	16	4	27	5	23	68	12	9	7	4
Mean length in cm.	21·1	(16·8)	20·14	20·68	19·13	(20·3)	8·0	(6·3)	8·5	12·05	14·25	(15·85)	(16·5)	(16·5)

TABLE VI (CONTINUED)

Length in cm.	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
3	..	..	..	..	..	..	..	..	..	..	..	..
4	..	..	..	..	..	2	..	..	..	..	..	..
5	..	..	..	..	..	13	..	..	..	..	..	..
6	..	..	..	..	..	41	1	..	..	..	..	..
7	..	..	..	..	..	36	..	..	..	..	..	..
8	..	..	..	..	..	39	2	..	..	..	..	1
9	..	..	..	..	..	21	4	..	..	..	..	..
10	..	..	..	..	..	14	11	..	2	..	..	1
11	..	..	..	..	..	12	19	1	2	..	..	..
12	..	..	..	..	..	6	11	5	..	..	..	1
13	..	..	..	..	..	5	7	18	6	..	..	1
14	1	..	..	..	..	..	3	23	7	1	1	1
15	..	..	1	..	..	..	6	13	4	..	2	..
16	..	..	..	..	..	..	1	6	12	1	4	1
17	..	..	..	..	..	..	..	..	11	1	12	2
18	..	1	..	..	..	..	..	..	3	3	11	1
19	2	..	..	..	..	..	..	..	1	1	12	1
20	1	..	..	..	..	..	..	..	1	2	4	..
21	..	..	..	..	..	..	..	..	..	..	6	1
22	..	..	..	..	..	..	..	..	..	1	2	..
23	..	..	..	..	..	..	..	..	..	..	1	1
24	..	..	..	..	..	..	..	..	..	..	..	..
25	..	..	..	..	..	..	..	..	..	..	..	..
26	..	..	..	..	..	..	..	..	..	..	..	..
No. of fish caught	4	1	1	..	..	189	65	66	49	10	55	12
Mean length in cm.	(18·5)	(18·5)	(15·5)	..	..	8·34	12·0	14·4	15·8	18·7	18·9	16·2

following months, the samples of fish were too small for great reliance to be placed on the results, but the fish seem to have attained a length of some 18 cm. before the run to the sea. The O-group fish were much more numerous in the summer of 1937: they appeared in June, and grew from a mean length of 8·34 cm. in that month to one of 18·9 cm. in November. This very rapid growth, which was observed not only in the whiting, but also in pout and pollack, may be partly accounted for by the fact that the gadoids have no winter fasting period while in the estuaries.

Gadus luscus L., the Pout

The length-frequency distributions of the pout in each month are shown in Table VII. The irregularity of the appearance of pout in the estuaries makes it difficult to arrive at conclusions on their growth and period of estuarine life. In the autumn of 1936, and winter of 1936–7, when pout were numerous in some months, the length frequency distributions showed unimodal curves, suggesting that a single year group made up the population. The mean length of this group increased from 13·5 cm. in September to 20 cm. in January. The disappearance of this length-group before April suggests a spring run to the sea similar to that of other gadoids.

In June 1937, a number of young pout, with a mean length of 5·9 cm., were

TABLE VII. *GADUS LUSCUS*: MONTHLY LENGTH DISTRIBUTION

Length in cm.	1935		1936											
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
4	..	..	..	..	..	..	1	..	..	..	..	..	..	..
5	..	..	..	..	..	..	2	..	..	..	..	..	..	..
6	..	..	..	..	..	..	..	..	2	..	..	..	..	..
7	..	..	..	..	..	..	..	..	..	..	..	..	..	..
8	..	..	..	..	..	..	..	..	..	..	..	..	..	..
9	..	..	..	..	..	..	..	..	..	3	1	..	..	..
10	..	..	..	..	..	..	..	..	..	1	..	..	..	..
11	..	..	..	..	..	..	..	..	..	..	2	..	..	..
12	..	..	..	..	..	..	..	..	..	..	6	2	..	..
13	..	..	..	..	..	..	..	..	..	..	4	4	..	..
14	..	..	..	..	..	..	..	..	..	..	2	7	..	1
15	..	..	..	..	..	..	..	..	..	..	1	16	..	..
16	2	..	..	..	..	..	..	..	..	..	..	27	..	..
17	..	..	1	..	..	..	..	..	..	..	1	26	..	1
18	..	..	..	..	..	..	..	..	..	..	1	14	..	..
19	5	..	..	..	..	..	..	..	..	..	..	4	..	1
20	..	..	..	..	..	..	..	..	..	..	..	1	..	..
21	..	..	..	..	..	..	..	..	..	..	..	1	..	..
22	..	..	..	..	..	..	..	..	..	..	..	..	..	..
23	..	..	..	..	..	..	..	..	..	..	..	..	..	..
24	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. of fish	7	..	1	..	..	..	3	..	2	4	18	102	..	3
Mean length in cm.	(18·69)	..	(17·5)	..	..	..	(5·2)	..	(6·5)	(9·75)	13·55	16·75	..	(17·2)

Length in cm.	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
3	..	..	..	..	2	1	..	..	..	..	..	..
4	..	..	..	..	..	2	..	..	..	..	..	..
5	..	..	..	..	..	15	..	..	..	..	..	..
6	..	..	..	..	..	5		..	..	..	..	..
7	..	..	..	..	..	4	1	1	..	..	..	..
8	..	..	..	..	..	1	1	..	..	..	..	..
9	..	..	..	..	..	..	..	1	..	..	..	..
10	..	..	..	..	..	..	..	..	1	..	1	..
11	..	1	..	..	..	..	..	..	1	..	1	..
12	..	..	..	..	..	..	..	..	2	..	10	..
13	..	..	..	..	..	..	..	..	1	..	11	..
14	..	1	1	..	..	..	..	..	1	1	10	..
15	..	..	..	..	..	..	..	..	2	..	4	..
16	1	..	..	..	..	..	..	..	1	..	8	..
17	1	..	..	..	..	..	..	..	1	..	6	..
18	4	2	..	..	..	..	..	..	..	..	3	..
19	3	1	4	1	..	..	..	..	..	..	2	..
20	11	1	4	..	..	..	..	..	..	..	1	..
21	5	3	2	..	..	..	..	..	..	..	2	..
22	2	..	..	..	..	..	..	..	..	..	..	..
23	..	..	..	..	..	..	..	..	..	..	..	..
24	..	..	..	..	..	..	..	..	..	..	..	..
No. of fish	27	9	11	1	2	28	2	2	10	1	59	..
Mean length in cm.	20·2	(18·4)	18·85	(19·5)	(3·5)	5·9	(7·75)	(8·5)	14·2	(14·5)	15·2	..

caught. After that the fish were rare again until November, when fifty-nine fish caught on November 2 had a mean length of 15·2 cm., nearly 1·5 cm. shorter than the 102 fish caught on October 30 in the previous year.

The only conclusion that may safely be drawn is that the estuaries are, at times, a nursery ground for young pout.

Gadus pollachius L., the Pollack

Pollack were found to haunt hard ground, where the bottom was stony and weed-grown. Except for very small summer fish, large numbers of pollack were never taken—probably owing to the small areas of suitable habitat. The study of the length-frequency distributions and mean lengths (Table VIII) suggests an estuarine history similar to that of the whiting; but, owing to the scantiness of the material, any conclusions are only tentatively put forward.

Young pollack were first observed in June in each year, when they were about 6·5 cm. long. Growth during the following autumn and winter was rapid; the length increment was about 12 cm. in 9 months. After a year of estuarine life most of the fish go down to the sea in spring.

As in the whiting, the recruitment of 1937 seems to have been larger than that of 1936.

Gadus morrhua L., the Cod

Cod were never numerous—only twenty-six were examined during the 26 months of the investigation. Fish as large as 35 cm. were twice taken, and once a juvenile fish of 6 cm.

Gadus minutus, L., the Poor Cod

Only two poor cod were taken before July 1937—a fish of 9·6 cm. on September 15 1936, and one of 8·2 cm. in March 1937. Between July and December 1937 twenty fish, from 8 to 15 cm. long, were caught. The small number of occurrences within the estuaries is curious, for in the waters off Plymouth the poor cod is "probably the commonest gadoid on the trawling grounds" (Ford, 1931).

Onos mustelus L., the Five-bearded Rockling

Occasional specimens of the rockling were netted, but only a few of them were examined in the laboratory. Two fish of 14 cm., opened in December 1937, contained fragments of crustaceans, and one a small goby in addition.

Feeding Habits.

The food of the gadoids during their estuarine life is shown in Table IX. *Crangon vulgaris* and mysids form the bulk of the food of all species, with small teleost fish next in importance. There is no winter fasting period. All the gadoids compete with one another, and with the flounder, for food.

TABLE VIII. *GADUS POLLACHIUS*: MONTHLY LENGTH DISTRIBUTION

Length in cm.	1935		1936											
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
3	..	..	..	..	..	..	..	1	..	..	..	..	..	..
4	..	..	..	..	..	..	..	..	..	..	..	..	..	..
5	..	..	..	..	..	..	..	2	..	..	..	..	..	..
6	..	..	..	..	..	..	..	18	..	..	..	..	..	..
7	..	..	..	..	..	..	..	10	..	..	..	..	..	..
8	..	..	..	..	..	..	..	..	..	..	..	..	..	..
9	..	..	..	..	..	..	..	..	2	3	..	..	..	..
10	..	..	..	..	..	..	..	..	1	1	..	..	..	1
11	..	..	..	..	..	..	..	..	1	1	..	..	..	1
12	..	..	..	..	..	..	..	..	2	3	..	..	..	..
13	..	..	..	..	..	..	..	..	..	1	1	..	1	1
14	..	..	..	..	..	..	..	..	..	..	..	..	3	3
15	..	..	..	..	..	..	..	..	..	..	1	4	3	1
16	2	..	..	..	..	..	..	..	..	3	..	3	2	1
17	..	..	..	..	..	..	..	..	..	..	..	1	3	2
18	1	..	..	1	..	1	..	..	..	..	..	1	1	2
19	3	..	..	7	..	..	..	..	..	..	..	..	1	2
20	2	..	1	4	..	..	..	..	..	..	..	1	..	..
21	..	..	1	3	..	..	..	..	..	..	..	..	..	1
22	3	..	..	1	..	..	..	..	..	..	..	..	..	..
23	..	..	..	..	..	..	..	..	..	..	..	..	..	1
24	..	..	..	..	..	..	..	..	..	..	..	..	..	1
25	..	..	..	..	..	..	..	..	1	..	..	..	..	..
No. of fish	11	..	2	16	..	1	..	31	7	12	2	10	14	17
Mean length in cm.	19·6	..	(21·0)	20·25	..	(18·5)	..	6·7	(11·0)	12·6	(14·5)	16·8	16·2	17·1

Length in cm.	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1	..	..	..	..	..	..	..	..	..	..	..	..
2	..	..	..	..	..	..	..	..	..	..	..	..
3	..	..	..	..	..	..	..	..	..	..	..	..
4	..	..	..	..	..	..	..	..	..	..	..	..
5	..	..	..	..	..	18	..	..	..	..	..	..
6	..	..	..	..	..	45	..	..	..	..	..	..
7	..	..	..	..	..	27	..	..	..	..	..	..
8	..	..	..	..	..	7	1	..	..	..	..	..
9	..	..	..	..	..	1	..	..	..	..	..	..
10	..	..	..	..	..	..	4	1	..	..	..	..
11	1	..	..	..	..	..	18	1	..	..	..	..
12	..	..	..	..	..	..	7	..	..	..	..	..
13	..	1	..	..	..	..	8	2	..	..	..	..
14	..	1	..	..	..	..	1	..	..	..	..	..
15	..	..	1	..	..	..	1	1	..	..	..	..
16	6	..	1	..	..	..	..	..	1	..	..	..
17	..	..	1	..	..	..	..	..	1	..	..	..
18	..	..	2	..	..	..	..	..	..	..	1	..
19	..	..	1	..	..	..	..	..	..	..	1	..
20	1	..	1	..	..	..	..	..	..	..	2	..
21	1	1	..	..	..	..	..	..	..	..	1	..
22	1	..	..	..	..	..	..	..	..	..	..	..
23	1	..	..	..	..	..	..	..	..	..	..	..
24	..	..	..	..	..	..	..	..	..	..	..	..
25	..	..	1	..	..	..	..	..	..	..	..	..
No. of fish	11	3	8	..	..	98	40	5	2	..	5	..
Mean length in cm.	18·0	(16·8)	(18·8)	..	..	6·7	11·8	(12·9)	(17·0)	..	(20·1)	..

TABLE IX. *GADIDAE*: OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism.

	G. merlangus		*G. luscus*		*G. pollachius*		*G. morrhua*		*G. minutus*	
	1936	1937	1936	1937	1936	1937	1936	1937	1936	1937
Number of fish containing recognizable food	158	197	57	82	87	76	16	5	1	24
Gobius minutus	1	4	..	..	8	2	..	1	..	..
Gobius microps	..	..	..	..	..	..	..	..	..	1
Gobius sp.	..	..	..	2	..	..	..	..	..	..
Clupea sp.	3	16	1	3	7	3	..	..	..	..
Teleost remains	13	23	7	1	15	11	4	1	..	..
Hydrobia ulvae	1	..	..	..	..	..	..	..	..	..
Gastropod fragments	..	1	..	..	..	..	..	..	..	..
Cardium edule	..	..	..	1	..	..	..	..	..	..
Carcinus maenas	2	..	2	9	..	..	1	..	..	2
Eupagurus bernhardus	..	..	..	..	..	..	1	..	..	..
Leander squilla and *Leander* sp.	..	1	..	1	..	..	5	..	..	..
Crangon vulgaris	103	125	48	55	33	11	10	3	..	11
Decapod larvae	..	..	..	7	..	..	..	..	..	..
Neomysis vulgaris	21	18	7	6	29	5	..	..	..	..
Schistomysis ornata	15	14	11	10	5	..	1	..	..	3
Praunus flexuosus	3	10	3	4	13	8	..	..	..	1
Mysid fragments	28	42	20	16	32	28	..	..	1	6
Caprella aequilibra	..	..	..	1	..	..	..	..	..	..
Pariambus typicus	..	1	..	..	..	..	..	..	..	..
Corophium volutator	..	1	..	2	..	1	..	..	..	8
Gammarus locusta and *Gammarus* sp.	12	8	1	9	16	18	1	..	..	1
Apherusa sp.	..	..	..	..	1	..	..	..	..	..
Amphipod fragments	4	1	1	..	8	20	1	..	..	1
Sphaeroma serratum and *Sphaeroma* sp.	..	..	..	..	4	..	..	..	..	..
Gnathiid larvae	1	..	..	..	1	..	..	..	..	..
Cyprids of *Balanus*	1	..	..	..	2	..	..	..	..	..
Temora longicornis	5	..	..	..	..	..	..	..	..	..
Copepod fragments	7	..	..	..	7	2	..	..	..	..
Crustacean fragments	35	12	3	19	28	5	1	2	..	3
Arenicola sp.	..	1	..	..	..	..	..	..	..	..
Spirographis spallanzani	6	..	..	2	..	..	..	..	..	..
Nereis diversicolor	..	1	..	..	..	1	..	..	..	1
Polychaete remains	1	1	..	1	..	2	..	..	..	..
Ova	1	..	..	..	..	..	..	..	..	..
Vegetable matter	..	1	..	..	..	..	..	..	..	..

Callionymus lyra L., the Dragonet

Dragonets were never numerous in the tuck-net hauls; 128 fish were caught during the investigation. Of this number, ninety-six (75 %) were taken between April and September. At West Mud dragonets were more numerous than on the Saltash marks. Twenty-nine fish caught at West Mud on August 8 1936 belonged to two length-groups: one of 3–7 cm., with a mean length of 5·6 cm. the second of 10–13 cm., with a mean of 11·9 cm. Fifteen fish taken on the same ground on June 25 1937, appeared to belong to a single length-group of 8–13 cm., with a mean length of 10·7 cm. Only one mature fish was taken, a male of 13 cm., at Saltash, in December 1935.

The food of the dragonet is shown in Table X: various molluscs, *Carcinus*, *Crangon* and gammarid amphipods are the food organisms most frequently taken: but this fish is remarkable for the variety of its diet. The width of this variety is illustrated by the fact that twenty nine different food organisms were found in 128 dragonets, and only twenty-five in 1157 flounders. Steven (1930) found the same catholic taste in food on the trawling grounds off Plymouth; but he found that Crangonidae were rarely caught, either because they were too agile, or because they live a little above the bottom where the fish usually hunts.

TABLE X. *CALLIONYMUS LYRA*: OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism. Number of fish containing recognizable food = 118.

	1936	1937		1936	1937
Calyptraea chinensis	1	..	*Corophium volutator*	3	4
Hydrobia ulvae	1	..	*Gammarus marinus*	1	..
Littorina sp.	1	..	*Gammarus locusta*	5	..
Cardium edule	8	5	*Gammarus* sp.	5	2
Paphia pullastra	2	1	Amphipod fragments	16	8
Spisula solida	1	..	*Sphaeroma* sp.	..	3
Scrobicularia plana	1	..	Gnathiid larvae	1	..
Macoma balthica	..	1	Cirripede cyprids	3	..
Pecten sp.	1	..	Copepoda	8	2
Mytilus edulis	7	..	Crustacean fragments	22	21
Molluscan fragments	2	2	*Spirographis spallanzani*	..	7
Carcinus maenas	10	11	*Melinna palmata*	1	1
Portunus sp.	..	1	Cirratulids indet.	1	..
Eupagurus bernhardus	3	2	*Nephthys hombergi*	1	1
Crangon vulgaris	3	25	*Phyllodoce* indet.	1	..
Decapod larvae	5	4	Polychaeta indet.	..	11
Neomysis vulgaris	1	1	Oligochaeta indet.	..	1
Mysid fragments	2	1	Hydroid fragments	..	2
Caprellid fragments	1	1	Algae	..	3

Dragonets are "very common on the sandy trawling grounds" off Plymouth (Ford, 1931). The relatively small numbers which are taken in the estuaries suggest that the brackish and muddy conditions of the Tamar and Lynher are not well suited to them and that they therefore do not make use of the sheltered waters as a nursery ground.

GOBIIDAE

It seems that there has been a change in the goby population of the Tamar and Lynher since 1928. Percival (1929), in his faunistic survey, made between June and November 1928, mentioned only *Gobius microps*, which he found to be "present in great quantities". The common goby of the period from November 1935 to December 1937 was *G. minutus*: of 179 small gobies examined between May and December 1937, 174 were *G. minutus* and 5 *G. microps*. *G. niger* was caught occasionally, *G. paganellus* once and *Aphya pellucida* four times.

Only the feeding habits of the gobies were investigated. Samples of

Gobius minutus large enough for the study of growth rates were not collected, and the other four species were not numerous enough to provide the necessary data. The food of the Gobiidae is shown in Table XI. Although so small a fish, *G. minutus*, feeding chiefly on shrimps and mysids, is a direct competitor with the flounder, bass and gadoids. On the other hand, the goby itself provides a meal for the larger fish of these competing species; and it is the principal food of the brill. Adult *G. minutus* fast in the breeding season.

TABLE XI. *GOBIIDAE*: OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism.

	Gobius minutus	*Gobius microps*	*Gobius niger*	*Gobius paganellus*
No. of fish containing recognizable food	86	4	20	1
Clupea sprattus	..	..	2	..
Hydrobia ulvae	..	..	1	..
Cardium edule	..	..	2	..
Scrobicularia plana	..	..	1	..
Lamellibranch fragments	..	..	1	..
Carcinus maenas	..	..	..	1
Crangon vulgaris	11	..	5	..
Decapod larvae	1	..	..	..
Neomysis vulgaris	16	..	1	..
Schistomysis ornata	2	..	..	..
Praunus flexuosus	1	..	..	..
Mysid fragments	5	1	..	..
Corophium volutator	4	1	..	..
Gammarus sp.	7	2	2	..
Amphipod fragments	5	..	..	..
Copepod fragments	6	..	..	..
Ostracod indet.	1	..	..	..
Crustacean fragments	20	..	4	1
Spirographis spallanzani	..	..	1	..
Polydora ciliata	1	..	..	..
Cirratulids indet.	3	..	..	..
Nephthys hombergi	1	..	1	..
Nereis diversicolor	5	2	1	..
Polychaete remains	5	..	4	..
Hydroid remains	..	..	1	..
Spawn	1	..	..	..
Algal fragments	..	..	1	..

	Aphya pellucida
No. of fish containing recognizable food	3
Teleost fragments	1
Schistomysis ornata	2

G. niger resembles *Callionymus* in the wide variety of its food, and eats more molluscs than most of the estuarine fish.

Agonus cataphractus L., the Pogge

Pogge were found on all the estuarine fishing grounds. On February 24 1936 big hauls of pogge were made on the Saltash marks; in a sample of fifty-five fish from this assembly, twenty-four were gravid females, 8–13 cm.

long, and twenty-nine ripe males, 8–12 cm. long. It is probable that these fish had come together to breed. Russell (1937) found post-larvae off Plymouth in the same month.

Pogge feed almost entirely on crustaceans as shown below, especially amphipods and young *Crangon vulgaris*. The stomachs of twenty of the ripe fish caught in February 1936 were examined; nineteen contained food, so there is obviously no fast at the breeding time.

Food of *Agonus cataphractus:* Number of occurrences of each organism

	1936	1937
Carcinus maenas	3	1
Crangon vulgaris	5	17
Schistomysis ornata	3	2
Mysid fragments	4	1
Corophium volutator	1	1
Gammarus locusta + *Gammarus* sp.	10	6
Melita palmata	7	..
Amphipod fragments	9	1
Crustacean fragments	7	1
Polychaete remains	1	..

Caranx trachurus L., the Horse Mackerel

Small horse mackerel are caught in the rivers in the late summer and early autumn. The length distribution of the fish was

July–Sept. 1936		July–Aug. 1937	
Length cm.	Number	Length cm.	Number
9	1	18	1
8	1	17	1
7	9	16	3
6	8	15	4
5	1	14	..
		13	3

The fish taken in 1936 had been feeding on *Neomysis vulgaris*, while those caught the following year contained the remains of small clupeoids, and crustacean and polychaete fragments. It may be that the latter fish belong to the same year-class as those caught in the previous summer; but this is only a presumption.

In addition to these small fish, two horse mackerel of 34·5 and 30·6 cm. were netted in September 1936; and two of 40·8 and 33·7 cm. were caught in a drift-net in October of the same year. One of these four contained several small clupeoids; the other three were empty.

Morone labrax L., the Bass

The bass is a fish which has been very little studied. The adults usually live close inshore on rocky coasts and off harbour bars, where the heavy, broken water makes it difficult to catch them by any method but rod angling. Some fish are netted in the estuaries and sandy bays of south Devon and Cornwall, and caught by line-fishermen around the Drift Rock off Tenby (Parker, 1934); but in general the bass is a quarry of the amateur rather than of the professional fisherman. The scientific literature of this species is exceedingly scanty, and is devoted chiefly to descriptions of the morphology and occurrence of the larvae.

In the Tamar numbers of immature bass are taken in the tuck-nets during winter: the best hauls are made where the bottom is stony and when a stiff onshore breeze is blowing. Aflalo (1904) recorded that large bass, also, come close inshore after strong wind, when the water is cloudy and disturbed. The inshore movements of the estuarine fish seem to take place only in daylight, for bass are rare in catches made during the night. It may be, however, that the absence of bass from the night hauls is due to an uprising from the bottom, similar to the nocturnal upward movements of hake (*Merluccius merluccius*) (Hickling, 1925).

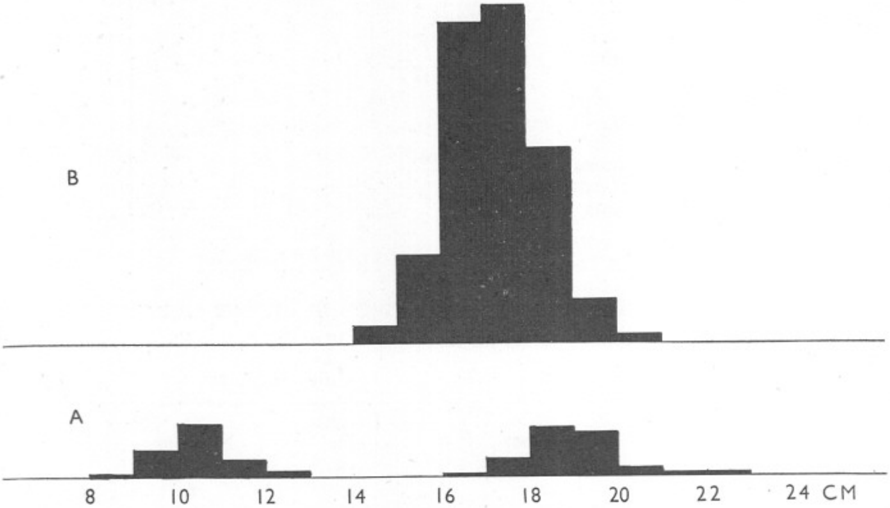

Fig. 16. *Morone labrax*; length frequency distributions. *a*, November 1935–April 1936. *b*, September 1936–April 1937.

The fishermen regard the bass as one of the most valuable fishes in the estuaries, for only the salmon commands a higher price.

Growth.

In the winter of 1935–6 the length-frequency histograms for the bass showed two clearly defined groups (Fig. 16 *a*), the smaller fish averaging about 10·5 cm. in length, the larger 19·0 cm. Fish of these two groups were caught regularly until the spring of 1936. There was practically no increase in length between November 1935, when the arithmetic mean lengths of the two groups were 10·5 cm. (11 fish) and 18·83 cm. (27 fish), and February 1936, when the means were 10·62 cm. (17 fish) and 19·1 cm. (25 fish). During the summer of 1936, few bass were caught—a large fish of 29 cm. in May, and four fish of 16·4, 15·8, 15·6 and 15·5 cm. in August.

In the autumn of 1936 and winter 1936–7, many bass were seined—454 fish between September 1936 and April 1937. With the exception of a single fish of 7·5 cm., caught in September, all these belonged to a single length-group (Fig. 16 *b*), corresponding with the larger of the two groups found in the previous year. The mean length of this group in September was 17·9 cm. (23 fish): by November it had increased to 18·35 cm. (34 fish): and by February to 18·47 cm. (127 fish). Through the summer of 1937 a few fish were taken in each month; the mean lengths of these very small samples showed a steady increase: to 20·5 cm. in June (2 fish), and 22·83 cm. (3 fish) in August. In the last months of 1937 only small numbers of bass were netted; the few fish obtained could be assigned to three different length groups of approximately 10, 18 and 26 cm.

The simplest interpretation of the length-grouping of young bass in the river is that there were two year-classes in 1935–6, the larger class being one year older than the smaller. The failure of the larger length-group in 1937, one year after a failure of the smaller group supports this view. Newly-hatched bass are rare off Plymouth; among fourteen post-larvae measured between 1925 and 1933 (Russell, 1935), those taken in April were from 4 to 7·5 mm. in length. The attainment of a length of 10 cm. within the first growth period is by no means impossible: herring, which never reach the size of adult bass, may grow to such a length within a year (Ford, 1928). It is therefore suggested that the "10 cm. long" fish are the O-group, and the "18 cm." fish the I-group. In the winter of 1935–6, both groups were well represented. In 1936, all the I-group fish appear to have gone down to the sea at the end of March, for many O-group bass were netted in April, but none of the larger size. In the winter of 1936–7, the I-group was strongly represented, but there was a complete failure in the recruitment of the stock. This lack of fish of the 1936 class was reflected in the winter of 1937–8 by a lack of I-group fish. The recruitment in 1937 was again a failure. Most of the fish of the 1935 class left the estuaries in the spring of 1937 as I-group fish, but a few remained through the summer, and as II-group fish were some 26 cm. long in the middle of winter 1937–8.

Patterson (1913) observed a rather similar length distribution of young bass in Breydon Water: "There were unprecedented numbers of small bass, locally known as 'sea perch', taken on Breydon Water in August and September (1913). In August they measured 4½ in. (11·4 cm.); some taken in October I measured at 7½ in. (19·05 cm.), an evident quick growth of 3 in. in 3 months." It is more probable that these fish actually belonged to different year-groups, the O-group and the I-group, rather than that an increment of 7·5 cm. should have taken place in so short a time.

Large bass are very rare in the estuaries; I saw only one big fish in more than two years' work. This was a specimen about 75 cm. long, taken in a salmon-net at Sheviock in July 1937. Holt & Byrne (1898) suggested that the estuaries might be a spawning ground of bass, but the complete lack of mature fish is against such a view. The tidal reaches of the rivers are a nursery ground, deserted for the sea before the gonads begin to mature.

Growth in the bass seems to take place during the summer months, with a period of no increase in winter. Ford (1937) found that the supraoccipital

TABLE XII. *MORONE LABRAX*: OCCURRENCE OF FOOD ORGANISMS

The figures give the number of fish containing the specified category of food organism for each month.

	1936											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	..	7	..	..	..	1	..	4	19	34	17	..
Teleost fish	..	..	..	..	..	..	..	..	1	5	2	..
Oikopleura sp.	..	..	..	..	..	..	..	..	1	..	..	..
Carcinus maenas	..	..	..	..	..	..	..	..	2	..	1	..
Leander sp.	..	..	..	..	..	..	..	..	..	..	..	..
Crangon vulgaris	..	1	..	..	..	1	..	3	16	19	12	..
Praunus flexuosus	..	..	..	..	..	..	..	1	3	..	..	..
Neomysis vulgaris	..	1	..	..	..	..	..	..	..	4	1	..
Schistomysis ornata	..	1	..	..	..	..	..	..	..	..	..	..
Mysids indet.	..	2	..	..	..	..	..	1	..	10	1	..
Sphaeroma sp.	..	..	..	..	..	..	..	..	..	..	..	..
Gammarus sp.	..	2	..	..	..	..	..	..	..	2	..	..
Corophium volutator	..	1	..	..	..	..	..	..	..	..	..	..
Amphipods indet.	...	1	..	..	..	..	..	..	..	1	1	..
Crustacea indet.	..	1	..	..	..	..	..	1	1	4	5	..
Nereis diversicolor	..	..	..	..	..	..	..	..	..	..	..	..
Phyllodoce sp.	..	..	..	..	..	..	..	..	..	..	..	..
Polychaeta indet.	..	..	..	..	..	..	..	..	..	..	1	..
Number of empty fish	..	7	..	..	..	0	..	0	2	8	1	..

	1937											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of fish containing recognizable food	11	13	20	7	..	1	1	3	1	..	4	2
Teleost fish	..	..	..	..	..	..	..	1	1	..	..	..
Oikopleura sp.	..	..	..	..	..	..	..	..	..	..	..	..
Carcinus maenas	..	..	1	1	..	..	..	1	..	..	3	..
Leander sp.	..	..	..	..	..	..	..	1	..	..	..	..
Crangon vulgaris	9	8	11	4	..	1	..	1	..	..	3	1
Praunus flexuosus	..	..	..	..	..	..	..	..	..	..	..	..
Neomysis vulgaris	..	..	1	..	..	..	..	..	..	..	..	..
Schistomysis ornata	..	..	..	..	..	..	..	..	..	..	..	..
Mysids indet.	..	..	..	..	..	..	..	..	..	..	..	1
Sphaeroma sp.	1	..	..	..	..	..	..	..	..	..	..	..
Gammarus sp.	..	2	6	..	..	..	1	..	..	..	..	..
Corophium volutator	..	..	..	..	..	..	..	..	..	..	..	..
Amphipods indet.	2	1	..	..	..	..	..	..	..	..	..	..
Crustacea indet.	2	1	3	1	..	..	1	..	..	..	..	..
Nereis diversicolor	4	2	3	1	..	..	..	..	..	..	1	..
Phyllodoce sp.	1	..	1	..	..	..	..	..	..	..	..	..
Polychaeta indet.	1	2	2	..	..	..	..	..	..	..	..	..
Number of empty fish	3	..	12	9	..	0	0	0	0	..	0	0

bone of this fish "exhibits growth zones of remarkable clarity". This phenomenon is consistent with a periodically interrupted process of growth.

Feeding Habits.

The bass is a hunter of active prey. Crustaceans, especially *Crangon vulgaris* and mysids, form the bulk of its food (Table XII). *Nereis diversicolor* and other polychaetes, and small teleost fish make up the rest of its diet. There is no marked change in feeding habits with increasing size. Some of the larger organisms are available only to the older fish, but throughout the period of estuarine life crustaceans form the bulk of the food consumed. In its feeding habits, the bass is a direct competitor with the flounder.

Scomber scombrus L., the Mackerel

In the autumn of some years, big hauls of mackerel are made in the estuaries. As many as 300 fish have been caught in one shot of a tuck-net on West Mud. The fishermen say that a good sprat year is also a good year for mackerel, as the mackerel follow, and feed on, the shoals of sprats.

Neither 1936 nor 1937 were "mackerel years". There were no fish at all in 1936, and only a few in 1937, when some fish were netted in Barn Pool, near the mouth of the Hamoaze in early August. Only eleven mackerel were caught during the investigation. These fish had all fed on sprats; one contained a single *Crangon vulgaris* in addition.

OTHER SPECIES

A variety of other species of fish are liable to occur in the Tamar Estuary, but only sporadically in small numbers. Those actually taken are recorded in Table XIII.

FISHES AND THE BIONOMICS OF THE ESTUARINE ANIMAL COMMUNITY

The life histories of the fishes caught in the estuaries have been considered species by species: it remains to consider the fish population as a whole, and as a part of the general community of estuarine animals. The essential organization of animal life in an estuary is that of a resident population providing food for a number of migratory predators. The period of estuarine life of these predators varies with the species, from about nine months in the case of a gadoid to three or four years in the flounder. In considering these immigrations of marine organisms three types of invasion may be distinguished—annual, irregular and sporadic.

The annual invasions are the means of recruiting the populations of those species of fish which are regularly resident within the rivers. In general the invasion by each species will take place at the same time each year. Most

TABLE XIII. RECORDS OF SPECIES OF WHICH SIX OR LESS INDIVIDUALS WERE CAPTURED

Species	Date and place of capture	Length cm.	Food	Notes
Raia clavata, Thornback Ray	8. viii. 36, West Mud	19·9 (across wings)	*Crangon vulgaris*, 6	♂
	7. x. 37, West Mud	*c.* 30·0	*Crangon vulgaris*	..
	2. xi. 37, Butterfly Ground	7·4 (across wings)	..	♀ Internal yolk-sac large: external yolk-sac still visible
Raia maculata, Spotted Ray	8. viii. 36, West Mud	11·4	*Crangon vulgaris*, 7	♀
Clupea alosa, Allis Shad	24. ii. 36, Butterfly Ground	47·5	One or two strands of Zostera, or grass	♂ Weight 1022 g.
Centronotus gunnellus, Butter Fish	26. vi. 37, West Mud	14·8	Crustacean fragments	..
Trachinus vipera, Lesser Weaver	24. ix. 37, Sheviock Wood	..	..	..
Arnoglossus laterna, Scald Fish	26. vi. 37, West Mud	8·2	*Crangon vulgaris* and amphipod fragments	..
Trigla gurnardus, Grey Gurnard	6. xii. 35, Saltash	11·3	*Neomysis vulgaris*, 10	..
	8. viii. 36, West Mud	8·9	*Crangon vulgaris* remains	..
Trigla hirundo, Tub Fish	28. xi. 35, Pier Ground	22·7	*Crangon vulgaris*, 2	..
	15. v. 36, Kiln Bay	13·7	*Crangon vulgaris*, 1 *Corophium volutator*, 1	..
	30. viii. 37, Kiln Bay	11·0	*Crangon vulgaris*, small, several	..
Trigla cuculus, Red Gurnard	2. x. 36, Kiln Bay	28·0	..	..
Cottus bubalis, Long-spined Sea Scorpion	16. xii. 36, Saltash	..	..	..
	8. xii. 37, Saltash	16·2 15·0	Empty Remains of a Teleost (?*Gobius* sp.) of *ca.* 80 mm.	..
Labrus bergylta, Bergylt	19. viii. 36, Pier Ground	..	..	Three fish
Crenilabrus melops, Gilt-Head	20. viii. 37, Pier Ground	11·3	*Carcinus maenas*, 1 *Nereis diversicolor*, 1 *Gammarus* sp., 1	..
Ctenolabrus rupestris, Goldsinney	6. vi. 36, Pier Ground	5·1 4·5	Copepod remains Copepod remains	..
Zeus faber, John Dory	13. viii. 37, Pier Ground	18·5	Empty	In the "old days" John Dories were caught under the ferry lights at Saltash: now they are considered to be very rare
Mullus surmulletus, Red Mullet	1. x. 36, Petre's	19·3 18·1	..	..
	23. ix. 37, Sandacre	8·5	Crustacean fragments	Ford (1931) records Red Mullet in the Lynher
Spinachia vulgaris, Sea Stickleback	Saltash	..	..	Several specimens were captured on rough ground near Saltash

species recruit their populations in the early summer, when the O-group come in from the sea; but the herring has two separate immigrations, the O-group in summer and the I- and II-group fish in the autumn. All those fishes which show an increase of population by regular invasion have a corresponding process of decrease by the return to the sea of the same fish at a later stage of their life history.

Other predators beside fishes come regularly to the estuaries. Every winter a number of cormorants (*Phalacrocorax carbo carbo*) feed daily in the Tamar and Lynher. Steven (1933) found that flatfishes formed nearly 40% of the numerical total of fishes taken by cormorants on the coasts of Cornwall, and that very nearly half of the fishes eaten by these birds were of marketable species. Observations made during the winter of 1936–7 showed that approximately 150 cormorants visited the rivers daily, and that each bird fed two or three times during the day. Since a cormorant can easily eat a 200 g. flatfish at a meal, and often takes considerably more, the steady toll which they exact from the fish population must be an ecological factor of some importance. Large numbers of wading birds visit the rivers each winter, and compete with the fish for such foods as *Cardium*, *Carcinus* and *Nereis*.

One other animal swarms in the estuaries each year, the scyphozoan *Aurelia aurita*. Allen (1931) records it as "most abundant in the estuaries in spring and summer". Percival (1929) found that "*Aurelia aurita* breeds extensively in the asexual stage on the mussel bed of Neille Point. The medusae regularly invade the river during the summer months...." In 1936 *Aurelia* was first seen on April 22, and by May 23 had become so numerous that a tuck-net could not be worked on the Kiln Bay ground, owing to the huge masses of jelly-fish which blocked the meshes and filled the cod-end. In early June the salmon fishers also were hindered by the great numbers of *Aurelia*. In the following year, *Aurelia* was not seen until May 5. It never became numerous in the lower part of the estuaries, and was not common enough to be a nuisance in the upper reaches until the end of June. Large numbers of juvenile *Aurelia*, preying directly on young fish, and the older medusae living on zooplankton (Lebour, 1923), introduce additional end-points into the food chains of estuarine animals.

The irregular invasions are of those species which appear in some years only—the mackerel is the best example. It is probable that the irregular migrants have a comparatively small effect on the resident fauna of the estuaries, and only appear when some organism suitable for their food is unusually abundant: for example, I am told by the fishermen that mackerel only appear when the numbers of young sprats and herring are exceptionally large.

Several sporadic invasions were seen during the period of the investigation. The most remarkable was the sudden appearance of large numbers of *Pleurobranchus membranaceus* in October 1936: none of the local fishermen had ever seen such a creature before, and some of them were of the opinion that the animal was "some kind of spawn". The immigration of this species, too large to be eaten by fish, probably has very little effect on the animal community in general, for it neither increases the supply of food for the predators nor the competition for food among them. On the other hand, an invasion of predatory animals, such as the cephalopods *Sepia officinalis* and *Alloteuthis subulata*, which appeared in the summer of 1937, must increase the competition for animal food. Alternatively, some invasions of smaller organisms may increase the supply of food—for example, in September 1937 *Caprella aequilibra* was found in the stomachs of several of the dabs and pout caught during one day's fishing.

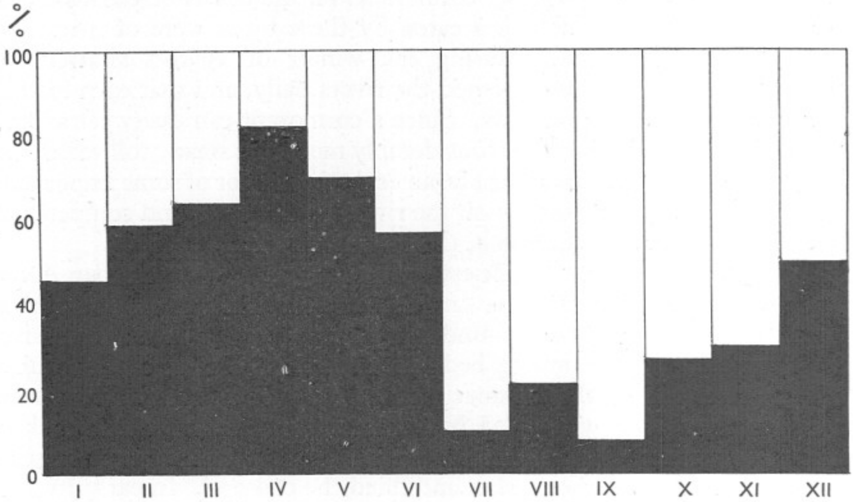

Fig. 17. Frequency of occurrence of *Schistomysis ornata* and *Neomysis vulgaris* in the food of estuarine fishes. (Expressed as percentages of the total monthly occurrences of *S. ornata*, black, and *N. vulgaris*, white.)

The number of species which are resident in the estuaries throughout their lives is small: and the number of different animals decreases with increasing distance from the sea. The composition of the resident invertebrate fauna varies from month to month. There is more than the obvious variation in numbers and size owing to the annual breeding season. Different species reach their maximum numbers at different times, and so bulk large or small in the diet of fishes at different seasons. This is well shown by the Mysidacea. Of the four mysids recorded by Percival, two, *Neomysis vulgaris* and *Schistomysis ornata*, are important fish foods. Fig. 17 shows the relative proportions in which these two species occur in fish stomachs from month to month. It will be seen that from February to June *S. ornata* occurs more frequently than *N. vulgaris*: that in the period July to November *N. vulgaris* is more numerous: and that in the depth of winter the two occur with equal frequency. The calculation was made from the combined figures for 1936 and 1937, from all species of fish. It may be suggested that this change in frequency of occurrence is due to a change in selection; but this explanation would be correct only in the improbable event of a simultaneous change in choice on the part of some twenty different species of fish. Percival says of *Schistomysis ornata* that it "had the shortest range and the least significance from the point of view of numbers". Since Percival's collections were made between June and November it seems probable that the period in which *S. ornata* was most numerous was missed, with the result that the importance of the organism in the estuarine fauna was not realized. Tattersall (1938) found *S. ornata* to be the dominant species in the winter maximum of mysids off Plymouth.

A result of the small number of wholly estuarine animals is that many kinds of fish are compelled to seek the bulk of their food in the ranks of a limited number of species. *Crangon vulgaris*, mysids, especially *Neomysis* and *Schistomysis*, and the polychaete *Nereis diversicolor*, are eaten by practically every species of fish in the rivers. It seems probable that there must be some competition for these commonest species.

On the basis of feeding habit, the fishes of the estuaries may be divided into four categories:

(1) Fish without competitors: the grey mullets are the sole example.

(2) Fish which feed to some extent upon the commonest organisms, but take the bulk of their food from species for which there is less competition: for example, the dab and the brill.

(3) Fish which feed to some extent on the commonest organisms, but have a wide choice of foods, and are thereby relieved from the effects of severe competition: for example, the plaice, the dragonet and *Gobius niger*.

(4) Fish which have many direct competitors for the bulk of their food: for example, the flounder, the bass and the gadoids.

On the first category it is necessary to make little comment. The grey mullets of the estuaries are exclusively vegetarian, and their food supplies are available for their use without competition from any other fish. The fundamental balance between the number of animals and the amount of food must be maintained: but the competition being entirely intrageneric, the grey mullet population is able to make full use of the available pasture.

The members of the second category are in a situation scarcely less favourable. The case of the dab is typical. When the young fish first enter the estuaries, they feed upon small crustaceans in direct competition with the juvenile members of other species. Within a few weeks, however, their diet begins to change, for the fish becomes large enough to feed upon the sabellid, *Spirographis spallanzani*, which is the staple diet of the species during estuarine life. Although some crustacean diet will always be taken, and though some other fish eat small numbers of *Spirographis*, the dab is largely freed from interspecific competition as soon as it becomes big enough to nip off and swallow a few sabellid tentacles. The total production of dab in any year must be to some extent controlled by the total production of worm. Were the supplies of *Spirographis* to fail, it is probable that the dabs could maintain themselves, and grow, on some other diet—for example, *Crangon vulgaris*. This, however, could only be done in the face of considerable competition from other species.

The fish of the third category obtain a measure of freedom from interspecific competition by a different method. The plaice, a typical fish of this category, feeds with apparently equal zest upon a large assortment of foods. For example, in the dab, only three groups of polychaete occurred ten or more times—*Spirographis*, *Polydora* sp. and cirratulids, and of the recognizable polychaetes, 93% were *Spirographis*: in the plaice, seven groups of polychaetes occurred ten or more times—*Spirographis*, *Ampharete grubei*, *Melinna palmata*, *Nephthys hombergi*, *Nereis diversicolor*, *Polydora* sp. and cirratulids—and *Nephthys*, the most numerous, made up only 21% of the recognizable forms. It was observed that fishes having a wide choice of foods were the only species which fed with any frequency upon molluscs.

It should, perhaps, be emphasized that a species is not limited to one of these categories. The dab shows a considerable width of choice in its food: but is most remarkable for its concentration upon one of many possible articles of diet.

There remain a number of fish, including some of those most numerous in the rivers, which are subject throughout their estuarine lives to steady interspecific competition for the bulk of their food. These are the fish which feed largely on *Crangon*, mysids and amphipods—the flounder has competitors for every item in its diet. The success of a year-group of any one of the fish in this category depends not only on the numerical strength of the recruitment of its own species, but on the size of the corresponding year-groups of its competitors.

It is, of course, possible that there is enough food for all the fish in the estuaries to grow at maximum speed, and that competition for food is more apparent than real. Extensive transplantation experiments with marked fish might reveal retarded growth within the estuaries, but could not show whether the hurtful competition was inter- or intraspecific. Observations made over a long period, in which numerical fluctuations in the year classes of different species and the growth rates of each year class were noted, would provide material from which inferences on the effects of competition might be made. From this two-year study of the estuaries one suggestion may be put forward. The growth rate of the flounder was found to be lower than that of populations in Europe: the growth rate of the dab seemed to be higher. It may be that there is a connexion, on the one hand, between the retarded growth of the flounders, and the steady competition for food which they must face, and, on the other, between the rapid growth of the dabs and their comparative freedom from interspecific competition.

The small number of molluscs eaten by the estuarine fishes is remarkable. In many localities plaice and dabs feed largely on molluscs: in the North Sea Todd (1915) found that plaice ate more molluscs than anything else, and that dabs competed with them for that diet. On the trawling grounds east of Plymouth, *Cultellus pellucidus* is an important food of the dab. Ford (1925) has pointed out that "before the potential value of a bed of lamellibranchs as food for fishes can become known, the precise food value of the successive stages in the life history of each lamellibranch must be determined". If the limited number of species of lamellibranch inhabiting the estuaries have rapid growth rates, they may very quickly become too large to be preyed upon by the immature flatfish. Of the five marine species listed by Percival (1929) four —*Mytilus edulis*, *Scrobicularia plana*, *Paphia pullastra* and *Cardium edule*—do, in fact, grow to a large size. It is known that the food taken by a fish is dictated by its hunting habits (Steven, 1930). Within the range of possibility of any one species there is usually a considerable variety of diets, and the food chosen may be dictated by two factors beside that of simple availability. The possible factors are "preference" and a habit-formation resulting from the interaction of this preference with availability. The fact that one article of diet may be preferred to another by a member of the higher vertebrates is a matter of common experience: and it is probable that a fish also will select one food rather than another, for no more reason than that it "likes" the chosen food. Scott (1922) found that in young plaice "individuals in a catch are found to have been feeding on one particular species, although it is quite obvious from the examination of the stomachs of their companions that species belonging to the same group and to other groups, were present". Wailes (1935) found that in the Pacific herring (*Clupea pallasii*) "there is evidence for belief in individual specialization on certain types of food". Allen (1938) found that brown trout (*Salmo trutta*) showed an individual selection of food organisms.

It is, moreover, possible to accustom fishes to a wholly unnatural diet—as witness the ordinarily vegetarian grey mullet in the Plymouth tank room, which have formed the habit of eating pieces of chopped squid, in the absence of vegetable food. If there are comparatively few molluscs of a sufficiently small size in the estuaries, the fishes may form a habit of eating other organisms, with the result that shellfish are taken in even smaller numbers than their density on the ground warrants.

The feeding habits of the members of an animal community may be closely observed. The food taken may be compared with the available supply, and special preferences or rejections noted. Changes in diet and similarities in diet may be listed: but, at the end, there must remain wide gaps in the exact knowledge of the relationships between the different species. It is rarely possible to say that the effect of one species upon another is wholly beneficial, or wholly destructive. Competition for a similar diet can only affect the competing organisms when there is not enough food for all of them to feed to repletion at all seasons of the year. When the food supplies for a species are inadequate, the reduction in numbers caused by a predator can only benefit the survivors. Cormorants removing 500–1000 fish a day from the estuaries may serve to increase the growth rate of those which are left: the loss from the point of view of numbers is severe: the loss in total weight of fish may not be great. Small *Aurelia aurita* reduce the number of the juvenile fish which have newly entered the estuaries: but the larger medusae compete with the survivors for zooplanktonic organisms. The effect of the scyphozoan upon the fish may be beneficial at one stage in its life history and is almost certainly detrimental at another. The large flounder which consumes a number of *Gobius minutus* removes so many of the competitors with the young fish of its own species.

If, on the other hand, the habitat be capable of supporting an excess of food for all the predators, the relationships between the members of the community are simplified. The effect of each predator upon its prey is wholly unfavourable, not only from the individual but from the specific point of view. Only investigations on an enormous scale—quantitative faunal surveys of vast extent, biochemical assays of the food value of every species, experimental studies of populations in captivity and of the dietetic demands of each member of the fauna—could reveal the exact balance that exists between the different members of an animal community. But even a limited investigation of that community can show the possibilities of competition between organism and organism, and the actual reactions of certain species to the sum of the environmental factors working upon them.

SUMMARY

The Saltash tuck-net is used in the estuaries of the Tamar and Lynher for seine netting on soft mud. The fishery is carried on during autumn and winter, from open boats with crews of two men.

Hauls were made with a tuck-net in every month between November 1935 and December 1937.

The fish population of the estuaries is essentially marine: its composition changes from month to month with the arrival from, or departure to, the sea of different species of fish. With the exceptions of salmon (*Salmo salar*), sea trout (*Salmo trutta*) and some of the Gobiidae, all the fishes of the estuaries go down to the sea to spawn.

The flounder (*Pleuronectes flesus*) is the typical fish of the estuaries. Flounders live in the estuaries until the onset of sexual maturity, when they go down to the sea to spawn: a few female flounders return to brackish waters after spawning. The growth rate of the flounder varies greatly from fish to fish. At two years old the mean length is about 11 cm., and at four years it is 18 cm. The food of the flounder consists of Crustacea and Polychaeta.

The other species of fish living in the estuary are listed, with remarks upon their periods of estuarine life, growth rates and food.

The relationships between the members of the estuarine fish community are discussed.

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THE ECOLOGY OF THE TAMAR ESTUARY
IV. THE DISTRIBUTION OF THE FAUNA AND FLORA ON BUOYS

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(Text-figs. 1 and 2)

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INTRODUCTION

In considering the fauna and flora of estuaries, particularly the question of penetration from the sea and zonation along the estuarine gradient, a study of the growth on floating buoys has a special significance. The buoys supply a habitat in which certain variables affecting the bottom fauna are eliminated. Not only is a substratum of a constant type provided, but because the buoys are floating the organisms attached to them are subjected to a constant degree of immersion, thus eliminating an important element in the fluctuation of the environment, due to the rise and fall of the tide, to which the fauna and flora of the shore is subjected. A series of buoys along an estuary, such as exists in Plymouth Sound and Hamoaze, virtually supplies an experimental series in which the only important environmental variables are *salinity conditions* and (to a much lesser degree) *turbidity* of the water.

According to Orton (1930), the black varnish coating of buoys provides more or less "innocuous surfaces". Buoys are primarily available only for sessile organisms such as barnacles, mussels, coelenterates, Bryozoa, ascidians and algae. But once the latter have settled, they collect among their crevices, byssi and holdfasts, quantities of silt and plant debris, and this in turn provides a foothold and food for amphipods, and to a lesser extent, worms. Animals such as *Ligia*, *Orchestia* and *Jaera*, which have no pelagic stage in their development, have slender chances of reaching the buoys in mid-river; while certain species, such as *Littorina littorea*, even though they have pelagic larvae, cannot withstand constant immersion (Flattely & Walton, 1922, p. 207). Colonization must be affected by the time at which the buoys are laid down (see Appendix I, p. 86), for this may happen when one species is breeding and it may have established itself before another, which breeds later, is able to gain a foothold. How far the present distribution is influenced by this fact it is difficult to say, but the possibility must not be overlooked. The longer a floating structure is in the water, the richer and more varied its fauna tends to be (cf. Orton, 1930; Fraser, 1938).

MATERIAL AND METHODS

A series of buoys extending from open sea (Mewstone) to typical estuarine conditions (Neal Point) was chosen. Certain physical and chemical factors for this area have already been discussed (Cooper & Milne, 1938, 1939; Milne, 1938). The buoys varied to some extent in size and shape, but all had some flat, vertical surfaces from which collections could be taken and zonation measured; their immersed portions varied from one to a little over two metres in depth. Buoys lie at their moorings from 12 to 15 months (see Appendix I) and then are towed gently to the wharf a little above Cremyll where they are scraped and repainted. Those mentioned here were examined immediately after they were raised from the water. There are other buoys closely neighbouring, or at the same level in the estuarine gradient as, each of the buoys named in Fig. 1. With the exception of New Rock, Panther and H 1 buoys, one to three of these were examined in each case as a check.

The following buoys, not shown in the map in Part I, are situated in relation to buoy D 4 as follows (approximately): Mallard, 1 km. west; New Rock, 3·2 km. south-south-west; Panther, 3·3 km. south; and Mewstone, 6·5 km. south-south-east. The Mallard and D buoys lie inside the Sound; while the New Rock, Panther and Mewstone lie outside the Breakwater.

Collections were made separately from each of the three plant zones, and from three different points in each zone. The dimensions of the areas scraped were governed by the uniformity of the distribution in the zone and by the size of the zone. In Zone III, where most of the fauna is concentrated, three squares of 20 cm. side were scraped. The macrofauna and macroflora only were studied; microfauna like copepods and Protozoa, and microflora like coating diatoms were omitted.

Horizontal Distribution in the Estuarine Gradient

The horizontal distribution on the buoys is given in Fig. 1. Neal Point is not necessarily the up-river limit of those organisms found on it, since no buoys were available for examination above this point. It seems reasonable to take the absence of species on Neal Point buoys which are present on H 15 as indicating their limit at H 15, even though there are no buoys above Neal Point, for the Hamoaze series (H 1–H 15 and Neal Point) was laid down and lifted about the same time.

The following have been omitted from Fig. 1; of these *A–E* are algae, the remainder animals:

List I

A. The filamentous green algae, unidentified, which are abundant on all the buoys in the series.

B. Fucoids, young stages, present on H 1–H 11.

C. *Ascophyllum nodosum* Le Jol, present on H 7 and H 11, and almost full grown on the former; strangely absent on the seaward buoys.

D. *Hypoglossum woodwardii* Kylin, found only on H 11, rare.

E. *Chylocladia* sp., on H 1, rare.

F. *Anomia ephippium* L., on Mallard buoy, rare.

G. *Idotea granulosa* Rathke, on Mallard and H 4 buoys, rare.

H. *Limnoria lignorum* (Rathke), in wood baulks protecting the surface of H 7, and tunnels only on H 11, common.

I. *Cellepora costazii* Audouin, common on Mewstone and abundant on New Rock buoys.

J. *Schizoporella hyalina* (L.), on Panther buoy, present.

K and *L*. *Cirratulus cirratus* (O. F. Muller) and *Polyophthalmus pictus* (Dujardin), on Panther buoy, present.

M. *Ophiothrix fragilis* (Abildgaard), on Mewstone, common but young, disk 3–5 mm.

N to *R*. *Gonothyraea loveni* Ellis & Sollander, *Opercularella lacerta* (Johnston), *Calycella* sp., *Campanulina repens* Allman, *Coryne* vel *Syncoryne* sp., all present but rare on H 7 and H 11 buoys, possibly present on others—but method of collection inefficient (see Appendix II).

S. *Tubularia larynx* Ellis & Sollander, similarly, but noticed in abundance on Panther and Mallard, and common on H 4, while adult stalks were present on Neal Point buoy. *Tubularia* dies off in winter.

T. *Thalassomyia frauenfeldii* Zett and *Clunio marinus* Hal, insect larvae (see Fig. 1), and possibly others, since investigation was not exhaustive.

In Fig. 1 the data for Mewstone buoy are also not included because there is a possibility that one or two species were missed, since the collection was made several hours after the buoy had been taken from the water. The species are listed below. Several of the marine species present on other open sea buoys are absent but Mewstone is more out of the zone affected by estuarine waters.

List II. *Mewstone Buoy*

Filamentous green algae, *a.*; *Ulva linza* var. *lanceolata* (Kutz), *a.*; *U. lactuca* var. *latissima* (D.C.), *c.*; *Laminaria digitata* Lamour, *a.*; *L. saccharina* Lamour, *c.*; *Mytilus edulis* L., *c.*; *Jassa falcata* (Montagu), *a.*; *Stenothöe monoculoides* (Montagu), *c.*; *Balanus*

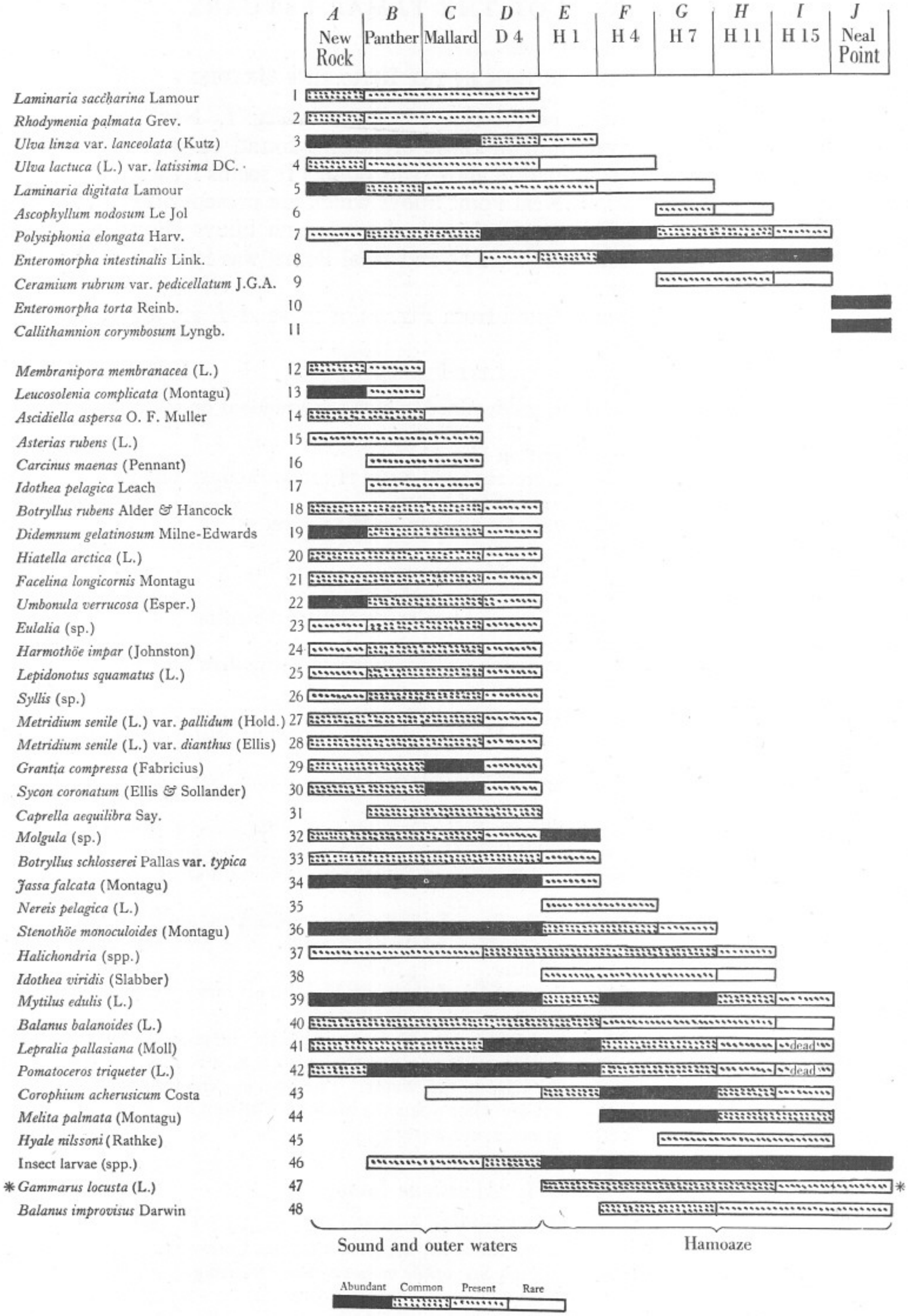

Fig. 1. Quantitative horizontal distribution showing limits on buoys in the Tamar Estuary, Plymouth Sound and outside.

* Later found that at Neal Point buoy (only) this was a var. of *Gammarus zaddachi* Sexton.

balanoides (L.), *c.*; *Lepralia pallasiana* (Moll), *c.*; *Cellepora costazii* Audouin, *c.*; *Pomatoceros triqueter* (L.), *c.*; *Ophiothrix fragilis* (Abildgaard), *p.*
(*a.* abundant; *c.* common; *p.* present.)

As in the Tees (Alexander, etc., 1935) it was found "that the range of species even of the same phylum differed greatly". A considerable difference is also evident in the resistance, i.e. penetrative power of two species of the same genus (cf. *Enteromorpha*, *Ulva*, *Laminaria*, *Idotea* and *Botryllus*). Since the Hamoaze series, H 1 to H 15 and Neal Point, were all laid during November–December 1935 and examined during February–March 1937, there were at least thirty species available for colonization of these buoys (see Fig. 1). This is the total species on all the buoys of the Hamoaze series. But the number of species present on each buoy was as follows (*A*, *B*, *N–S* in list I, and insect larvae are omitted.)

H 1	H 4	H 7	H 11	H 15	Neal Point
19	17	19	18	10	4

Moreover, there is not one species which is present on all the Hamoaze series, though five—*Polysiphonia elongata*, *Enteromorpha intestinalis*, *Mytilus edulis*, *Balanus balanoides*, *Corophium acherusicum*—are present on H 1 to H 15.

In the Tamar there is a great deal of suspended silt and this increases up-river. It is sometimes suggested that animals with delicate ciliary or pore mechanisms (suspension feeders) will be limited by suspended silt. The sponges, Coelenterata, Polyzoa and tunicates, together with *Mytilus*, *Pomatoceros* and *Balanus* may be classed as suspension feeders. The numbers of suspension and non-suspension feeders on each buoy in the series were as follows:

Buoy	Suspension feeder	Non-suspension feeder
Panther	19	14
Mallard	15	16
D 4	14	11
H 1	7	7
H 4	6	8
H 7	6	8
H 11	6	6
H 15	3	5
Neal Point	1	2

Fig. 1.
Buoys and their positions

In the map in Part I, it will be seen that the mouth of the estuary (zero position) is taken as being Devil's Point. The position of the buoys relative to this are as follows:

Sound and Outer Waters	*A.*	New Rock, 3·2 km. S.S.W. of D 4
	B.	Panther, 3·3 km. South of D 4
	C.	Mallard, 1·0 km. West of D 4
	D.	D 4, Drake's Island, 1·9 km. from zero position
Hamoaze	*E.*	H 1, 1·2 km. up river from zero position
	F.	H 4, 2·25 km. ,, ,, ,, ,,
	G.	H 7, 3·3 km. ,, ,, ,, ,,
	H.	H 11, 4·9 km. ,, ,, ,, ,,
	I.	H 15, 6·0 km. ,, ,, ,, ,,
	J.	Neal Point, 9·25 km. ,, ,, ,,

The five species of hydroid (*N–R*, List I) on H 7 and H 11 buoys, and *Tubularia larynx* on H 4, are omitted. Thus on the Tamar buoys, just as in the bottom fauna of the Tees, Tay and Tamar estuaries (Alexander, *et al.*, 1935) there is no marked difference between the penetration of the two groups.

Although the relative abundance as well as the range is shown in Fig. 1, it must be clearly understood that too much stress must not be laid on the former since no detailed counts were made. The figure is only intended to indicate trends in density. In any case, the size-composition would be necessary to show the degree of ecological success. Generally the organisms become less numerous and smaller towards the lower end of their salinity range, as very obviously shown without measurement by *Laminaria* and *Mytilus*. Where there is a tendency to lesser density, not size, towards the seaward end of the range, e.g. in *Polysiphonia*, *Halichondria*, *Lepralia*, *Pomatoceros* and *Corophium*, this must be partly due to competition for space. Those organisms which do penetrate the estuary have some of the space normally shared with those which do not, since fewer species come in than drop out. Thus (excluding *A*, *B* and *N–S* in List I, and insect larvae) it is found that of the 39 species present on the Panther buoy, only 34 penetrate to the Mallard (37), 30 to D 4 (31), 14 to H 1 (19), 10 to H 4 (17), 9 to H 7 (19), 7 to H 11 (17), 4 to H 15 (10), and 0 to Neal Point (4). (The figures in brackets represent the total number of species present on the buoys with the exceptions noted above.) For example *Polysiphonia elongata* becomes denser at D 4 where the other algae, *Laminaria digitata* and *L. saccharina*, accompanying it in Zone III are becoming scarce; *Halichondria* similarly at D 4, where *Sycon compressum* and *Grantia compressa* are beginning to fall away. Of course the competition is not necessarily within a phylum only. Numbers are also reduced when one species gives place to another with a certain amount of overlapping, especially where those species have similar habits: this occurs where *Jassa falcata* begins to give place to *Corophium acherusicum* at H 1 (both live in tubular galleries in silt); and to a lesser extent with the two species of barnacles. A very abrupt changeover with no overlapping is seen where, at H 15, *Polysiphonia* is completely replaced by *Callithamnion* in Zone III, and *Enteromorpha intestinalis* by *E. torta* in Zone II. Zonation, as pointed out by Elton (1927), is more clearly marked in plants than in animals.

The occurrence of *Nereis pelagica* at H 1 and H 4 only, and not seawards of this, is explained by the fact that on these buoys a few had got a foothold in empty nailholes in the protecting wood baulks. But the presence of such truly marine organisms as *Gammarus locusta*, *Ascophyllum nodosum* and fucoids on Hamoaze buoys and their absence on more seaward buoys is not so easily explained. Fig. 1 shows that *Molgula* is common on all seaward buoys but tends to decrease towards the Hamoaze; just inside however, at H 1 buoy, it suddenly attains an extraordinary abundance, to a large extent crowding out *Mytilus* and *Polysiphonia*. After H 1 it drops out abruptly on buoys, though it is found opposite H 4 in St John's Lake.

The following are the dominant forms grouped roughly in order of their importance:

In the Sound and Outer Waters:

(i) *Mytilus*, *Jassa*, *Ulva*, *Polysiphonia*, filamentous green algae.

(ii) *Laminaria*, worms and Bryozoa, *Tubularia*.

In the Hamoaze and up to Neal Point:

(i) *Mytilus*, *Corophium*, *Enteromorpha*, *Polysiphonia* (replaced, as noted above, by *Callithamnion* at Neal Point).

(ii) *Lepralia*, *Pomatoceros*, *Gammarus*.

Speaking generally for the whole series, the dominant forms are filamentous green algae, *Ulva*, *Enteromorpha*, *Polysiphonia*, *Mytilus* and amphipods. The mussel competes with the algae, chiefly *Polysiphonia*, with which it shares Zone III.

ENVIRONMENTAL CONDITIONS

Salinity, temperature and hydrogen-ion concentration are discussed more fully in Part III of this series (Milne, 1938). Current and wave action are similar on the H 1–H 15 series of buoys; a little more wave action might be expected at those buoys between Devil's Point and the Mallard, though the current is much the same; Panther, New Rock and Mewstone buoys are subject to the violence of the open sea. The current in the Hamoaze and Sound, reversing with the tide, varies from $1\frac{1}{4}$–$2\frac{3}{4}$ knots. Suspended matter, always present in greater quantity than in the sea, increases up-river and during winter or spate conditions (Cooper & Milne, 1938). The sides of the buoys are perpendicular so that silt will not easily be deposited. There are no industrial effluents in the Tamar and only a relatively small amount of crude sewage. The hydrogen-ion concentration seldom falls as low as pH 7·5 even at H 15. Diurnal fluctuation of the temperature of the water passing the buoys is small but the seasonal range increases up-river—at Saltash the extremes may be 2–4° C. higher or lower than those at the Breakwater. Organisms on the buoys are subject to constant immersion, and this, as noted before, excludes certain species. This condition, however, avoids desiccation and large fluctuations in temperature, but lays the organisms open to more protracted and greater salinity fluctuation than on an equivalent point on the shore. Various workers have shown that certain marine organisms can be accustomed to salinities steadily decreasing to that of freshwater, provided the process is sufficiently gradual. Rate as well as range of salinity fluctuation is therefore important. Part III shows how this varies from high to low water, daily, fortnightly and seasonally from the exceptionally rainy winter of 1936–7 to the rather dry summer of 1937, so that most contingencies are covered. There is a progressive increase in the range of fluctuation in an up-river direction. Differences such as 12·8 ‰ (9 atm. of osmotic pressure) at Saltash, and 5·5 and 5·2 ‰ (3·5 atm.) at Drake's Island and the Breakwater respectively may have to be withstood in 6 hr. (tide) at springs in winter;

while summer conditions are more stable, the corresponding figures being 1·8 $^{\circ}/_{\circ\circ}$ (1·5 atm.) and 0·2 and 0·3 $^{\circ}/_{\circ\circ}$. Maximum ranges within one tidal cycle were 33·7–7·6 $^{\circ}/_{\circ\circ}$ at Saltash, 33·7–19·5 $^{\circ}/_{\circ\circ}$ at Drake's Island, and 34·9–26·6 $^{\circ}/_{\circ\circ}$ at the Breakwater.

Fischer-Piette (1931 *et seq.*) has shown that salinity is by far the most important agency controlling estuarine distribution. He demonstrated that horizontal limits fluctuate according to rainfall (i.e. lowering of salinity) summer and winter and from year to year.

With the aid of Fig. 1 in the present paper and Table II in Part III, and the map in Part I, some idea of the resistance of certain species to salinity fluctuation may be formed.

FLUCTUATION OF LIMITS WITH FLUCTUATION OF ENVIRONMENT

There was an exceptionally high rainfall and therefore a correspondingly low salinity in the winter of 1936–7. Towards the end of this rainy period skeletons of *Pomatoceros* and *Lepralia* were present at H 15, while living specimens were found on H 11; similarly, *Limnoria* tunnels were found to be occupied at H 7 but empty at H 11. This withdrawal of limits is undoubtedly due to a steepening of the estuarine gradient at this time (Fischer-Piette, 1931). Crawford (1937, p. 651) in the years immediately preceding states "in 267 specimens counted at random from Neal Point Buoys there was found

Corophium acherusicum	259	*Gammarus zaddachi*	2
C. insidiosum	3	*Melita palmata*	1
Jassa falcata	2		

Idotea viridis and *Hyale* were also present." Of these, only *Gammarus zaddachi* was present when the buoys were examined in March 1937.

But this rainy winter did not cause the retreat of all organisms. Percival's (1929) lists of intertidal organisms were made during and after a dry summer,* while after the wet winter (1936–7) the writer noted the intertidal penetration of seven of his species:

	Penetration in kilometres	
Species	1928	1937
Molgula sp.	2·0	2·0
Mytilus edulis	13·3	13·3
Littorina littorea	9·4	9·4
L. rudis	9·4	9·4
Balanus balanoides	13·3	11·0
Halichondria spp.	9·4	5·0
Littorina obtusata	9·4	11·0

Four species had maintained their position, two had retreated and one had actually advanced. With the exception of one retreating species, *Halichondria*,

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* Percival does not mention the rainfall of the preceding winter.

and one static species, *Molgula*, the remainder are all able to close up and possibly escape harm while awaiting the return of suitable conditions (see later).

COMPARISON WITH PREVIOUS WORK

Orton's (1930) list of the chief organisms growing on or in experimental material—floating rafts, and piles fixed at L.W.S.T.—in Cawsand Bay and Plymouth Sound differ from the present findings chiefly because some of the material was not subject to constant immersion, and most of his rafts were in the sea three times as long as the Admiralty buoys.

Percival's (1929) distribution of intertidal and bottom species in the Tamar are compared in Table I. There are differences both in numerical order of and extent of penetration. If salinity alone were the limiting factor then at least the numerical order of penetration would be the same. The distribution on buoys ought to be the best indicator of order of penetration, or resistance to the salinity gradient, of those animals able to live on buoys: for while the substratum of the shore is irregular in many ways, thus bringing other factors into play, that on the buoys is constant in texture and slope. Organisms on the shore generally penetrate farther than those on buoys (Table I). This is believed to be due chiefly to the greater and more protracted salinity fluctuation on the buoys than on a corresponding point on the intertidal area or bottom. Mussels were absent on the Neal Point buoys in spring 1937, while the richest bed in the Plymouth district lies directly beneath them on the bottom.

TABLE I. COMPARISON OF EXTENT OF PENETRATION OF SPECIES COMMON TO THE STUDIES OF PERCIVAL (1929) AND THE PRESENT PAPER

Distances given in kilometres up-estuary (+) or down-estuary (−) from zero position at Devils' Point (see map in Part I).

(*Gammarus locusta* is omitted because Percival did not recognize *G. zaddachi* as a separate species.)

Intertidal and Bottom 1928	km.	Buoys 1937	km.
Carcinus maenas	+21·7	*Balanus balanoides*	+6·0
Ascidiella aspersa	+14·0	*Melita palmata*	+6·0
Botryllus schlosserei	+13·6	*Lepralia pallasiana*	+5·0
Pomatoceros triqueter	+13·6	*Pomatoceros triqueter*	+5·0
Melita palmata	+13·3	*Botryllus schlosserei*	+1·0
Balanus balanoides	+13·3	*Jassa falcata*	+1·0
Lepralia pallasiana	+11·0	*Harmothöe impar*	−2·0
Jassa falcata	+ 9·4	*Metridium senile*	−2·0
Ophiothrix fragilis	+ 9·4	*Ascidiella aspersa*	−3·0
Harmothöe impar	+ 9·4	*Carcinus maenas*	−3·0
Metridium senile	+ 7·7	*Cirratulus cirratus*	−5·3
Cirratulus cirratus	+ 5·4	*Ophiothrix fragilis*	−7·5

The effect of rainfall conditions on extent of penetration is discussed in the preceding section.

Fraser (1938) investigated the fauna of buoys submerged for one year in the Mersey Estuary in a salinity gradient varying from sea conditions down to

27·4‰. This resembles salinity conditions in the Sound and Outer Waters at Plymouth. The fauna in the Mersey is poorer in number of species than the Tamar; sponges, polyzoa and *Carcinus maenas* are absent in the former. Throughout the range in the Mersey estuary, *Mytilus edulis*, *Harmothöe imbricata*, *Lepidonotus squamatus*, *Nereis pelagica*, *Podocerus variegatus* and *Asterias rubens* are common; *Metridium senile* and hydroids, *Balanus crenatus*, and ascidians are less common; *B. balanoides* is practically absent. *Jassa falcata* is common at the seaward end of the range (cf. Tamar). The density of *Asterias* and *Nereis* here contrasts with their paucity in the Tamar. Apart from geographical position, the pollution and possibly the silt suspension factors, the former of which is much greater in the Mersey, may largely account for the differences.

The various comparisons made illustrate the difficulty of attributing the limiting factor to salinity alone.

Vertical Distribution

The flora of the buoys showed a particularly clean-cut vertical zonation. The dimensions of the various belts are given in Table II; the data are averages from 2 to 4 buoys (except for Panther where only one buoy was examined) and three measurements were made on each buoy.

TABLE II. WIDTH OF THE ALGAL ZONES ON THE BUOYS IN CENTIMETRES

Zone III was limited by the depth of the buoy.

Buoy	Zone I	Zone II	Zone III
Panther	0–17·8	17·8–35·6	35·6–127·0
Mallard	0–18·6	18·6–35·6	35·6–218·5
D 4	0–17·8	17·8–35·6	35·6–111·8
H 4	0–10·2	10·2–25·4	25·4–127·0
H 7	0– 9·7	9·7–22·3	22·3–246·6
H 11	0– 8·0	8·0–18·0	18·0–183·1

Uppermost was a narrow belt of filamentous green algae unidentified. This belt, termed Zone I, was present on all the buoys.

Just below was a slightly wider belt, Zone II, occupied by *Ulva* or *Enteromorpha*, or both. *Ulva* (2 spp.) was present from Mewstone to H 4 and *Enteromorpha* from Panther to Neal Point. *E. intestinalis* was completely replaced by *E. torta* at Neal Point buoys, while the two species of *Ulva* are present together for some part of their horizontal range, though *U. lactuca* finally outstrips *U. linza* in penetration of the estuary.

Below this again was a very much wider belt, Zone III, where *Polysiphonia elongata* was dominant. *Polysiphonia* was absent at Mewstone, present from New Rock to H 15, and completely replaced by *Callithamnion corymbosum* at Neal Point. A few brown algae—chiefly *Laminaria* spp., and other red algae—such as *Rhodymenia* and *Ceramium*, were present also in Zone III. Moreover, on the seaward buoys, some fronds of *Ulva lactuca* tended to spread downwards a few centimetres and mingle with *Polysiphonia*, but the latter was by far the dominant.

Thus Zones I and II were occupied solely by green algae, while Zone III was occupied predominantly by red, and to a lesser extent by brown.

Both the size and density of fronds tended to increase a little downwards in each zone. Zone II was more luxuriant than Zone I, and Zone III than Zone II.

No macrofauna was present in Zone I; in Zone II a few species were present, especially *Stenothöe*, insect larvae, and occasionally *Idotea*; but the greater part of the fauna, including the species in Zone II, was confined to Zone III. The macrofauna increased in abundance with depth below the surface, reached its maximum at about 50 cm., and maintained that abundance to the bottom of the buoy.

Colman (1933, p. 454) and Orton (1929, p. 278) give the upper limits of certain algae in normal habitats in the Plymouth district. Below, these limits are compared with those on the buoys by giving the least distance in metres below E.H.W.S.T. at which they grow on the littoral; and regarding the surface mark on the buoys as E.H.W.S.T. Unfortunately, in their works only three species could be found which occur on the buoys but they are examples from the green, upper brown, and lower brown algal zones normal to the shore.

Species	Shore (Colman)	Shore (Orton)	Buoys
Enteromorpha sp.	..	0·34	<0·08
Ascophyllum nodosum	1·61	1·56	0·18
Laminaria digitata	4·55	5·22*	0·22

* Orton refers to *Laminaria* spp.

According to Newton (1931) *Polysiphonia elongata*, *Ceramium rubrum*, *Callithamnion corymbosum* and *Rhodymenia palmata* live in rock pools between tidemarks as well as below low water mark which is the usual habitat of "red" algae; but Hamel (1923) gives −25 m. Chart Datum as the depth at which *Rhodymenia palmata* has been found growing at St Malo. Nevertheless the table above shows that there is an extraordinary compression of zonation on the buoys.

This compression of the normal littoral algal zonation must be due chiefly to light conditions on the buoys and to a lesser extent to constant immersion. Since buoys float, waves have practically no uncovering action. Algae are influenced by emersion just as animals are (Fischer, 1928; Baker, 1910; and others). Brown algae such as *Ascophyllum* and fucoids, being intertidal, are at a disadvantage owing to constant immersion, while most of the reds, and to a lesser extent some of the browns such as the species of *Laminaria*, are naturally constantly immersed in their normal habitat. *Ascophyllum* and fucoids only appear on buoys in the Hamoaze to which the laminarians do not penetrate. Where other conditions are suitable, then, the laminarians must oust the other algae which are not so fitted to withstand the constant immersion of Zone III. The compression of the zonation even in the open sea at Mewstone buoy emphasizes the importance of tidal action in controlling zonation on the shore.

Vertical Zonation of the Algae and Illumination

Børgesen (1908) states that sublittoral algae raise their vertical limit in caves where illumination is poorer than on the shore. In the estuary light penetration is much less than in the open sea (Cooper & Milne, 1938). On proceeding from the sea inwards, not only does the total amount of light penetrating become progressively less but its composition changes with depth. "In marked contrast to the open sea, red light penetrates as well or better than green, and blue is cut down most rapidly" (p. 526).

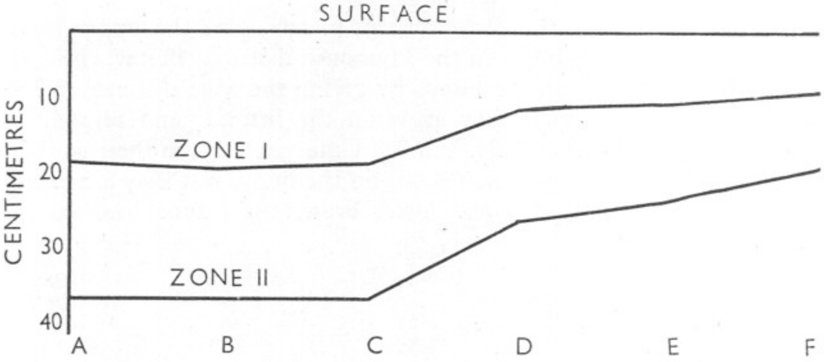

Fig. 2. Lower limits of upper algal zones on buoys. *A*, Panther; *B*, Mallard; *C*, Drake's Island D 4; *D*, H 4, Hamoaze; *E*, H 7, Hamoaze; *F*, H 11, Hamoaze.

On the Mewstone buoy, where conditions are more or less those of the open sea, there is the typical triple zonation mentioned above, but Zone III contains no red algae, *Laminaria* only being present. The lesser penetration of light in the Sound possibly favours the (red) *Polysiphonia* and *Rhodymenia* so that in this situation they establish themselves and tend to oust *Laminaria* in Zone III. Light conditions are more or less uniform in the Sound but penetration decreases abruptly on entering the Hamoaze and continues to decrease up-river (at least to Neal Point buoy). The algal zonation follows the light conditions closely, for the bottom limits of Zones I and II are fairly constant in the Sound but rise abruptly on entering the Hamoaze and rise steadily on proceeding up the Hamoaze (Fig. 2 and Table II).

Daylight factors* at the zonal boundaries found by the author on the buoys in Plymouth Sound and on Hamoaze No. 7 buoy were presented in our earlier papers (Cooper and Milne, 1938, 1939). They suggested forcibly that the

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* From here to the end of this section I am indebted to Dr L. H. N. Cooper for assistance.

depths of the boundaries are very largely conditioned by the daylight factors. Although we have zonal data for two other Hamoaze buoys, Nos. 4 and 11, we have light records only at Nos. 1, 7 and 15. Approximate extinction coefficients have been calculated for the water near buoys Nos. 4 and 11 on the assumption that the extinction coefficient for a given wave band varies linearly with the distance between two buoys, not too far apart. Thus

$$\mu_{\lambda(\mathrm{H4})} = \frac{\mu_{\lambda(\mathrm{H1})} + \mu_{\lambda(\mathrm{H7})}}{2}$$

and

$$\mu_{\lambda(\mathrm{H11})} = \mu_{\lambda(\mathrm{H7})} + \frac{1{\cdot}5}{2{\cdot}6}\left[\mu_{\lambda(\mathrm{H15})} - \mu_{\lambda(\mathrm{H7})}\right].$$

Using such values for the extinction coefficients, the daylight factor at each buoy and on each occasion, *F*, has been calculated from the equation

$$F = 100\left(\frac{I_{\lambda_1}e^{-\mu_{\lambda_1}d} + I_{\lambda_2}e^{-\mu_{\lambda_2}d} + \ldots + I_{\lambda_9}e^{-\mu_{\lambda_9}d}}{I_{\lambda_1} + I_{\lambda_2} + \ldots + I_{\lambda_9}}\right),$$

where I_{λ_1}, etc., represent the spectral energy of a given wave-band in air, and $I_{\lambda_1} + I_{\lambda_2} + \ldots + I_{\lambda_9} = 1$.

Since in 1937 the medium red filter, S 66, was not available, the rather large gap between the S 61 and S 72 filters has had to be closed by taking the mean values of the extinction coefficients as measured for those two filters (μ_M; see Cooper & Milne, 1938, p. 510) and adding 0·6 as an approximate distilled water correction factor at 660 mμ (μ_{DW}). The daylight factors so obtained are presented in Table III together with those from Plymouth Sound and Hamoaze No. 7 buoy. Both light transmission and zonation in Plymouth Sound were sufficiently uniform for us to amalmagate our results into one group, in itself evidence for our thesis.

TABLE III. DAYLIGHT FACTORS AT ZONAL BOUNDARIES ON BUOYS (1937)

	Plymouth Sound	Hamoaze			Weighted mean
		H 4	H 7	H 11	
	Boundary of Zones I and II				
Depth in metres ...	0·180	0·102	0·097	0·080	..
June 17 (high water)	78·3	82·5	80·0	84·4	80
June 23 (low water)	76·4	79·4	77·8	76·9	77
February 18 (high water)	65·4	71·4	69·8	73·4	70
	Boundary of Zones II and III				
Depth in metres ...	0·356	0·254	0·223	0·180	..
June 17 (high water)	62·3	62·2	61·8	72·9	64
June 23 (low water)	59·2	56·7	56·5	55·2	57
February 18 (high water)	43·7	45·0	45·0	50·1	45
	Bottom of buoy (within Zone III)				
	(Mallard)				
Depth in metres ...	2·19	1·27	2·47	1·83	..
June 17 (high water)	7·4	11·0	0·97	3·1	..
June 23 (low water)	5·5	6·8	0·35	0·29	..
February 18 (high water)	0·85	2·1	0·020	0·15	..

On June 17 1937, the estuary was optically almost uniform from Hamoaze No. 7 buoy as far up indeed as Neal Point buoy, a condition no doubt somewhat rare and accounting for the high daylight factors calculated for Hamoaze No. 11 buoy on that date. The rest of the additional data serves but to confirm our view that the zonation of algae on buoys in Hamoaze and Plymouth Sound is mainly, if not entirely, governed by the daylight factors.

The factors for the very turbid estuary at low water on February 16 1937, have not been calculated. Conditions must have been so adverse for photosynthesis that even quite considerable fluctuations in absolute light intensity may be safely ignored.

We may summarize the range of daylight factors found within the three zones, excepting times of winter spate, thus:

	Daylight factor %
Zone I	70–100
Zone II	45– 80
Zone III	> 1– 64

Discussion

In an ecological study one is always confronted by the doubt that the environment has not been correctly assessed by merely choosing (of necessity) what are thought to be the most important factors. The relative importance of environmental factors ought therefore to be discussed.

The sea (tide) brings plankton and nutrient salts* while the river brings detritus and possibly nutrient salts also. Thus detritus and plankton feeding animals apparently find no lack of their foods in the estuary, but for plants the opacity of the water must soon limit photosynthesis. Considering the relative bulks of sewage and water in the estuary basin together with the speedy rate of renewal of the latter by tide and river, sewage here is probably innocuous since it will be quickly diluted and swept away. Thus the Tamar has a relatively clean estuary and oxygen concentration probably never falls so low that it could be a significant factor alone. Sponges and Polyzoa are absent on Mersey buoys, and though present on seaward buoys are not generally exuberant in the Tamar. The latter estuary, though well oxygenated, contains a high silt content, and the Mersey, besides being polluted, seems to have a higher one still. The dominance of mussels in both estuaries may thus be explained, for, as Fischer-Piette notes (1935, p. 155), "the mud which accumulates between their shells and among their byssus threads soon eliminates animals which require clean water, like many sponges, Bryozoa, Hydrozoa, and compound ascidians".

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* Generally speaking: "So far as nutrient salts are concerned conditions in Plymouth Sound are usually better than those of the open sea at the same season" (Dr L. H. N. Cooper).

Huntsman (1918) has shown that a combination of comparatively high temperature and low salinity influenced the vertical distribution of certain marine species, so that the temperature gradient in the Tamar may be more important than some factors. But undoubtedly salinity is the chief limiting agency, outweighing all others (see Fischer-Piette 1931). Yet all the other factors even though they may be thought harmless* of themselves (because of their usually small range of variation and their apparently negligible difference from sea conditions) must help both singly and collectively to make salinity a greater or lesser limiting factor. It is well known that one physical or chemical factor may affect the action of another. This point is emphasized by a comparison of intertidal penetration of marine species in several estuaries of similar salinity gradient (Tees, Tay, Tamar and La Rance in France): there are broad similarities, but there are also striking differences both in extent of penetration and in the order in which the organisms drop out. These differences or at least the latter difference would be absent if salinity were the only limiting factor. Fischer-Piette's (1931) "salinity" is really rainfall which includes *p*H, temperature, current and suspended matter changes. In nature, then, one can only speak of a chief limiting factor. In a clean estuary the chief one is salinity.

Mytilus certainly (unpublished work) and *Balanus*, *Pomatoceros* and *Lepralia* possibly, can close up and wait for the return of suitable salinity conditions; but that amphipods, coelenterates and algae in the Tamar can withstand osmotic changes up to 9 atm. four times in 24 hr. and often for several days at a time without their tissues disrupting is remarkable. Atkins (1916, p. 179) has shown that *Ascophyllum nodosum* in seawater of osmotic pressure 22·6 had an osmotic pressure of 23·6 atm. after 24 hr. in the dark in the laboratory; on being placed in diluted sea water (10·7 atm.) the same thallus, after 3½ hr., was at 13·4 atm. Thus "alteration of the medium...leads to a very rapid readjustment of pressure through the diffusion outwards of salts". Atkins goes on to say that "injurious effects...are occasioned by fluctuations which are too rapid for the proper adjustment to be effected". Although the changes at Saltash (H 15) are large at certain times, they are never so abrupt as this (being spread gradually over 6 hr.) and never so large (9 atm. as opposed to 12).

The horizontal distribution of algae in the different zones may be partly affected by the spectral composition (as well as the daylight factor) of the penetrating light since this changes in the up-river direction. But probably the horizontal gradients in salinity and temperature have some influence as well as light in this connexion. While the zonal boundary curves of flora on buoys are undoubtedly a function of the light factor, it may be that these other factors also influence the *absolute* limit of vertical distribution for it is conceivable that salinity and temperature may affect the metabolism of the plant cell and thus its capacity for photosynthesis. Some of the invertebrate

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* (Cf. Fischer-Piette, 1931.)

population are possibly also limited in their distribution by that of the algae in which they dwell (cf. Russell, 1936, p. 6).

Owing to the limited time available, seasonal variations in distribution on the buoys could not be investigated, but the Tees Survey Report (Alexander, etc., 1935) states that "apart from the normal seasonal changes which occur in the abundance of various organisms, such as the dying away of hydroids in winter and the seasonal maxima of insect larvae, no seasonal changes were observed in the fauna and flora of the (Tees) estuary".

My thanks are due to the authorities of H.M. Dockyard, Devonport, for facilities afforded for the examination of the buoys; and also to the staff of Plymouth Laboratory, especially to Dr L. H. N. Cooper.

Summary

Buoys differ from the intertidal area in that they are constantly immersed near the surface of the water and the slope and texture of their surface is constant. The horizontal and vertical distribution of the macrofauna and macroflora on a series of buoys stretching from the open sea up the Tamar estuary is given.

There are differences in estuarine penetration even among species belonging to the same genus. Distribution is likely to be affected by the time of laying the buoys and the period in the water. But the six buoys farthest from the sea were laid down and lifted at approximately the same time. For these, at least thirty species were available for colonization, but little more than half that number was found even on the most seaward; and the number decreased up-river.

Although there is more suspended silt in the estuary than in the sea and although this increases up-river, the penetration of suspension and non-suspension feeders is similar.

Generally organisms become less numerous and smaller towards the up-river end of their range. Where there is a tendency to lesser density (not size) in a species towards the seaward end of the range, this is largely due to competition for space. Those organisms which do penetrate the estuary have some (new species come in) of the space normally shared with those which do not. Density also decreases where one animal gives way with overlapping to another of similar habits. There is usually no overlapping and no density decrease where replacement occurs in plants.

Dominants on these buoys are filamentous green algae, *Ulva*, *Enteromorpha*, *Polysiphonia*, *Mytilus* and Amphipoda. *Mytilus* competes with the algae.

Salinity seems clearly to be the main limiting factor. Range of fluctuation alone may be less important than range plus rate of fluctuation. Average salinity decreases and range and rate of fluctuation increases in the up-river direction. Salinity data, however, do not suffice to explain all the observed

facts of distribution so that other chemical and physical factors must be taken into account in association with salinity. Organisms such as amphipods and algae, which cannot close up to await the return of suitable conditions like *Mytilus*, sometimes withstand 12 °/₀₀ fluctuations (9 atm. of osmotic pressure) four times in 24 hr. at springs in winter.

Data are given which show the observed salinity-fluctuation-tolerance of certain organisms in the Tamar. After an exceptionally rainy winter, certain organisms on buoys withdrew their limits a little down-river. On the shore, though some had retreated, others maintained their position, while one had actually advanced from the position it occupied after a dry summer some years previously. With two exceptions all these could close down like *Mytilus*, though whether they could escape the bad conditions like the latter, is not known, for one, *Balanus balanoides*, had retreated.

Comparisons are made with other work in the Tamar. Differences in numerical order and extent of penetration on shore and buoys indicate that the salinity factor is conditioned by other factors which differ in the two habitats. The fact that organisms penetrate farther up-river on the shore arises largely from the greater and more protracted salinity fluctuation on the buoys compared with an equivalent point on the shore or bottom.

The vertical algal zonation normal to the shore is much compressed on the buoys. This is due mainly to light penetration and to a lesser extent to constant immersion. Light penetration decreases up-river and the zonal boundaries exhibit a corresponding approach to the surface in the up-river direction; this is shown to be mainly, if not entirely, governed by the daylight factor. Spectral composition also changes up-river but that the composition of the flora changes likewise may be due partly to salinity and temperature gradients.

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APPENDIX I. DATES OF LAYING AND EXAMINATION OF BUOYS

Name of buoy	Laid down	Examined
Mewstone	Jan. 1936	Feb. 11 1937
New Rock	Jan. 1936	May 4 1937
Panther	Jan. 1936	May 3 1937
Mallard	Apr. 1936	Apr. 23 1937
D 4	Apr. 1936	June 10 1937
H 1	Dec. 1935	Feb. 5 1937
H 4	Dec. 1935	Feb. 16 1937
H 7	Dec. 1935	Feb. 22 1937
H 11	Dec. 1935	Feb. 17 1937
H 15	Nov. 1935	Feb. 10 1937
Neal Point	Dec. 1935	Mar. 9 1937

APPENDIX II. NOTES ON IDENTIFICATION

The species are as in the Plymouth Marine Fauna (1931), and *A Handbook of the British Seaweeds* (Newton, 1931). In some cases it was impossible to give more than the generic name either because the specimen was in a bad state of preservation (especially the smaller coelenterates) or the systematics are confusing (e.g. *Molgula* and *Halichondria*—of the latter, L. R. Crawshay of the Plymouth Laboratory holds that there may be several species at Plymouth all formerly called *H. panicea*). I am indebted to the following for aid in identification:

E. W. Sexton, G. I. Crawford and G. M. Spooner—certain Crustacea.
L. R. Crawshay—certain sponges.
H. B. Moore—Balanids.
D. P. Wilson—certain worms.
Professor Stephenson—*Metridium* sp.
W. J. Rees—small coelenterates.
Professor Lily Newton—certain algae.
Professor Theinemann—insect larvae.

THE REACTIONS OF CERTAIN MYSIDS TO STIMULATION BY LIGHT AND GRAVITY

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INTRODUCTION

Delage (1887) was the first to show that the statocysts of mysids have a balancing function. Since then various authors have made further contributions to the problems of orientation and movement in this group, notably Bethe (1895), Bauer (1908), Menke (1911), von Buddenbrock (1914) and Fraenkel (1931). We still, however, lack any comprehensive account of the behaviour of mysids under laboratory conditions; in particular, attention does not seem to have been paid to the difference in behaviour when "light-adapted" and when "dark-adapted", and also, the tactile sense of these creatures appears to have been disregarded.

The present paper is an attempt to fill some of these gaps and to suggest certain correlations between the behaviour of mysids as seen in the laboratory and in the sea. The following account deals mainly with observations on *Hemimysis lamornae*, but other species, for example *Mysidopsis gibbosa* and *Paramysis arenosa*, have been observed. There do not appear to be any significant differences in behaviour between these species.

The observations recorded here were begun at the Marine Station, Millport, and continued in the zoological laboratories of the University of Glasgow and later at University College, Cardiff. I wish to thank Mr F. S. Russell, F.R.S., for his interest and advice during the course of the work, and Prof. W. M. Tattersall for the identification of certain mysids.

THE REACTIONS OF MYSIDS TO LIGHT

Light Adaptation

Franz (1911) and Fraenkel (1931) have described how *Hemimysis lamornae* behaves when light-adapted. The individuals are seen to swim to and fro in the direction of the incident light. One of the chief peculiarities of this reaction is the regularity of the change from positive to negative phototaxis. Each excursion persists for an approximately equal amount of time so that the animal is seen to be swimming backwards and forwards through the same area of water. The reversal of the taxis involves reorientation of the animal so that it is always swimming head foremost. In some degree this appears to parallel the spontaneous change of sign of phototaxis found by Clarke (1932) in

Daphnia, although here one direction of movement was primary, and the movements in the secondary direction were not so long in extent and were of shorter duration. Moreover, in *Daphnia* reorientation is not involved, for Clarke (1932) found that the direction of the excursion was controlled by the postural angle of the antennae, the same orientation of the body to the light source being maintained throughout.

Fraenkel (1931) shows that this movement of mysids is telotactic in nature and not topotactic; for, if two light sources are supplied so that the incident rays cross at right angles they react to one and neglect the other.

From my own observations I conclude that this reaction, as described above, takes place only when light is falling horizontally; for when the lighting is from above the mysids tend to remain on the bottom or very close to it and similar horizontal excursions appear to be made in any direction.

It should also be mentioned here that the phototactic reactions described above are only shown by those mysids which are swimming freely in the water. The conditions under which they swim a few inches from the bottom have been discussed by Cannon & Manton (1927) who point out that in *Hemimysis lamornae* it is a habit, under certain conditions (principally lack of food material suspended in the water), for the animals to descend and stir up the bottom deposit. In this attitude the head is directed vertically downwards and I have not been able to detect any response to light.

The Response to Light of Dark-Adapted Individuals

The subject of this section does not appear to have been dealt with by previous workers, except somewhat briefly by Menke (1911).

Mysids may be dark-adapted in an ordinary photographic dark room and their movements may then be watched by means of a dull red light to which they do not react. This method has been used by other observers (see von Buddenbrock, 1914).

Mysids of all the species investigated showed a much greater tendency to leave the bottom in darkness than in light. A few minutes after the room light was extinguished they were found to be swimming freely in their tank. Under these conditions they may rise to the surface of water contained in tubes of a metre or more in height. This reaction is best classified as a negative geotaxis.

If, when mysids which are dark-adapted are swimming freely in their tank, a light is switched on, they immediately swim to the bottom of the tank with great rapidity and even appear to be trying to swim through it. It is important to note that this downward movement is made quite irrespective of the direction of the stimulating light source; the light stimulus is equally effective from above, from below or horizontally. The movement is always downwards even if this involves approaching the light source. It seems quite impossible to classify this response as any type of phototaxis and, therefore, it may be regarded as light inducing a positive geotaxis.

This effect of light on dark-adapted mysids is in marked contrast to the response to the same stimulus which is exhibited by planktonic forms or by bottom-living creatures, such as cumaceans, which lack definite receptor organs of gravitational stimuli. For in these latter animals the response can be classified in terms of phototaxis alone.

In the mysids we have gravitational and light stimuli acting together, and the response, which is a resultant of these two may be classified as a special instance of telotaxis.

Fraenkel (1931) defines telotaxis (p. 82) as the "assumption of a position so that a certain region of the receptor apparatus is acted upon by the stimulus". Here, where there is a combination of gravitational and light stimuli, it is possible to regard the light as stimulating the animal to assume such a position that a definite region of the gravitational receptor apparatus is acted upon by the stimulus of gravity. Alternatively, it is possible to argue that this response should be regarded as an example of mnemotaxis. Whichever is the correct view in terms of taxes, it seems clear that we are concerned with a combination of stimuli. To demonstrate this, the statocysts, which are the receptors of gravitational stimuli, can be removed.

Observations on Mysids with the Statocysts removed

The Removal of the Statocysts

In small mysids such as *Hemimysis lamornae*, it is only practicable to remove the uropods entire. In larger species it is easier to remove the ramus of the uropod containing the statocyst without damaging the other ramus. However, the results did not differ whichever method was adopted, but the latter operation probably affects the physiological condition of the specimen less.

It cannot be pretended that the operation is anything but severe; in my experience it was unusual for a specimen which had been so treated to live for more than a few (three or four) days. Delage (1887) apparently did not meet with this difficulty. Bethe (1895) recorded that in a mysid from which he removed the uropods a change in the posture of the abdomen was noted; he does not say to what species it belonged. A similar change of posture was especially looked for in *H. lamornae* but no such change was noted.

Behaviour of Mysids without Statocysts

Since Delage (1887) first removed the statocysts of mysids to prove their orientating function, similar experiments have been carried out by various of the authors already mentioned, particularly by von Buddenbrock (1914) who made an exhaustive study of their orientation.

Von Buddenbrock came to the conclusion that if the statocysts of mysids are removed normal orientation is maintained, in the light, by the eyes working through the "dorsal light reflex"; and in the dark, by a "general position reflex". The exact working of this general position reflex is not fully understood, but in the absence of light and with the normal gravitational receptors removed, it suffices to keep the creature correctly orientated even if the body has been unbalanced by the unilateral removal of one of the antennae.

A point of interest, to which little attention seems to have been paid, is that, when the statocysts of a mysid have been removed and it then reorientates itself to light by the dorsal light reflex it will usually become negatively phototactic and move away from the light (a few instances of positive phototaxis under these conditions have been met with). It will be realized that to orientate with the dorsal surface to the light and then move away from the light source interferes seriously with normal movement; for it means that the creature is moving with the ventral surface, and not the head, foremost. When positively phototactic the mysid similarly orientates itself with the dorsal surface towards the light source and then moves towards it dorsal side first.

This orientation and movement can be produced in any plane. By lighting from below the animals can be induced to turn on their backs and swim upwards ventral side foremost.

A variation of this behaviour has been met with in some specimens of *H. lamornae*. Here after the animal has reorientated itself with its back towards the source of light it makes the excusion by swimming head foremost as is normal, and then at the end of the excursion coming to rest with the dorsal surface again directed towards the source of light.

The phototactic nature of the movements of the individuals which behaved in this way was very striking.

The behaviour of dark-adapted mysids whose statocysts had been removed, seemed to differ somewhat from that of the normal individuals in that they did not appear so active in the absence of light; a slight negative geotaxis appeared to exist although Menke (1911) did not apparently find this to be so.

It should be noted here that there are certain practical difficulties which were met with in making the observations. It was found that *H. lamornae* from Plymouth sent to Cardiff did not appear to respond as readily as this species and others did when sent to Glasgow from Millport. It is believed that this may be due to a different physiological condition correlated with the fact that this species lives in the tanks at Plymouth, but that when supplied from Millport it was taken with other mysids from the sea. Another difficulty is the very strong tactile sense possessed by these animals, contact with the sides and bottom of the tanks interfering seriously with the responses that were being studied; this point will be dealt with more fully below.

To conclude this section it is necessary to point out that the behaviour of mysids whose statocysts have been removed becomes more easily explained in terms of phototaxis than in the normal animals; and approximates, under experimental conditions, both to that of planktonic creatures, such as decapod larvae, and to that of such bottom-living animals as cumaceans, where orientation and movement are both controlled by the direction of light.

The Importance of the Tactile Sense

The responses of mysids are observed when they are swimming freely in the water, but a number of collisions with the sides and bottom of the vessel containing them are inevitable. With normal specimens this is not important as they quickly leave the sides and care is taken not to stimulate them when they are in contact with a solid object. When the statocysts have been removed the tactile sense becomes very important; specimens often remaining in contact with the sides or bottom of the vessel for long periods and sometimes it is necessary to remove one forcibly from the side into midwater in order to apply a stimulus. It may be mentioned here that those without statocysts appear to lose the ability to use the ordinary escape reflex of mysids in which the abdomen is sharply flexed under the head and thorax, causing the animal to jump in the water. It is not that the loss of the uropods makes the sudden flexure valueless, it is apparently not attempted at all. Also the conclusion has been reached that these specimens without statocysts do not stand on their heads trying to swim through the bottom of the vessel as has been described above; or at least it is not such a conspicuous part of their activities as it is in normal creatures.

In order to demonstrate the importance of the statocysts and to overcome the difficulty introduced by the tactile sense the following experiment, in which the animal is allowed to remain in contact with a surface throughout, has been devised.

The mysid is drawn up into a glass tube in which it can move freely but is always in contact with some part of the glass. For *H. lamornae* tubing $\frac{1}{5}$ in. (or 5 mm.) in diameter is sufficient. When the tube is entirely filled with water it is held horizontally, the water being prevented from running out by means of corks or the presence of the experimenter's fingers. The light should be dim, or better, red. The tube is now revolved around its long axis; if the mysid is a normal one it will preserve its original orientation with respect to gravity by creeping round the tube as it is turned. If, however, the animal has had its statocysts removed it remains clinging to the wall of the tube and makes little or no effort to retain a definite orientation with respect to gravity and thus revolves with the tube.

DISCUSSION

The two most important points which arise from the foregoing observations and experiments are (1) that the normal orientation and tactile responses of mysids are the result of stimulation by both light and gravity, and (2) that if the gravitational receptors are removed the behaviour becomes more like that of a planktonic crustacean, or a cumacean; and further that, as may be expected in a bottom-dweller, the tactile sense is important.

Since Tattersall (1936) has summarized the available information concerning the vertical movements of mysids in the sea, it is interesting to compare these field results with the observations made in the laboratory.

It seems that certain species are to be met with in the plankton both by day and by night and that an upward movement takes place during darkness. The behaviour of this group of species is paralleled by many planktonic crustacea other than mysids such, for instance, as decapod larvae. In addition there is another group of species which live on the bottom during the day and at night tend to rise into the plankton; in the majority of species they do not rise above twenty metres from the bottom, although one, *Anchialina agilis*, was found by Russell to rise right to the surface about midnight. The behaviour of this latter group, especially that of *A. agilis* is paralleled to a certain extent by some other bottom-living crustaceans, namely cumaceans.

This behaviour, which has been found to take place in the sea, can be correlated with the laboratory observations if it is assumed that the rising at night is due to a negative geotaxis which is reversed and becomes positive in the presence of light. Whether this is the correct interpretation or not it does draw attention to the importance of geotaxis as a possible factor in vertical migration.

The explanation of the diurnal vertical migration of the plankton along the lines of "taxes" is a difficult subject which is as confused to-day as ever, so it is not intended to discuss the matter at all fully here, but merely to point out where the evidence derived from mysids may be of value.

Russell (1927) writing of the difficulty of differentiating between geotaxis and phototaxis, as, of course, in the sea they would both be acting in a vertical direction, remarks "a downward movement may as well be interpreted as a negative phototropism as positive geotropism". In mysids, as a result of the experimental work, it does seem possible to differentiate between phototaxis and geotaxis. Here the influence of light would appear to act through geotaxis. Clarke (1936), as a result of his work on *Daphnia* and further work in the sea, is inclined to seek a similar explanation of migration through a combination of geotactic and phototactic stimuli.

Some authors are inclined lightly to dismiss the influence of gravity, for in the laboratory the control of the direction of movement is found in the great majority of planktonic animals to be under the influence of light. Spooner (1933) has drawn attention to the orientating function of light. This directional effect of light is, however, really the dorsal light reflex, or its equivalent (e.g. an "anterior light reflex" in some animals where the head is directed towards the light), but because this is the strongest reflex present and overpowers others that may exist, it does not show that a gravitational stimulus acting through a general position reflex is not present. In fact it would be only through some such mechanism that orientation would be preserved through the hours of darkness. That gravity is reacted to by *Daphnia* was shown by Clarke (1930) and the present writer has shown elsewhere how the zoea larvae of Brachyura retain an unstable orientation in the absence of light (Foxon, 1934), and it seems likely that the behaviour of *Apus* quoted by Lochhead (1936) may belong to the same category.

It is known that the conditions of laboratory investigation differ markedly from those found in the sea, particularly as regards the composition and intensity of light. Russell (1927) has pointed out that the contradiction, that whereas in the sea most planktonic creatures make a downward movement in the day but in the laboratory move towards light, can be resolved when the intensity of light is taken into account. From this then it can be assumed that a downward movement would be caused by a negative phototaxis and would continue until a certain lower intensity of light was reached; the upward movement would not, however, take place when the light stimulus was entirely removed unless orientation was maintained and upward swimming took place. Therefore a negative geotaxis must be postulated for upward movement in the dark. As the evidence that normal orientation is maintained in the dark is growing, this assumption does not appear to be unwarranted.

As regards mysids it seems reasonable to assume from the evidence brought forward here that the downward movement is a reversal, in light, of a negative geotaxis which persists in darkness. That is, that it is a combined phototactic and geotactic response. That this is the mechanism involved in other groups of animals cannot be assumed without the greatest caution.

It has been noted above that the behaviour of mysids in the sea is closely paralleled by that of planktonic forms of decapod larvae and bottom-living cumaceans according as to whether the particular mysid is planktonic or benthic. In the laboratory, however, the behaviour of cumaceans (see Foxon, 1936) and decapod larvae on the one hand is quite different from that of normal mysids on the other, for both the former groups display strong phototactic reactions which completely obscure any signs of geotaxis. Thus the behaviour of cumaceans and decapod larvae is more like that of mysids whose statocysts have been removed. It appears most probable that, although in the sea the vertical movements of cumaceans on the one hand and mysids on the other hand are roughly parallel, the actual mechanisms producing these results may vary in the two groups. To quote Russell (1927) once more, he says (p. 253), "The writer is not going to generalize on the actual method by which the animals keep around the optimum. It may be phototropism, geotropism or acceleration and inhibition of motion. It may be a combination of all. From the evidence of laboratory experiments it may differ for different animals...." From the evidence at present brought forward it seems probable that more often than has been generally thought, these vertical movements are a result of a combination of light and gravitational stimuli (inhibition of motion is not a likely factor for reasons brought forward elsewhere; see Foxon, 1934). In addition it appears that these stimuli may not always work in the same way. In the majority of animals, as for instance in decapod larvae, light seems to have a simple phototactic effect, and in others (mysids), to work mainly through geotaxis.

SUMMARY

Light-adapted mysids as exemplified by *Hemimysis lamornae* display phototelotaxis which regularly alternates in sign from positive to negative and *vice versa*. This reaction may be disturbed by other activities such as feeding; it only takes place in horizontal illumination.

Dark-adapted mysids display negative geotaxis. When a light stimulus is given this geotaxis is reversed in sign irrespective of the direction of the incident light.

When the statocysts of the mysids are removed their responses are much more like those of planktonic creatures. In the light normal orientation is maintained by the "dorsal light reflex", and in darkness by the "general position reflex". In the darkness a feeble negative geotaxis is sometimes seen. In light, phototaxis is seen in both light-adapted and dark-adapted conditions; in the majority of cases it is negative but on occasion has been seen to be positive.

The sense of touch is very important and introduces certain observational difficulties. An experiment to show the relation of the statocysts to gravitational stimuli and overcoming this difficulty has been devised.

The vertical movements of mysids in the sea have been compared with the laboratory observations and it is shown that this behaviour can be interpreted as caused by negative geotaxis which is reversed in the presence of light.

It is suggested that certain planktonic forms retain their orientation in darkness by means of the "general position reflex" and that their upward movements exhibited in the dark are due to a negative geotaxis.

Although the reactions of normal mysids in the laboratory are markedly different from those of such animals as cumaceans and decapod larvae, in the sea a general similarity between their behaviour exists. It is suggested that this similarity of behaviour in the sea is brought about by stimuli acting in somewhat different ways, and that this difference of method accounts for the differences found in the behaviour in the laboratory. Thus whereas in mysids light is regarded as altering the sign of a pre-existing negative geotaxis, in the other groups it seems that a simple phototaxis (negative) acting in opposition to a weaker negative geotaxis causes a downward movement in light which is reversed in darkness.

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CHANGE IN INHERITANCE IN ECHINOID HYBRIDS

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(Text-figs. 1–6)

In their classical study on experimental hybridization of the echinoids *Echinus esculentus*, *E. acutus*, and *Psammechinus miliaris*, Shearer, de Morgan & Fuchs (1914) found that the hybrid larvae with *P. miliaris* eggs showed one type of inheritance in the years 1909–11, but another in the year 1912. The authors suggested that the peculiar temperature conditions of the sea water prevailing at Plymouth that year may have affected the germ cells of *P. miliaris*. In the summer of 1932, when studying heterosperm merogones of *P. miliaris* and *Echinus esculentus* at Plymouth (Hörstadius, 1936), I also reared hybrids of *P. miliaris* ♀ × *E. esculentus* ♂ to metamorphosis. It was surprising to find that the larvae that year showed a third and fourth type of inheritance, an account of which will be presented in this paper, together with some remarks on possible causes of the different results of the crosses.

According to Shearer, de Morgan & Fuchs (1912, 1914) the plutei of *E. esculentus* possess, at a late larval stage, both anterior and posterior epaulettes, almost always a pedicellaria at the posterior end of the larva, but no green pigment masses. The larva has a body that is deeper than it is wide, the posterior pole being comparatively flattened.

As regards the fully-formed pluteus of *E. acutus*, the three authors state that it has a rather smaller body, with more slender and divergent arms than *E. esculentus*, but resembles the latter in all essential features, such as the development of the epaulettes and of the pedicellariae. They further point out that, owing to the similarity of the characters of this species and *E. esculentus*, their hybrids afford no information of value in the study of heredity.

The late larva of *P. miliaris* is described as being of a different general shape from that of *E. esculentus* and *E. acutus*. The width of the body is greater than its depth, and the posterior pole is more rounded. The arms are comparatively short. Unlike the two species mentioned above, the *P. miliaris* larva has no posterior epaulettes and no posterior pedicellaria, but four masses of green pigment are developed in the anterior epaulettes.

In the following table I have tried to collect all the results regarding the characters of green pigment, posterior epaulettes, and posterior pedicellaria. Absence of a character is marked 0, presence +. As Shearer, de Morgan & Fuchs call attention on several occasions to the fact that the posterior pedicellaria may occasionally be lacking in the pure larvae of *E. esculentus* and *E. acutus*, as well as in hybrids with eggs from these species, the + in the corresponding column is placed in parentheses. Usually when a character has not been expressly mentioned in the text of the papers quoted, it is represented by a note of interrogation, but if from the drawings or indirectly from the text, or from personal information, it has been possible to conclude something in regard to the presence or absence of the character in question, a + or o has been put in the table, but followed by a mark of interrogation. The general shape of the body cannot be included as a character in the table, as too many deviations occur even within one species.

		Green pigment	Posterior epaulettes	Posterior pedicellaria
	E. esculentus	o	+	(+)
	E. acutus	o	+	(+)
	P. miliaris	+	o	o
1909–11	*E. esc.* ♀ × *P. mil.* ♂	o	+	(+)
	E. acutus ♀ × *P. mil.* ♂	o	+	(+)
	P. mil. ♀ × *E. esc.* ♂	+	o	o
	P. mil. ♀ × *E. acutus* ♂	+	o	o
1912	*E. esc.* ♀ × *P. mil.* ♂	o	+	(+)?
	Exceptional culture	o	2 or 1 or 0	?
	E. acutus ♀ × *P. mil.* ♂	o	+	(+)?
	Exceptional culture	o	2 or 1 or 0	?
	P. mil. ♀ × *E. esc.* ♂	o	+	o?
	Exceptional culture	+	o	?
	Exceptional culture	o	2 or 1 or 0	?
	Exceptional culture	o	o	+
	P. mil. ♀ × *E. acutus* ♂	o	+	o?
1914	(*E. esc.* ♀ × *E. acutus* ♂) ♀ × *P. mil.* ♂	o	+	?
	P. mil. ♀ × (*E. esc.* ♀ × *E. acutus* ♂) ♂	o	+	?
1932	*P. mil. Z*-type ♀ × *E. esc.* ♂	o	o	o or +
	P. mil. S-type ♀ × *E. esc.* ♂	o	o	o
	One exception	o	o	+

During the years 1909–11 Shearer, de Morgan & Fuchs (1911, 1912, 1914) found that the inheritance in the hybrids was invariably maternal, the larvae in reciprocal crosses thus being different. As seen from the table, the hybrids *E. esc.* ♀ × *P. mil.* ♂ had no green pigment, but possessed posterior epaulettes and, most of them, the posterior pedicellaria also. In these respects they thus resembled the pure *E. esculentus* and *E. acutus* plutei. The shape of the body, however, was not so deep and flattened at the aboral pole as that of *E. esculentus*, nor so wide as that of *P. miliaris*. The arms were also rather intermediate in form.

The hybrids *P. mil.* ♀ × *E. esc.* ♂, like the normal *P. miliaris* plutei, were characterized by the green pigment and the complete lack of posterior epaulettes and posterior pedicellaria. Occasionally a group of mesenchyme cells could be observed at the posterior pole of the larva, as if in an attempt to form a pedicellaria. The pluteus had not so wide a body as in pure *P. miliaris*, and the arms were longer, but the general appearance was similar to this species.

As seen from the table, crosses between *E. acutus* and *P. miliaris* gave exactly the same pattern as when *P. miliaris* was hybridized with *E. esculentus*.

In the season of 1912, also at Plymouth, the inheritance was different from that of previous years, the offspring of crosses with *P. miliaris* eggs being as a rule paternal, not maternal (Shearer, de Morgan & Fuchs, 1912, 1914). As seen from the table (under 1912), this gave a dominance of the *E. esculentus* characters over those of *P. miliaris* in both reciprocals of the cross. In general form the hybrids were of the *E. esculentus* type and most of them (a few exceptions will be dealt with below) had posterior epaulettes but had not developed any green pigment masses. The three authors do not refer to the posterior pedicellaria in their material from 1912. It has been mentioned above that the inheritance of this pedicellaria follows that of the posterior epaulettes, but that it is not a very reliable feature, as it sometimes fails to make its appearance in pure *E. esculentus* larvae, and sometimes also in the hybrids *E. esc.* ♀ × *P. mil.* ♂ 1909–11 [(+) in table]. Although the presence or absence of the posterior pedicellaria in the *E. esc.* ♀ × *P. mil.* ♂ hybrids in 1912 is not, so far as I can find, indicated in the text of the papers, we can nevertheless conclude from the drawings (1912, text-fig. 4; 1914, pl. 22 figs. 74–76, text-fig. 11) that it was developed in some larvae, whereas in others it only seems to have been represented by a group of mesenchyme cells (1912, text-fig. 4; 1914, pl. 22, fig. 73, text-fig. 11). As to the frequency of the posterior pedicellaria in this cross, we know nothing. This character has therefore been marked (+)? in the table.

In the only drawing of a larva of the reciprocal cross, *P. mil.* ♀ × *E. esc.* ♂ 1912 (1912, pl. 18, fig. 9; 1914, pl. 22, fig. 77), there is no posterior pedicellaria present, only a group of mesenchyme cells, and no such pedicellaria has been expressly mentioned by Shearer, de Morgan & Fuchs in any of their plutei with eggs of *P. miliaris*, neither in the pure *P. miliaris* larvae, nor in the other hybrids. On the other hand, it has to be mentioned that Shearer, de Morgan & Fuchs, in the very last sentence of their paper of 1914 (p. 344), write: "If our investigations at Plymouth had been confined to the summer of 1912 alone, we should have arrived at the same conclusion as Loeb, King, & Moore, that certain characters are definitely dominant, namely the posterior ciliated epaulettes and posterior pedicellariae, while the green pigment is recessive." Loeb, King & Moore (1910) worked with other species and characters. As this statement has no support in the descriptions of the experiments, *P. mil.* ♀ × *E. esc.* ♂, it is not clear whether it refers only to the cross *E. esc.* ♀ × *P. mil.* ♂ (and also here it is not valid for all cases, cf. the above paragraph) or whether it is intended to hold good also of the cross *P. mil.* ♀ × *E. esc.* ♂.

It is important to notice that when *P. miliaris* was crossed with *E. acutus* in the year 1912 the same change in inheritance occurred as when it was crossed with *E. esculentus*. Thus *E. acutus* ♀ × *P. mil.* ♂ gave, as in 1909–11, no green pigment, but posterior epaulettes. As regards the posterior pedicellaria, nothing is mentioned in the text, but according to the drawings (1912, text-fig. 3; 1914, pl. 22, fig. 78, text-fig. 12) it seems to have developed. One exceptional culture will be mentioned below. Contrary to the results of 1909–

11 the cross *P. mil.* ♀ × *E. acutus* ♂ inherited the *E. acutus* characters, having no green pigment, but possessing posterior epaulettes. To judge from pl. 18, fig. 7, and text-fig. 3 (1912), as well as pl. 22, fig. 79, and text-fig. 12 (1914), no posterior pedicellaria was developed, but in some larvae a group of mesenchyme cells. The results were thus identical with those of the crosses *P. miliaris* and *E. esculentus*. Both with *E. esculentus* and *E. acutus* sperms added to *P. miliaris* eggs the inheritance was maternal in 1909–11, paternal in 1912.

In 1912 the results were not as uniform as they had been in 1909–11, as a few cultures showed exceptions (small type in table). While the majority of the hybrids *E. esc.* ♀ × *P. mil.* ♂ were of the form of *E. esculentus*, the larvae in one exceptional culture had the general shape of *P. miliaris*, with a broad body, domed aboral end, and short arms. In this cross only four larvae exhibited the typical combination of two posterior epaulettes and lack of green pigment. In eight larvae only one of the posterior epaulettes developed, and in eleven larvae none. Exactly the same type of exception occurred in one of the crosses *E. acutus* ♀ × *P. mil.* ♂, as all the larvae had the maternal absence of green pigment, but some had both posterior epaulettes, some had an epaulette on one side of the body only, and others had neither posterior epaulette.

In the crosses with *P. miliaris* ♀ and *E. esculentus* ♂ two kinds of exceptions were observed in 1912. In one culture ten plutei were of purely paternal form, having no green pigment but posterior epaulettes (0+), while twenty-five were of the purely maternal (*P. miliaris*) type in general form and in developing green pigment masses but no posterior epaulettes (+0, small type in table). In another culture the larvae instead were—like those of all other cultures of this cross in 1912—of the *E. esculentus* type in general form, and they all also had the paternal absence of green pigment; but they differed among themselves with regard to the development of the posterior epaulettes. Eighteen had both posterior epaulettes, five developed only one posterior epaulette, and nine had none. These latter (no pigment, one or no posterior epaulette) thus showed the same combination of characters as the exceptions among *E. esc.* ♀ × *P. mil.* ♂ and *E. acutus* ♀ × *P. mil.* ♂ the same year (see above).

As seen from the figures (quoted above), the posterior pedicellaria was generally present in the exceptional larvae of the cross *E. esc.* ♀ × *P. mil.* ♂ 1912. As regards the occurrence of posterior pedicellariae in the exceptional cultures *P. mil.* ♀ × *E. esc.* ♂, there is no information in the papers.

In view of the uncertainty concerning the posterior pedicellaria in 1912, I wrote to Dr Shearer for further information, and he kindly gave me the following particulars. As the records from 1912 were not available, Dr Shearer could not answer definitely for each combination, but said that some hybrids in 1912 had a posterior pedicellaria although they did not go through metamorphosis, their development being very slow and irregular. Even if this should refer to the cross *P. mil.* ♀ × *E. esc.* ♂, it seems that the statement in the last sentence of the three authors' paper, quoted above—that the posterior pedicellaria was definitely dominant in 1912—must be a slip, as evidently most hybrids did *not* develop this organ. In his letter Dr Shearer mentions a fact of great interest. In a cross with one lot of *P. miliaris* fertilized eggs with *E. esculentus* sperms about 7 % of the larvae developed a posterior pedicellaria, but neither green pigment nor posterior epaulettes. Thus we here meet with a new combination, oo+. The reason why these larvae were not mentioned in the paper was that they did not develop in a normal way, as they did not produce proper *Echinus* rudiments. They were therefore considered as non-viable. Moreover, many of these posterior pedicellariae were not complete, as parts of the organ, e.g. one jaw, would sometimes be missing. Although the larvae of the type oo+ thus were not quite normal, and the posterior pedicellaria was often malformed, we add this combination to the exceptions in our table.

The change of inheritance in 1912 was thus as follows. In the majority of the crosses of *P. miliaris* ♀ with *E. esculentus* or *E. acutus* ♂ the inheritance was opposite to that of previous years, being paternal (o+) in 1912 instead of maternal (+o) in 1909–11. Only in one culture, *P. mil.* ♀ × *E. esc.* ♂ 1912, some of the larvae inherited both characters from the female parent (+o). In 1912 there was, moreover, another type of exception, which occurred three times, in three different crosses: *E. esc.* ♀ × *P. mil.* ♂, *E. acutus* ♀ × *P. mil.* ♂, and *P. mil.* ♀ × *E. esc.* ♂. With lack of green pigment was combined the lack of one (o1) or of both (oo) posterior epaulettes. Shearer, de Morgan & Fuchs point out (1914, p. 308) that this shows that the two characters pigment and posterior epaulettes are not necessarily bound to be inherited in a special combination from the same parent, although this happens in the majority of larvae (+o or o+). For some individuals (oo) inherited the absence of green pigment from one parent (♀ or ♂) and the absence of the posterior epaulettes from the other (♂ or ♀). "The characters are thus of the nature of unit characters and independent of one another." The larvae with only one posterior epaulette were called mosaic hybrids. Finally, in one lot of *P. mil.* ♀ × *E. esc.* ♂ hybrids a posterior pedicellaria could (according to private information) be formed in a few larvae lacking both green pigment and posterior epaulettes (oo+); but these larvae were rather abnormal and were therefore not mentioned in the papers.

In 1914 some of the hybrids raised by Shearer, de Morgan & Fuchs in the year 1912 became sexually mature, but only those of the cross *E. esc.* ♀ × *E. acutus*. ♂. Unfortunately the F_2 generation of this cross afforded no information as to inheritance of the late larval characters, since the latter are alike in the two species. For that reason it was to be expected that a cross between this *E. esculentus-acutus* hybrid and pure *P. miliaris* would give the same result as when *P. miliaris* is crossed with either *E. esculentus* or *E. acutus*. Fuchs (1914) succeeded in rearing the larvae of both the reciprocal crosses, *E. esc.-acutus* ♀ × *P. mil.* ♂ and *P. mil.* ♀ × *E. esc.-acutus* ♂. The inheritance of the larval characters was the same as in the hybrids of the pure species in

1912: thus the *E. esculentus* or *E. acutus* characters dominated over those of *P. miliaris* in both reciprocal crosses (0+ in table). The general shape of the larvae is not described, nor is the posterior pedicellaria mentioned. This author has kindly told me in a letter that he cannot give any further information on this point, as he has no pre-war records left.

When I arrived at Plymouth at the end of May 1932, most of the *E. esculentus* obtained had already shed their sexual products. It was, however, possible to make a few fertilizations. A culture of *E. esc.* ♀ × *E. esc.* ♂ exhibited, in the late larval stage, the normal features: no green pigment but posterior epaulettes and a posterior pedicellaria. Likewise pure *P. miliaris* larvae were of the normal type (+00). The cross *E. esc.* ♀ × *P. mil.* ♂ never reached later stages, but the hybrids *P. mil.* ♀ × *E. esc.* ♂ showed a good development. Of the latter cross two fertilizations were made. The *P. miliaris* females used were rather different.

Lindahl & Runnström (1929) have studied the variation of *P. miliaris* at different localities. They describe two types from the Swedish coasts. The *Z*-type belongs to more shallow water. These sea urchins cannot stand a high salinity. They grow considerably larger than those at greater depths. Their colour is mostly olive green, with violet spine-points. The sea urchins of the *S*-type are much smaller, their spines comparatively longer, their colour lighter, greyish yellowish to brownish and reddish, their spines also with violet points. They live in water of a higher salinity than those of the *Z*-type, although they seem not to be too well adapted. The gonads of the *S*-type are comparatively larger than those of the *Z*-type, and the eggs of the former are larger than those of the latter. Lindahl & Runnström believe that these two types are only phenotypically different. For further information as to variation in size, shape and colour, distribution, sexual periods, influence of temperature, salinity, light, differences in habits, etc., I refer to the paper by Lindahl & Runnström (1929).

These two authors studied material from several European localities, among others from Plymouth. Dr J. H. Orton had told them that besides the larger *P. miliaris* collected at low tide small specimens were dredged from greater depths. When Lindahl & Runnström (1929, p. 421) received material from the Eddystone grounds they found these small sea urchins surprisingly like the *S*-type from the deeper waters of Sweden, while, on the other hand, the animals from shallow waters in both countries also showed great similarities.

One of the fertilizations *P. mil.* ♀ × *E. esc.* ♂ in 1932 was made with the large eggs of a small, light-coloured *P. miliaris* from Eddystone, thus of a sea urchin closely resembling the *S*-type. We may call this culture the *S*-culture. For the other fertilization a large, olive green *Ps. mil.* ♀, of the *Z*-type, was used. This animal had, however, not been recently brought in, but had lived for some time in an aquarium. This culture will be mentioned as the *Z*-culture. The larvae were put in plunger jars with outside sea water. They were examined at intervals individually, and some were reared through metamorphosis. Others were preserved at a late larval stage, and from these the drawings have been made. The young metamorphosed sea urchins were not reared.

The larvae of the *S*-culture grew larger than those of the *Z*-culture (cf. Figs. 1, 2, with 3–6). The body is broad and the posterior end rather rounded, as in *P. miliaris*. The arms, however, are long and divergent as in *E. esculentus*. Just as the species characters are mixed in regard to the shape of the body and arms, so also the more definite late larval features are combined in an unusual way. Twenty-six plutei showed the paternal absence of green pigment and maternal absence of posterior epaulettes and posterior pedicellaria (ooo). It might be said that this lack of all the three larval characters is due to bad condition of the larvae. This can, however, hardly be true. The plutei were very uniform, regular in shape and had a normal *Echinus* rudiment, as seen from Figs. 1 and 2. One pluteus developed differently, having a posterior pedicellaria, thus oo+ (small type in the table).

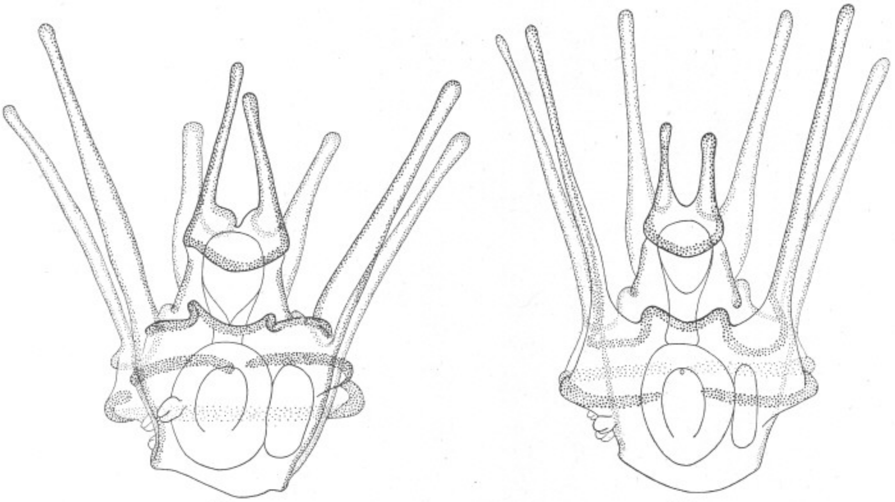
Fig. 1. Fig. 2.

Figs. 1 and 2. Hybrids of *Psammechinus miliaris* ♀ from Eddystone (so-called *S*-type) × *Echinus esculentus* ♂. Fertilization May 27, preserved July 1, 1932.

The *Z*-culture numbered forty-six larvae. They were not as uniform in shape as those of the *S*-culture. I have not records of all larvae in this respect, only of those preserved. Many of them have a rather high and narrow, square body like an *E. esculentus*. (Figs. 3–5). In spite of the absence of the posterior epaulettes, its posterior end is not rounded as in *P. miliaris*. If these features point towards *E. esculentus*, the arms are, however, not as divergent as in this species, but they are, on the other hand, comparatively longer than those of *Ps. miliaris*. Then there are some intermediate types leading to plutei of a pronounced *P. miliaris* type (Fig. 6). In these larvae the body is broad and its posterior part more domed. The arms are comparatively short, although some of them may be longer than is general in pure *P. miliaris* plutei. As regards the body shape, the larvae in the *Z*-culture are thus less uniform than those of the *S*-culture. Some more resemble the male, some the female parent. But in both cultures the features are more or less mixed. If we now turn to the three characters dealt with in our table, we find thirty-one plutei devoid of all of them (ooo, Figs. 5, 6), as the great majority in the *S*-culture. But ten larvae possessed a well-developed posterior pedicellaria (oo +, Figs. 3, 4). Only four of these are in the preserved material. In those four larvae the posterior pedicellaria is combined with an *E. esculentus*-like body. Whether

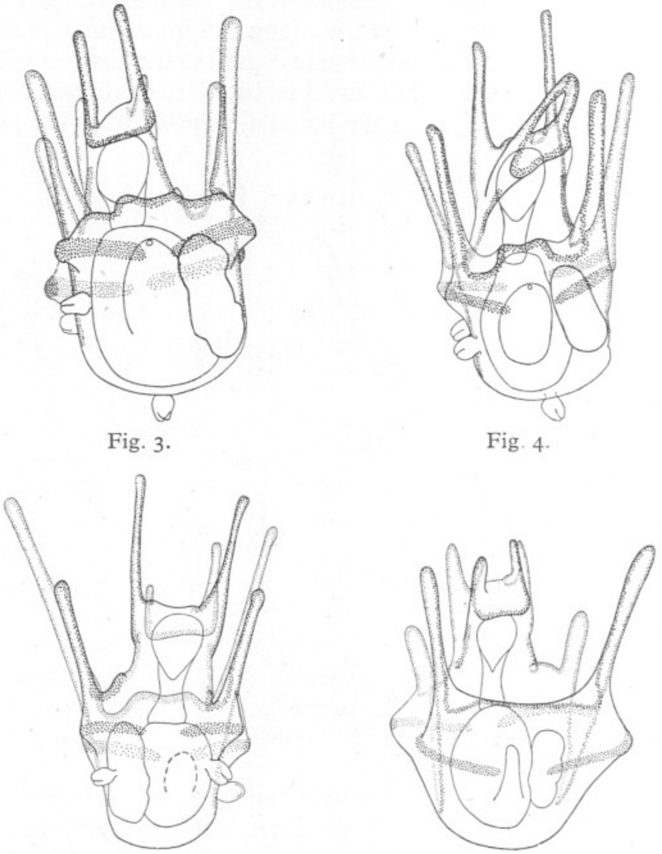

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Figs. 3–6. Hybrids of *Psammechinus miliaris* ♀ from the shore (*Z*-type) × *Echinus esculentus* ♂. Fertilized June 6, preserved July 20 1932.

this was so in the other six larvae I do not know. Finally, in five plutei there was a small pigmented protrusion in place of a posterior pedicellaria. One larva is peculiar in having—beside two pedicellariae on the right side —a pedicellaria also on the left side, although the *Echinus* rudiment is well developed (Fig. 5).

These results are interesting in several respects. We have mentioned above that the *S*- and *Z*-forms of *P. miliaris* are different in regard to both external characters and habits, but that the differences have been considered to be only of a phenotypical nature (p. 104). Nevertheless, we find a marked difference between the hybrids from *S* eggs and those from *Z* eggs. The former are large and of a uniform type (Figs, 1, 2), the latter look smaller and have the *E. esculentus* and *Ps. miliaris* characters mixed in different ways in different individuals, but none has the general appearance of the *Z* larvae (cf. Figs. 1, 2 with Figs. 3–6).

In 1932 the combinations of the characters green pigment, posterior epaulettes, and posterior pedicellaria, were neither those of 1909–11, nor those of the most common type of 1912 or 1914. Our most frequent type in 1932 was 000, which type occurred only as the exception in three cultures of 1912, and we recall that it then appeared in the three different crosses *E. esc.* ♀ × *P. mil.* ♂, *E. acutus* ♀ × *P. mil.* ♂, and *P. mil.* ♀ × *E. esc.* ♂. But the larvae in these exceptional cultures did not develop in a very normal manner. This rather universal combination (000) was thus dominant in 1932, both with the *S* eggs (twenty-six larvae) and the *Z* eggs (thirty-one larvae). It would seem from the three exceptional cultures in 1912, in which the larvae were not particularly healthy, that the lack of all three of these larval characters might be just a sign of a bad condition of the larvae. But I do not think that it necessarily is so. As seen from the drawings, our larvae were in good condition, and many of these 000 larvae went through metamorphosis. The development of a posterior pedicellaria in some of the larvae without both green pigment and posterior epaulettes (00+) represents a new type, hitherto not mentioned in the literature and only known through Dr Shearer's kind information. In our cultures the larvae were perfectly healthy, and the posterior pedicellaria well developed, while the 00+ larvae from 1912 were evidently very irregular (cf. above). Thus the two combinations of 1932, 000 and 00+, in 1912 appeared only as exceptions and in rather abnormal larvae, but in 1932 they represented the only types and the larvae were in excellent condition. It thus seems to me that in the larvae of 1932 there was a different combination of factors expressing themselves from that in the healthy hybrids of previous years.

To summarize, the crosses with *P. miliaris* eggs in 1909–11 invariably gave +00, in 1912 and 1914 mostly 0+0, but some not very healthy larvae showed the exceptions +0?, 01?, 000 or 00+. In 1932, 000 and 00+ were the rule. What can have caused these changes in inheritance? Shearer, de Morgan & Fuchs (1914) suggest that the change of inheritance in 1912 must have been due to some factor affecting the eggs of *P. miliaris* during their growth and maturation, as the same change was found whether sperms of *E. esculentus* or of *E. acutus* were used. The three authors found that the cause was not the relative ripeness of the eggs, as crossing at the beginning, middle, and end of the breeding period of each species gave no difference in inheritance. They further point out that the change was not due to changed conditions at, or after, fertilization, as changed alkalinity of the sea water and different laboratory temperatures had no influence. That the general physiological condition of the *P. miliaris* eggs was different in 1912 is indicated, according to the same authors, by the ill-health of pure cultures of this species, and by the low percentages of fertilization in crossing with *P. miliaris* ♀ that year. An investigation of the cytology of the crosses established that a true fusion of male and female pronuclei invariably took place. As to a possible elimination of chromosomes in the segmentation stages, Shearer, de Morgan & Fuchs did not succeed in correlating the character of inheritance with such eliminations. They suggest that the peculiar temperature conditions of the sea water at Plymouth in the season 1911–12 may have played a part in bringing about the change in inheritance.

If we compare the temperature data given by Shearer, de Morgan & Fuchs (1914, text-fig. 17), the curve for 1912 shows a lower temperature than those of 1909 and 1910 in the middle of February, but a higher temperature in April and May. The difference is hardly more than 1° C. On the other hand, the curve for 1911 is decidedly lower than that for 1909. It seems to me that the difference in heat from January to June is greater between the years 1909 and 1911 than between 1909 and 1912. At Naples *Paracentrotus lividus* has a breeding season extending over the whole year, i.e. each individual is probably ripe several times each year, both winter and summer. The winter temperature of the Mediterranean at Naples is 13° C., the summer temperature 26° C. The eggs taken out of an animal in the winter cannot develop normally at the summer temperature, and *vice versa* (Hörstadius, 1925). But the animals adapt themselves and their eggs to this considerable change of 13° in a few months. I can hardly believe that the small differences in temperature to which Shearer, de Morgan & Fuchs refer can be such as to affect the eggs of *P. miliaris* in any considerable way, the more so as the temperature during the following part of the breeding period (to October or November) is normally still higher than in May and June 1912, as the sea water in the summer reaches a temperature of about 16° C., while the curves given only reach about 13° C. at the beginning of June.

In 1914 Fuchs (1914) obtained the same inheritance as in 1912. He used hybrids *E. esc.* ♀ × *E. acutus* ♂ as one parent, but this difference ought not to be of great importance, for these two species have the same characters and the crosses *P. miliaris* eggs with either *E. esculentus* or *E. acutus* sperms gave the same result in 1909–11 and 1912 respectively. If the temperature conditions in 1912 were the cause of the change in inheritance that year, we ought to have had the same temperature variations in 1914, as the results of the crosses were the same as in 1912. Mr F. S. Russell, of the Plymouth Laboratory, has kindly provided me with the corresponding weekly temperatures at the end of the Promenade Pier in the year 1914 (from the Plymouth Meteorological Observatory). If these data (given below) are plotted on Shearer, de Morgan & Fuchs text-fig. 17 we find that the curve for 1914, up to the middle of February, is practically identical with that of 1910. From the middle of February onwards (to about June 1) the curve of 1914 is nearest to that of 1909, but on the whole shows about 0·7° F. (0·5° C.) a higher temperature than that year. It lies between the curves of 1909 and 1912, and is therefore the one that during these months most closely resembles that of 1912. The temperatures in 1914 thus do not show the extremes of 1912, neither the particularly low temperature in February, nor the high temperature in the spring, but, on the other hand, the curve of 1914 is the one coming nearest to that of 1912, being in a way intermediate between this one and those of 1909–11.

Week ending	Temp. ° F.	Week ending	Temp. ° F.
Jan. 3	47·6	Mar. 21	47·6
10	48·0	28	48·0
17	46·6	Apr. 4	50·6
24	45·3	11	49·5
31	45·9	18	50·7
Feb. 7	47·9	25	52·2
14	47·5	May 2	53·0
21	47·2	9	52·8
28	47·0	16	53·3
Mar. 7	46·7	23	56·0
14	48·0	30	54·5

As our *Z* female in 1932 had been kept for some time in the aquarium tanks, and as we do not know how long it had been living there, a comparison of the sea-water temperatures of 1932 with those of previous years is not of much value. However, it may be mentioned that in 1932 the temperature in January and February was much higher than in any of the years 1909–14, whereas in March–May it was lower than any other year except 1911. The conditions are thus the contrary of those of the extreme year 1912.

Mr Russell has kindly sent me records of the bottom temperatures of E 1, ten miles south-west of Eddystone. There are no records for the bottom temperature at the Eddystone (from where our *S*-type female had been taken), but it is likely to have been very similar to E 1. The sea water at this depth is generally warmer in the winter and cooler in the spring and summer than at the Promenade Pier. In 1932 this tendency was still more obvious at E 1. Here the temperatures were: Jan. 1, 11·25° C.; Feb. 11·00°; March, 8·9°; April, 8·5°; May, 9·0°, and June 1, 9·6°. The divergence from the mean of about 10 years is, for the same months, as follows: Jan. +0·75°, Feb. +1·40°, March 0°, April −0·5°, May −0·6°, and June −0·7° C. Thus 1932 was rather abnormal, being at first considerably warmer than normal and then colder, both at E 1 and the Promenade Pier.

Although the curve for 1914 is fairly similar to that of 1912 and the same results were obtained for these two years (0+) it is not quite clear that the temperature is the direct cause of the change of inheritance. It seems to me that the differences in temperature are too small to be of any probable importance. Moreover, some of the exceptions in 1912, which, too, are considered to have been due to the temperature conditions, were the rule in 1932, when the *S*-type had been exposed to unusual temperatures, differing from the normal in an exactly opposite direction from those in 1912 or 1914. The same holds for the shore temperature, but this fact is not significant, as we do not know how many days the *Z* female had been kept in the tank. Thus it is impossible to say anything with certainty as regards the possible role of the temperature.

In their description of the physical conditions of the sea water Shearer, de Morgan & Fuchs (1914, p. 272) mention a fact of interest. While according to them the *p*H of the outside sea water is generally 8·15–8·25, the tests in the spring of 1912 showed only about 7·9. The alkalinity is of great importance for the function of sexual products. Mortensen (1913) found that artificial fertilization was possible in *Holothuria nigra* only after the *p*H of the sea water had been raised, and this method has been widely used. To give another example, the maturation of the eggs in the annelid *Pomatoceros triqueter* is initiated when the eggs from the acid body fluid are shed in alkaline sea water (Hörstadius, 1923). The influence of *p*H on the mobility of sperms and maturation of eggs naturally does not indicate that a lower *p*H affects the sexual products during their development in the body, particularly as the inner milieu is probably rather stable even if slight external changes in *p*H occur. But this factor ought to be mentioned, as well as the small changes in temperature.

The fact that the hybridization of *P. miliaris* eggs gave the same change of inheritance in 1912, whether sperms of *E. esculentus* or *E. acutus* were used, does not necessarily prove that the change was due to some factor affecting the eggs of *P. miliaris* during the period of their growth and maturation. Environmental influences during the larval development are not excluded. Shearer, de Morgan & Fuchs state that the change of inheritance was not due to varied conditions during or after fertilization, as changed alkalinity and different laboratory temperatures had no influence. But other factors are conceivable. The three authors used Berkefeld filtered "tank water" for rearing their larvae (1914, p. 275). This means sea water taken from the supply circulating through the tanks of the aquarium. This water circulates for a considerable time. For this reason we must reckon with a greater or lesser amount of excretory products of all kinds in the water. To what extent such products accumulate, and how soon they break down we do not know; but it is possible that they occur in different concentrations at different times and may have some influence. Furthermore, the tank water in the Plymouth Aquarium is treated with lime ($Ca(OH)_2$) in order to replace the loss of calcium caused by the animals in the aquaria. For this reason tank water may vary in several respects at different times. Thus other factors than change of temperature and alkalinity may possibly have affected the eggs and larvae during development. And that the change of inheritance occurred with the use of *P. miliaris* eggs might be due to the *P. miliaris* eggs being particularly sensitive to environmental factors during development. However, it does not seem very probable that the cause of the change of inheritance is to be found in external factors during larval development.

A considerable literature deals with the variation of sea-urchin hybrid larvae. Many different species have been used, and usually only the skeleton has been studied. The results are very contradictory. For example, Herbst (1906*b*), Tennent (1911), Loeb, King & Moore (1910) ascribed differences in dominance to changes in alkalinity, while Koehler (1916) repudiated any influence of alkalinity. Herbst (1906*a*) thought the relative ripeness of the germ cells to be of no importance, but found the temperature during development to affect the type of the hybrid larvae, but there is also, according to Herbst, an inner factor to take into consideration. On the other hand, in 1898 Vernon attributed the differences in inheritance to seasonal differences in the ripeness of the germ cells; and so did Koehler (1916), who also expressly denied Herbst's statement that a higher temperature caused a development more similar to the mother. v. Ubisch (1932), and Nümann (1933) found an excess of skeletal elements when the temperature was raised. For a review of this vast literature, see Nümann (1933).

The only safe conclusion from all these investigations seems to be that the amount of skeleton produced is increased by higher temperature during larval development and that the skeletal characters in most sea-urchin larvae are not sufficiently definite to be relied upon. Furthermore, it seems highly probable that the type of inheritance depends upon an inner factor, the physiological condition of the germ cells, but we do not know whether this is a consequence of the age of the germ cells or of the season or of some factor other than the temperature influencing the animals during the development of their sexual products. Thus Nümann (1933) found both hybrid larvae of intermediate type and those resembling the mother at the same time in the season, only by using eggs of different females. Furthermore, it must be pointed out that eggs of different females, taken the same day from the same habitat—according to the experiences from developmental physiology—are often very different in their sensitiveness to different physiological agents, such as animalizing or vegetativizing substances, radiation, etc. (see Hörstadius, 1935; Lindahl, 1936; and others).

Shearer, de Morgan & Fuchs realized that the skeletal characters were too variable to be reliable for an investigation of inheritance in hybrids of *Psammechinus* and *Echinus*. They therefore studied the presence or absence of other organs. In regard to the presence or absence of green pigment, posterior epaulettes, and posterior pedicellaria, too, we probably have to maintain the suggestion made by several previous authors (cf. above) that the differences are due to some unknown inner factor. The temperature may have played a part in affecting this factor, but it can hardly be the temperature alone that is responsible for the changes in inheritance reviewed in this paper: in 1912 four different combinations were found, and two of them returned in 1932, although the temperature of the sea was quite different. It would be of interest if, for a sequence of years, crosses of *P. miliaris* *S*-type and *Z*-type with *E. esculentus* and *E. acutus* could be further studied at Plymouth, and the results compared with the physical conditions of the sea water.

SUMMARY

In 1932 crosses were made at Plymouth between *Psammechinus miliaris* ♀, both *Z*-type (from the shore) and *S*-type (from Eddystone), and *Echinus esculentus* ♂. The larvae from the *S* eggs differed in size and shape from those from the *Z* eggs (cf. Figs. 1, 2 with 3–6). None of the hybrid plutei possessed the green pigment of *P. miliaris*, nor the posterior epaulettes of *E. esculentus*. Some of the larvae (Figs. 3, 4) had a posterior pedicellaria, like *E. esculentus*, in others this organ was missing (Figs. 1, 2, 5, 6). Some of these plutei were preserved, others went through metamorphosis. Healthy larvae of these combinations (oo+ and ooo) have not hitherto been described. The results are compared with those of previous authors (see table, p. 100). Some possible causes of change of inheritance in different years are discussed.

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NITROGEN AND PHOSPHORUS REQUIRED FOR THE GROWTH OF PHYTOPLANKTON

By H. W. Harvey, Sc.D.

(Text-figs. 1–2)

When offshore water, collected during the early part of the year, is enriched with nitrate, phosphate and an iron salt and is kept in a north window, a growth of phytoplankton develops. After a few days the plant community changes; typical planktonic diatoms give way to pennate forms while flagellates and other unicellular algae tend to become numerous. The colonial alga *Phaeocystis* continues growth and some species of centric diatoms, as *Skeletonema*, persist longer than others.

Similar changes in the community have been described by Allen & Nelson (1910) who differentiate between the true plankton forms which flourish in the sea and the "aquarium forms which invariably take possession when present in mixed cultures, whilst the plankton forms are killed off. Why is it that, although species of the second class are always present in small numbers in plankton taken from the sea, they are there altogether outnumbered by the true plankton forms, whereas under conditions such as those of our experiments they invariably succeed in gaining the upper hand?"

This change appeared to start at about the time when, owing to photosynthesis by the increasing population of diatoms, the hydrogen-ion concentration fell and, collaterally, the partial pressure of dissolved carbon dioxide was reduced to a fraction of its normal value. By varying the quantity of excess base, some evidence was obtained which suggested that it was the reduced carbon dioxide pressure rather than increase in *p*H which caused the change in the community. Experiment showed that by keeping the partial pressure of carbon dioxide (and *p*H) within reasonable bounds, considerable growths of typical planktonic communities would develop. These were free or almost free from flagellates and were similar in composition to the diatom communities occurring at that time in the sea but many hundred times more dense.

These growths were obtained by bubbling a rapid stream of washed and filtered air through the water, reducing the light during particularly bright weather if the *p*H rose unduly, and by limiting the supply of one or other nutrient salt. In this way it was possible to obtain natural planktonic populations of such density that they had utilized 200 mg./cu. m. of available phosphorus at room temperature in March. With longer and brighter days later in the year, such dense populations were not always obtained; the rate at which they utilized CO_2 being, presumably, greater than the rate of supply from the air bubbles, and the change in community set in before so much nutrient was utilized. It was also found desirable to add a source of silica more readily available than from the glass walls of the flask; a solution of waterglass neutralized with hydrochloric acid proved satisfactory for this purpose.

Using this method of experiment it was possible to make various observations concerning the nutrient requirements of typical phytoplankton communities. Such communities include bacteria.

The number of bacteria occurring in nature in sea water rich in phytoplankton is greater than water poor in phytoplankton (Waksman *et al.*, 1933); there is reason to believe that some of these bacteria are epiphytic. It seems desirable therefore, in investigating the requirements of a phytoplankton community, to consider it as composed of both plant cells and bacteria, some of which may even play a part as symbionts. Indeed it is impossible to do otherwise in practice; it is not certain that marine diatoms have yet been obtained in culture free from bacteria.

On the other hand, it is necessary to consider how far these dense populations of phytoplankton grown from crude sea water resemble, not only in their plant species, but also in their bacterial content, communities occurring naturally in the sea.

When sea water is transferred to a glass vessel there is a rapid growth of bacteria. It has been shown that this growth is more rapid and greater the smaller the vessel, and depends upon the relation between the area of glass—water interface and the volume (Lloyd, 1937). ZoBell has suggested that organic matter dissolved in the water is adsorbed on the interface, where its localized concentration permits the bacteria to develop. Waksman *et al.* (1933) have followed the increase in numbers of both diatoms and bacteria in a culture, finding that the ratio of bacteria to diatoms increased from 3 : 1 to 20 : 1.

Although, in culture, the phytoplankton population becomes several, often many, hundred times more dense than in the sea, it seems probable that the supply of nutrient salts arising from bacterial decomposition of organic compounds proceeds at a rate, relative to the phytoplankton population, which is greater than would occur in nature.

THE RATIO OF NITROGEN TO PHOSPHORUS UTILIZED

A preliminary experiment was made in which a sample of sea water was enriched with ample phosphate, iron and silica. Portions of this were further enriched with 0·25, 0·5, 1·0 and 2·0 mg./l. nitrate N. After 5 days (March 20–25) in a north window, there was a growth of diatoms in all the flasks, the increased growth due to 0·25 mg./l.N. being very marked, and the growth due to higher concentrations only somewhat greater. After a further three days there was a regular apparent gradation in growth in the five flasks, the population density appearing to be doubled due to a doubling in quantity of added nitrate nitrogen. The community contained *Thalassiosira* two spp., *Skeletonema* *costatum*, *Lauderia borealis*, *Ditylum Brightwelli* and *Phaeocystis*, which together formed the dominant species.

Samples were taken from each flask and the phytoplankton separated by centrifuging. Their yellow-green pigment was dissolved in acetone and the colours compared with standard colours (Harvey, 1934). The linear relation between pigment in the diatoms and nitrate N added is shown in Fig. 1.

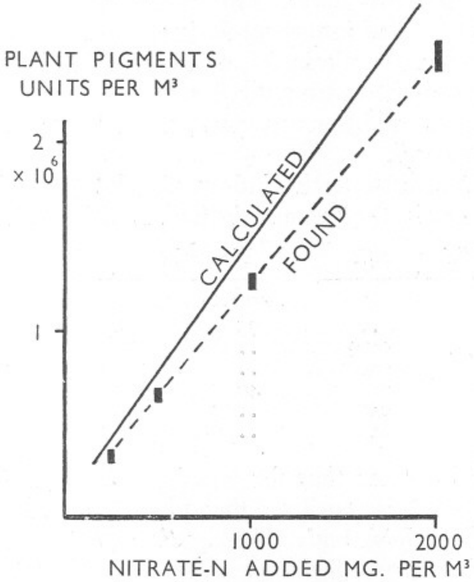

Fig. 1. Diagram showing quantities of plant pigment in phytoplankton grown on varying quantities of nitrate.

It had been found during the spring of 1934 that net-caught diatoms contained, on the average, 1000 units of plant pigments per 0·08 mg. phosphorus (Harvey *et al.*, 1935).

The following analyses of diatoms from the English Channel and American coast suggest an average content of nine times more nitrogen than phosphorus diatoms as they occur naturally in the sea.

	Ratio N/P by weight
English Channel, mixed diatom community, 3. iv. 34†	9·6
,, ,, mainly *Rhizosolenia*, 15. v. 34†	7·7
,, ,, mainly *Rhizosolenia*, 24. v. 34†	7·0
Bay of Fundy, *Thalassiosira Nordenskioldii**	13·4
Off Nova Scotia coast, mixed diatom community*	6·9
Average	9

† Cooper (1937*a*). * Redfield (1934).

Hence it may be concluded that, as a rough average value, diatoms occurring naturally contained some 1400 units of plant pigment per milligram of nitrogen.

Applying this value to the present experiment, the calculated line shown in Fig. 1 was drawn.

The result of the experiment suggests that the *method* is suitable for biological analysis, provided that growth is slow, at a reasonably cool temperature and that the flasks receive similar illumination.

In the next experiment a sample of sea water was enriched with iron and silica and divided into two parts. One part was enriched with 0·2 mg./l. phosphate P and subdivided into three flasks; to one of these no addition was made, to another 0·5 mg./l. nitrate N, and to the third 1·0 mg./l. nitrate N. The other part was enriched with 2 mg./l. nitrate N and subdivided into three flasks; to one of these no addition was made, to another 0·05 mg./l. phosphate P, and to the third 0·1 mg./l.

After varying periods in a north window, samples were taken from the flasks and the plant pigment in the contained diatoms estimated.

Addition mg./l.		Plant pigment units per litre		
N	P	After 4	6	8 days
2·0	..	75	89	..
2·0	0·05	..	865	801
2·0	0·1	..	1600	1641
..	0·2	40	44	..
0·5	0·2	..	932	800
1·0	0·2	..	1865	1600

The experiment indicates that for equal production of diatoms roughly nine times more nitrate N was utilized than phosphate P. *Thalassiosira gravida*, *Lauderia borealis*, *Biddulphia regia*, *Phaeocystis*, *Chaetoceros* two spp., *Ditylum Brightwelli* and *Skeletonema costatum* were dominant; *Thalassiothrix nitzschioides*, *Asterionella japonica*, *Nitzschia* sp., *Rhizosolenia alata*, *Bacillaria paradoxa* and *Streptotheca thamensis* were also present.

The experiment was repeated and gave a result which indicated that 10·4 times more nitrate N was utilized than phosphate P. In this water *Thalassiosira gravida*, *Lauderia borealis* and *Chaetoceros* two spp., formed the bulk of the production.

DIRECT UTILIZATION AND PREFERENCE FOR AMMONIUM

It has been shown that ammonium can be utilized as a source of nitrogen by the unicellular algae *Carteria* (Schreiber, 1927), *Chlamydomonas* (Braarud & Föyn, 1930) and *Chlorella* (Pearsall & Loose, 1937), in cultures free from bacteria. Several species of marine diatoms with their associated bacteria have also been found to utilize it. On the other hand the distribution of ammonium in the sea does not provide any clear evidence that it is utilized as such by phytoplankton, but, as pointed out by Cooper (1937 *b*), this is not remarkable on account of the complex changes in which it is continuously taking part.

Since the productivity of any area of the sea may be limited by the rate at which utilizable nitrogen is set free in the processes of digestion and decay, it is a matter of interest whether a phytoplankton community can use the earlier products of nitrogenous breakdown as well as the final product, which is nitrate.

A number of experiments have been made in which quantities of ammonium N up to 2·0 mg./l. have been added in place of nitrate N. The resulting growth was similar in quantity and composition to that brought about by an equal quantity of nitrate N. The same waters enriched with ammonium but kept in the dark during the period of the experiment were found to have undergone no detectable decrease in ammonium or increase in nitrate. There was no material change of ammonium to nitrate or nitrite.

This provides evidence that communities of diatoms such as occur in the spring can utilize ammonium directly.

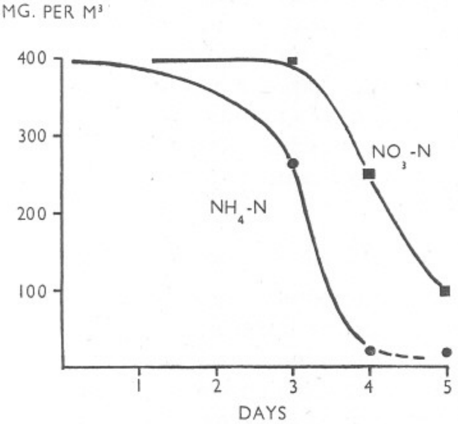

Fig. 2. Diagram showing fall in concentration of nitrate- and ammonium-nitrogen due to the growth of phytoplankton.

In some of the experiments, growth of the diatoms appeared to be slightly more rapid when supplied with ammonium than with an equal quantity of nitrate N. Pearsall & Loose (1937) had found that *Chlorella* would use ammonium-nitrogen more rapidly than nitrate N when grown in a solution containing equal quantities of both.

An experiment was therefore made with crude sea water adding equal quantities (0·4 mg./l.) of ammonium and nitrate N, mixed together, as a source of nitrogen. Analyses made at intervals during the growth of the resulting diatoms, gave values which are shown in Fig. 2. Most of the ammonium was used before there was any appreciable utilization of nitrate. *Thalassiosira gravida* and *Rhizosolenia delicatula* were dominant; *Eucampia zoodiacus*, *Skeletonema costatum*, *Phaeocystis* and *Chaetoceros* sp. being also present.

It appeared possible from this result that the more rapid utilization of ammonium was not merely due to the more rapid diffusion of its ion than of the nitrate ion. In order to investigate this possibility an experiment was made where the added nitrogen consisted of 30 mg./l. nitrate N and 0·5 mg./l. ammonium N. When the growth of diatoms had reached a population density which appeared on inspection similar to a growth which had utilized between 0·5 and 1·0 mg./l.N, analysis showed that the ammonium N had been reduced, from the 0·5 mg./l. added, to *ca.* 0·025 mg./l., possibly less. A sample of the same enriched water had been kept in the dark and this was found to have suffered no appreciable change in ammonium content. From this result it is concluded that the diatoms utilized nearly all the ammonium before any material quantity of the nitrate was used, although the latter was sixty times more concentrated at the beginning of the experiment, and many times more towards the end. That bacteria had not converted the ammonium to nitrate or nitrite was indicated by the analysis of the same water kept in the dark.

The possibility remained that the algae themselves converted nitrate to ammonium in the external medium. Warburg & Negelein had found that ammonium was produced in a nitrate solution in which *Chlorella* were suspended and kept in the dark. Experiments failed to show that marine diatoms did this; very small quantities of ammonium were found in the nitrate-enriched sea water in which the diatoms had been kept in the dark for several days, but not more than might be accounted for by breakdown of the diatoms.

UTILIZATION OF UREA AND URIC ACID

Experiments showed that nitrate or ammonium, added as a source of nitrogen, could be replaced by both urea and uric acid. With the former, growth was usually slower than with an equal quantity of nitrate N, and the final crop or total production of diatoms was in some cases less. With uric acid growth was slower and the final crop materially less, not more than 50 % in some cases.

It was found that if a subsample of the water with added urea or uric acid was kept in the dark during the course of the growth experiment, there was only an insignificant increase in its ammonium content. It would appear from this that most of the urea and uric acid was utilized directly. The phytoplankton community which developed with nitrogen added as nitrate, ammonium, urea or uric acid was similar in composition, with the exception of one experiment where the two latter sources of nitrogen led to a greater proportion of *Skeletonema costatum*, the other dominant species present being *Thalassiosira* two spp., *Lauderia borealis* and *Ditylum Brightwelli*.

AMINO-ACIDS AS A SOURCE OF NITROGEN

Although amino-acids have not been identified as occurring in sea water, their presence is probable, derived both from the early stages of the breakdown of organic matter and from the excreta of invertebrates. Baldwin (1937) cites analyses of the excreta of seven species, where amino-acids account for 14 %

of the total nitrogen. Moreover, significant quantities of dissolved amino-acids have been determined in lake water, amounting to some 0·08 mg./l.N (Peterson *et al.*, 1925).

Nitrogen in this form can be utilized by bacteria-free cultures of *Carteria* (Schreiber, 1927) and of *Chlamydomonas* (Braarud & Föyn, 1930); there is no knowledge whether marine diatoms, such as form the bulk of most phytoplankton communities, can utilize them directly, that is without previous breakdown to ammonia.

In an experiment where amino-acetic acid and where α-amino-propionic acid were added to crude sea water as a source of nitrogen, the resulting growth of diatoms was indistinguishable from the growth in a flask supplied with an equal quantity of nitrate N. It was found that ammonia was being set free in the water more rapidly than the diatoms were using it. In other experiments with α-amino-propionic acid growth was not always so rapid as with nitrate and in some cases the crop was slightly less. Similar results were obtained using β-amino-propionic acid and using proline as initial sources of nitrogen. With *l*-leucine variable small growths were obtained, the best growth was roughly one-third of that obtained with an equal addition of nitrate nitrogen. In this experiment it is noteworthy that no growth took place due to an equal addition of *d*-leucine nitrogen.

These experiments show that some amino-acids can be used by communities of marine diatoms with their associated bacteria, but provide no evidence whether they can be used directly without deamination in the external medium.

Kreps (1934) has presented evidence that some changes in the nitrogen and phosphorus cycle in sea water may be brought about through the agency of catalysts or enzymes. With the aim of finding whether such caused any material part of the deamination which occurred in these experiments, or whether the ammonium set free was due almost entirely to bacterial breakdown, crude sea water and the same after passing through a Seitz filter were added to α-alanine and the solutions kept for 5 days. A very heavy production of ammonium had taken place in the crude sea-water solution, but no detectable production in the solution made with Seitz filtered water.

Trimethylamine Oxide

This substance has been found in the urine of a marine teleost, forming 28 % of the total nitrogen (Baldwin, 1937) and is doubtless a potential source of combined nitrogen in sea water. Several experiments failed to show any increased growth of phytoplankton due to its addition to samples of crude sea water.

Organic Phosphorus Compounds

The productivity of an area of the sea is limited *inter alia* by the rate at which phosphorus, in a form which phytoplankton can use, is returned, after the death of organisms, to the upper layers. Sea water contains organic phosphorus compounds in solution in addition to phosphate; Redfield *et al.* (1937) have shown how these dissolved organic compounds accumulate in the water during the summer and are mostly broken down to phosphate during the winter. Their chemical nature is unknown. Surmise suggests that much nucleic acid must pass into the water during the course of a year from the sperm and ova shed by the animal population. Gardiner (1937) has shown the rapid regeneration of phosphate by copepods feeding on phytoplankton, but the proportion which is excreted as phosphate and which may be returned to the water as phospho-proteins and glycerophosphate compounds in partially digested faeces is unknown.

With these considerations in view, the effect of adding sodium nucleinate, caseinate and glycerophosphoric acid to crude sea water, in place of phosphate, has been tried. Sodium nucleinate brought about a similar growth and crop of diatoms to that brought about by an equal addition of phosphate P. A subsample kept in the dark showed on analysis that phosphate had been rapidly formed from the nucleinate. No such dephosphorulation occurred in water which had passed a Seitz filter, so it appears that marine bacteria very rapidly attacked nucleic acid.

The addition of caseinate led to a similar final growth, but growth was slower. The addition of glycerophosphate had no apparent effect.

It is noteworthy that none of these compounds give the Atkins-Denigès phosphate reaction.

Throughout these experiments thorough "bacteriological" precautions against possible contamination of the water samples were not taken, as the chance of such affecting the results seemed negligible.

I am indebted to Miss M. Mare for the identification of many diatom species and to Mr R. J. Harrison for analyses of the phosphorus compounds used.

SUMMARY

A method is described for obtaining growths of phytoplankton in samples of crude sea water, similar in composition but several hundred times more dense than phytoplankton communities occurring in the sea.

The ratio of nitrogen to phosphorus utilized by such communities has been determined.

They use ammonium in preference to nitrate, although the latter may be many times more concentrated than the former.

They use urea and uric acid as sources of nitrogen.

Certain amino-acids when added as sources of nitrogen were attacked by the bacteria in the community and either the ammonium set free or both the ammonium and the amino-acid were used by the phytoplankton. Others, as *d*-leucine, were not utilized, or, as *l*-leucine, only slowly utilized.

Sodium nucleinate and caseinate were rapidly broken down when added to crude sea water by bacterial action, and the phosphate produced utilized by phytoplankton. There was no significant utilization of glycerophosphate.

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PHOSPHORUS AND IRON IN *SAGITTA SETOSA* AND *SAGITTA ELEGANS*

By R. J. Harrison

Gonville and Caius College, Cambridge

(Text-fig. 1)

Cooper (1939) reported much more iron in *Sagitta setosa* than in *S. elegans*. The analyses had been made in different years, while for *S. setosa* only one sample had been examined and this may conceivably have been contaminated. In the spring of 1939 the problem was accordingly attacked afresh.

METHODS

To reduce the likelihood of contamination, the galvanized iron bucket of the ring trawl was replaced by a glass breffit from which the animals were removed by a glass pipette on to a filter paper; from this they were transferred by a glass seeker to a tared micro-beaker. Each sample was dried overnight in an aluminium-lined electric oven at 110° C. After weighing, concentrated sulphuric acid (0·1 ml.) was added, and the mixture heated at 120° C. for 1 hr in a hot-air bath made from a fire-clay crucible. The carbonaceous residue was oxidized with Merck's perhydrol which was found to contain a negligible amount of phosphorus and no iron; three to four drops were sufficient. The solution was then made up to 25 ml.

The method used for estimating the phosphorus was similar to that used by Cooper (1934) except that the addition of the stannous chloride followed that of the acid molybdate reagent.

The iron was estimated by the 2:2′-dipyridyl method (Cooper, 1935). Economy of this rather expensive reagent was achieved without loss of accuracy by the following procedure. Ten ml. of sample were treated with 0·1 ml. $4N$ hydrochloric acid and 0·2 ml. 10 % sodium sulphite as reducing agent. After 1 hr 0·5 ml. of a 0·2 % solution of dipyridyl in $N/50$ hydrochloric acid together with 0·4 ml. of a $10N$ solution of ammonium acetate were added. Four hours later the samples were compared with a standard (3·75 μg. Fe in 10 ml. water) in a Kober colorimeter.

Table I shows that there was a gradual decrease in the amount of iron in *S. setosa* until February 24. During this period the *Sagitta* were all immature, being mostly in stage II (see Russell, 1932, p. 133). In March the iron content was still somewhat low, but in April it had risen almost to that of the first sample. In the samples taken in March and April the *Sagitta* were more mature.

TABLE I

Sample no.	Date of capture	No. of animals analysed	Stage	Length in mm.	Dry weight of one animal mg.	Dry weight / Wet weight %
			Sagitta setosa			
17*a*	13. ii. 39	12	II	11–12	0·251	8·82
17*b*	13. ii. 39	12	II	11–12	0·242	8·83
17*c*	13. ii. 39	12	II	11–12	0·277	9·28
18*a*	21. ii. 39	18	I–II	10–13	0·196	9·20
18*b*	21. ii. 39	21	I–II	10–13	0·182	8·89
18*c*	21. ii. 39	12	I–II	10–13	0·189	..
22	24. ii. 39	63	II	10–12	0·183	11·10
23	10. iii. 39	20	II–III	..	0·219	8·70
25	14. iii. 39	27	III	..	0·269	..
27	1. iv. 39	50	II–III	..	0·268	..
			Sagitta elegans			
24	10. iii. 39	11	III	13–15	0·362	10·90
26	14. iii. 39	25	III	..	0·371	..

Sample no.	% composition on dry weight		Content of one animal		Ratio in mg.-atoms Fe/P
	P	Fe	P µg.	Fe µg.	
			Sagitta setosa		
17*a*	0·88	0·118	2·20	0·29	..
17*b*	0·83	0·120	2·01	0·29	0·076
17*c*	0·89	0·120	2·46	0·33	..
18*a*	0·79	0·084	1·55	0·16	..
18*b*	0·85	0·081	1·56	0·15	0·053
18*c*	0·79	0·092	1·49	0·17	..
22	0·99	0·043	1·81	0·08	0·025
23	1·20	0·085	2·63	0·19	0·039
25	0·99	0·059	2·66	0·16	0·033
27	1·00	0·108	2·68	0·29	0·061
			Sagitta elegans		
24	1·25	0·086	4·54	0·31	0·038
26	1·16	0·029	4·30	0·11	0·014

The numbers of *S. setosa* caught in half-hour oblique trawls with the 2 m. stramin ring trawl over the period of the observations are given below. These figures were kindly given me by Mr F. S. Russell.

Date	Numbers of *S. setosa*
8. ii. 39	9620
13. ii. 39	8030
21. ii. 39	571
27. ii. 39	199
6. iii. 39	22
14. iii. 39	91
20. iii. 39	3
27. iii. 39	..

It is noteworthy that the numbers of *Sagitta* decreased very considerably towards the end of February. This decrease was probably due to the dying off of the brood that had lived over the winter.

Fig. 1 shows the logarithms of the numbers of *S. setosa* in the ring trawl hauls and the ratios Fe/P plotted against time. This figure and Table I show clearly that as the numbers of *S. setosa* decreased, the content of iron, both absolutely and relatively to phosphorus, also fell away. Finally only a few individuals of higher iron content were found.

The sequence of generations in the life cycle of *S. setosa* is not clear (Russell, 1933), but it is possible that by April individuals of a different generation from that in February are prevalent. If this be so it is perhaps significant that in April the iron content was high. It is not possible to draw definite conclusions from the results, but the decrease in iron content during the period of dying off of the February population may perhaps suggest that the viability of *Sagitta* is associated with their content of iron. At any rate we have definite indications that the iron content may vary considerably from time to time and that, therefore, the problem is well worth following throughout the successive generations of *Sagitta* during a year.

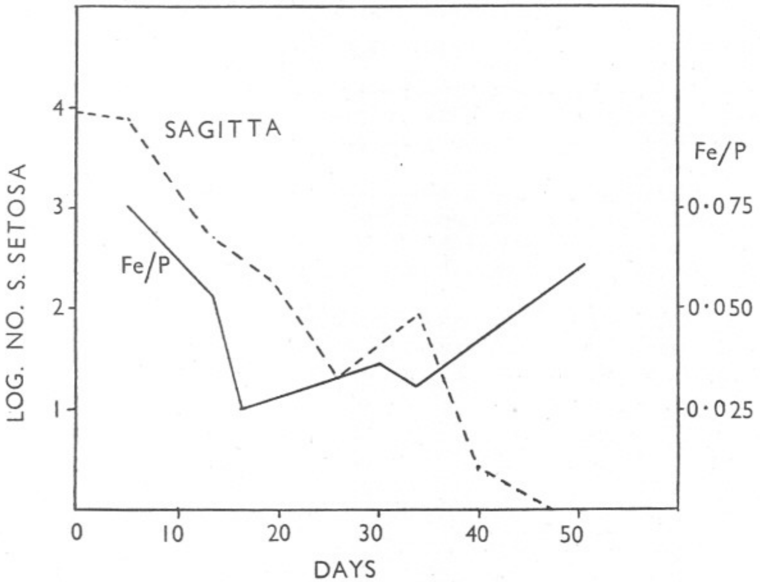

Fig. 1. Numbers of *Sagitta setosa* in ring trawl catches plotted logarithmically (——); and ratio of iron to phosphorus in mg.-atoms (– – –), during the period of observations.

S. elegans was scarce during the whole period of the investigation, but the only two samples with sufficient numbers for analysis showed a considerable decrease in iron content between March 10 and 14.

The high iron content found by Cooper in *S. setosa* in May 1934 has not yet been reproduced, the amount of iron appearing to be of the same order in the two species.

My thanks are due to Mr F. S. Russell, F.R.S., for suggesting the problem and for assistance in the sampling and to Dr L. H. N. Cooper for much helpful advice on the chemical technique.

SUMMARY

The amount of iron and phosphorus in *Sagitta setosa* and *S. elegans* has been estimated. As the winter population decreased in numbers the iron content per animal also decreased, rising again in what may have been the next brood.

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ON THE FAUNAS INHABITING INTERTIDAL SEAWEEDS

By John Colman, M.A.
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(Text-figs. 1–3)

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INTRODUCTION

While I was Student Probationer at the Plymouth Laboratory I started an examination of the faunas associated with seaweeds on Church Reef in Wembury Bay. I set out to find there the limits of distribution of as many intertidal species as possible, to estimate the numbers of each species present in each weed, and to compare, both qualitatively and quantitatively, the faunas of the various weeds with each other. I have omitted the phylum Protozoa.

First of all it was necessary to find out the limits of the zones of seaweed in relation to tidal levels, and this part of the work has been described in a previous paper (Colman, 1933). While the seaweeds were being surveyed, samples of them were collected whose animal contents formed the material for the present paper. It is therefore necessary to recapitulate briefly the methods and results of that survey.

Wembury Bay lies between the Great Mewstone and Gara Head just to the eastward of Plymouth Sound, and is mostly less than 5 fathoms (9 m.)

deep (see Map, Fig. 1). It is partly sheltered by the Great Mewstone from the full weight of south-westerly gales, but is exposed to considerable seas from the southward. Church Reef projects about a quarter of a mile towards the middle of the bay, and is almost entirely covered at high-water of spring tides. On its landward parts it supports dense growths of algae and lichens.

The zonation of the seaweeds was examined on a system of four linear traverses. Three of them radiated out from a high point near the middle of the reef which I have called Central Rock or C.R. Each traverse was marked out by triangular holes cut in the rock at intervals of about 45 ft. (14 m.). Some of these marks are still visible after nine years. Traverse A, 222·5 ft. (67·9 m.), lay towards the Coastguard look-out on Gara Head; Traverse B, 367·5 ft. (111·6 m.), towards the Great Mewstone; Traverse C, 382 ft. (116·0 m.), towards Wembury Church. In addition, a fourth line, Traverse D, was laid out from the landward end of Traverse C for 198 ft. (60·3 m.) in an easterly direction. A and B reached low-water mark on the east and west sides respectively of the reef, C was almost all between high- and low-water neaps, and D went above the limits of marine algal vegetation. Table I gives the details of the four traverses. Their approximate positions on the reef are

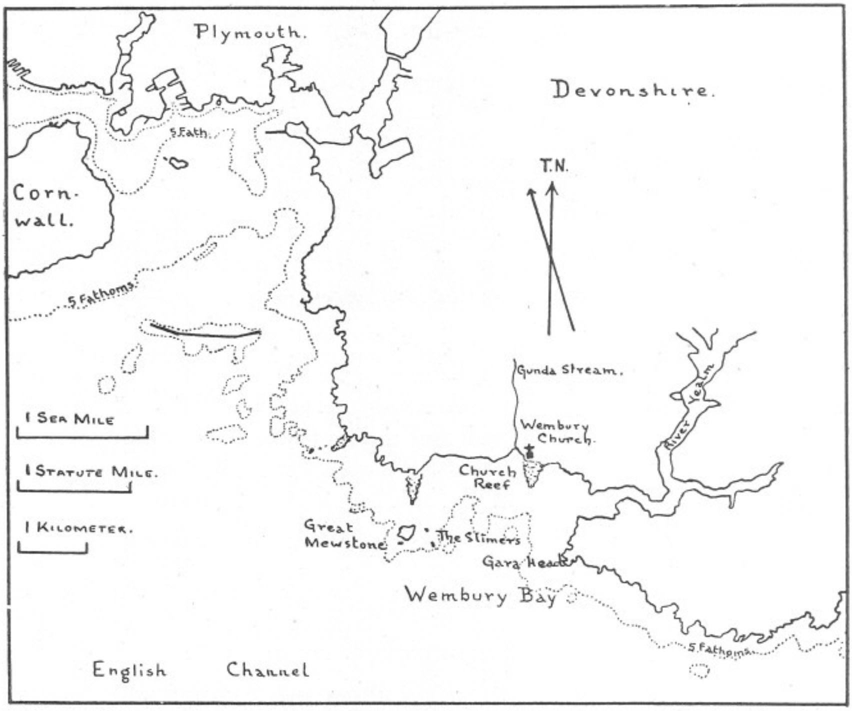

Fig. 1. Map showing the position of Church Reef in the Plymouth District.

shown in the Map, Fig. 2, which is taken from the Devonshire sheet CXXX 6 of the 1 in 2500 Ordnance Survey. Each traverse was levelled to the nearest hundredth of a foot by Mr Michael Spender, using as starting and finishing point a bench mark, 20·56 ft. (6·27 m.) above Ordnance Datum, on the south-west corner of the house adjoining Wembury Hill, and 2·70 ft. (0·82 m.) from the ground.

TABLE I. DIMENSIONS AND TRUE BEARINGS OF TRAVERSES

Traverse ..	A		B		C		D	
True bearing ..	159°		245°		4°		94°	
	Feet	Metres	Feet	Metres	Feet	Metres	Feet	Metres
C.R. to Mark I	50	15·2	43·5	13·3	65	19·8	..	..
CVII to DI	..	..	..	..	..	..	60	18·3
I to II	52	15·8	44	13·4	41	12·5	61	18·6
II to III	39·5	12·0	41	12·5	42	12·8	57	17·3
III to IV	35	10·6	41	12·5	44	13·4	20	6·1
IV to V	46	14·0	74	22·5	67	20·4	..	..
V to VI	..	..	35	10·6	64	19·5	..	..
VI to VII	..	..	30	9·1	59	17·9	..	..
VII onwards	..	..	59	17·9	..	..	..	..
Total*	222·5	67·9	367·5	111·6	382	116·0	198	60·3

Table II shows the tidal data for Devonport, which are applicable also to Wembury Bay. In this survey all heights are given relative to Ordnance Datum. This is a fixed level throughout Great Britain, whereas Chart Datum, which is about mean low-water springs, varies from place to place according to the range of the tides.

The tidal levels are not directly applicable in the field, on account of the "splash" or "wash" zone formed by breaking waves. This zone raises the effective level of the sea by an amount difficult to compute exactly, but which I estimate to be on the average about 2 ft. (0·6 m.) on Church Reef. In the previous paper (Colman, 1933, p. 453) I used the term "splash-zone",

TABLE II. TIDAL LEVELS AT DEVONPORT, 1930, IN RELATION TO ORDNANCE DATUM

	Predicted levels		Allowing for wash zone of 2 ft. or 0·6 m.	
	Feet	Metres	Feet	Metres
Extreme high-water springs	+ 8·68	+2·65	+10·68	+3·25
Mean high-water springs	+ 7·28	+2·22	+ 9·28	+2·82
Mean high-water neaps	+ 3·83	+1·15	+ 5·83	+1·75
Extreme (lowest) high-water neaps	+ 2·18	+0·66	+ 4·18	+1·26
Ordnance Datum	0·0	0·0	..	..
Mean sea-level	− 0·27	−0·08	+ 1·73	+0·52
Extreme (highest) low-water neaps	− 2·82	−0·86	− 0·82	−0·26
Mean low-water neaps	− 3·82	−1·16	− 1·82	−0·56
Mean low-water springs	− 8·24	−2·51	− 6·24	−1·91
Chart Datum	− 8·42	−2·62	..	..
Extreme low-water springs	−10·42	−3·25	− 8·42	−2·65

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* See note on page 183.

following Orton (1929). Recently, however, Stephenson (in Bokenham, Neugebauer & Stephenson, 1938, p. 129) has amplified the conception of the "splash-zone" and modified the terminology. He divides the region affected by wave action into three zones:

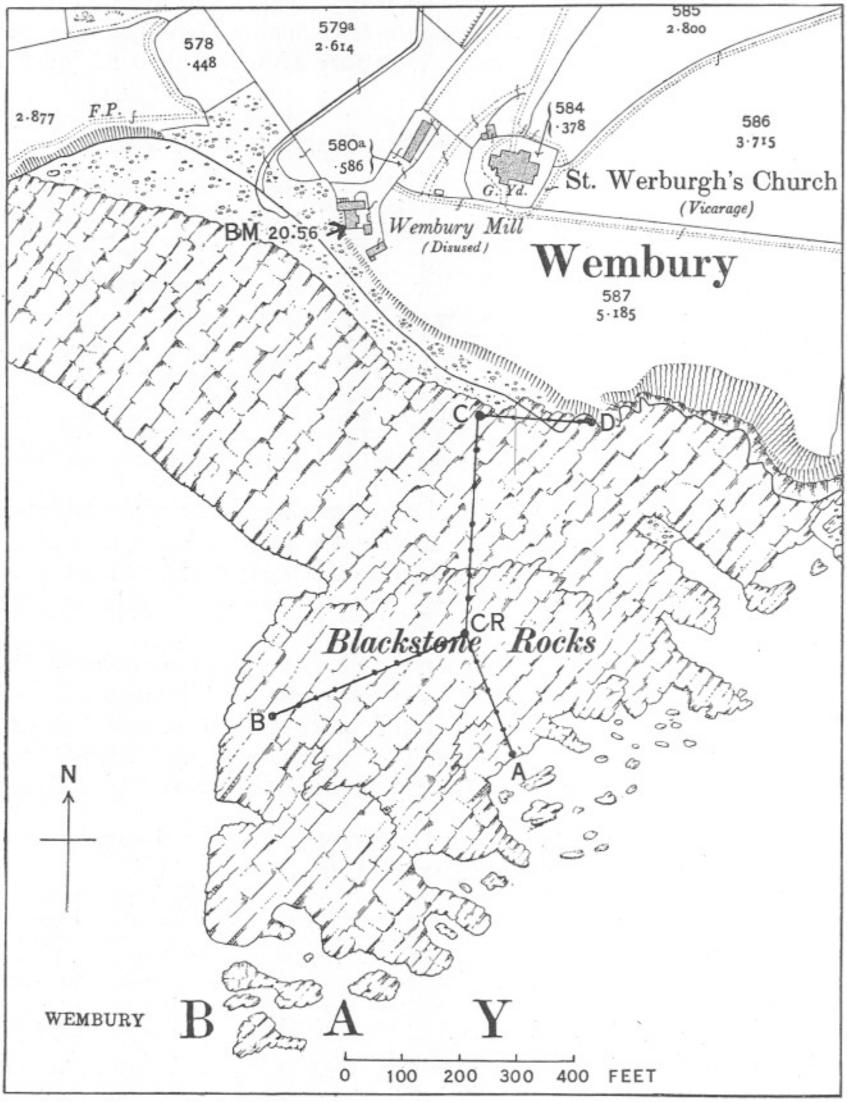

Fig. 2. Positions of the traverses and marks on Church Reef.

(*a*) The *wash zone*, immersed by each wave and effectively almost as wet as though completely submerged; this is the same as my "splash zone".

(*b*) The *splash zone*, splashed by individual drops but not by whole waves. I do not think that this zone is of much significance at Wembury, because owing to the shallowness of the bay the waves break before washing onto the reef in the region I surveyed, and do not throw up much heavy spray. I realize, however, that on coasts subjected to heavy wave action breaking directly on the rocks, as on much of the South African shore, this zone will have very real significance. I will therefore refer henceforward only to a *wash zone* on Church Reef.

(*c*) The *spray zone*, reached by spray in the form of fine mist in heavy weather. This zone again will be important in regions subjected to really heavy seas, but I do not take it into account in Wembury Bay. On-shore gales in the Plymouth district are usually accompanied by heavy rain which will mitigate to a large extent the effects of salt spray, while dry gales are usually off-shore, from the north-west.

When the distribution of animals and plants is given below in terms of tidal levels, it will be assumed that these levels have been raised 2 ft. (0·6 m.) by the wash zone.

Samples of seaweed were taken more or less at random along each traverse, the exact position and height of each sample being determined. From Traverse A there were taken nine samples of four species of weed; from Traverse B, eighteen samples of five weeds; from Traverse C, ten samples of four weeds; from Traverse D, thirteen samples of three weeds. There were thus fifty samples in all. They were divided among eight different seaweeds, which can now be listed, giving for each the number of samples and the limits of distribution on Church Reef, the heights being given above or below Ordnance Datum (see Table II). Each sample was given a number consisting of a letter referring to the plant, and a numeral. In this paper the samples will always be referred to on this system.

Pelvetia canaliculata (five samples, A1 to A5); from +7·49 ft. (2·3 m.) down to +4·91 ft. (1·5 m.), or from half way between mean high-water springs and neaps down to just above extreme (lowest) high-water neaps.

Fucus spiralis (six samples, B1 to B6); from +5·79 ft. (1·9 m.) down to +3·19 ft. (1·0 m.), or from mean high-water neaps down to a foot below extreme (lowest) high-water neaps.

Lichina pygmaea (four samples, C1 to C4); from above +6 ft. (2 m.) down to +0·04 ft. (0·0 m.), or from above mean high-water neaps down to just above extreme (highest) low-water neaps.

Fucus vesiculosus (three samples, D1 to D3); all just above mean low-water neaps); limits of distribution not determined.

Ascophyllum nodosum and *Polysiphonia lanosa* (twelve samples, E1 to E12); from +3·40 ft. (1·0 m.) down to −4·11 ft. (−1·3 m.), or from just below extreme (lowest) high-water neaps down to half-way between mean low-water neaps and springs. These two algae are treated as a unit, since wherever *Ascophyllum* occurs on Church Reef, *Polysiphonia* is growing as an epiphyte upon it.

Fucus serratus (ten samples, F1 to F10); from +1·40 ft. (0·4 m.) down to −8·6 ft. (−2·6 m.), or from mean sea-level down to extreme low-water springs.

Gigartina stellata (four samples, G1 to G4); from −5·0 ft. (−1·5 m.), or from above mean low-water springs, down to below all tide-marks.

Laminaria digitata holdfasts (six samples, H1 to H6); from −6·23 ft. −1·9 m.), or from mean low-water springs, down to below all tide-marks.

Table III shows the date of collection, position on the traverses, height on the shore and weight, of each sample, and the Map, Fig. 3, shows their distribution along the traverses. The samples were measured by damp weight, and no allowance has been made for differential water loss by evaporation at the various levels on the shore, though it must be considerable as between, say, *Pelvetia canaliculata* and *Fucus serratus*. The weight of the sample in each case

TABLE III. PARTICULARS OF THE FIFTY SAMPLES OF EIGHT SPECIES OF WEED

Seaweed	Sample no.	Weight in g.	Date	Position on traverse in m.	Height relative to O.D. in m.
Pelvetia canaliculata	A 1	197	30. vi. 30	D I 11·2 D II	+1·52
	A 2	52	10. vii. 30	D III 4·6 D IV	+1·95
	A 3	51	11. vii. 30	D II 2·1 D III	+1·76
	A 4	53	6. i. 31	D I 18·3 D II	+2·01
	A 5	97	20. iii. 31	D I 7·3 D II	+1·49
Fucus spiralis	B 1	408	24. vi. 30	D I 0·9 D II	+1·18
	B 2	94	10. vii. 30	D II 1·8 D III	+1·67
	B 3	80	11. vii. 30	D I 5·2 D II	+1·37
	B 4	93	6. i. 31	D I 0·3 D II	+1·15
	B 5	56	6. i. 31	D II 0·6 D III	+1·17
	B 6	77	20. iii. 31	D I 7·0 D II	+1·49
Lichina pygmaea	C 1	11	5. ix. 30	C R 11·5 A I	+0·06
	C 2	12	5. ix. 30	C R 0·9 A I	+1·34
	C 3	14	7. i. 31	C R 1·8 B I	+1·51
	C 4	24	20. iii. 31	C R 1·5 B I	+1·51
Fucus vesiculosus	D 1	87	15. vii. 30	C V 13·7 C VI	−0·40
	D 2	78	15. vii. 30	C V 11·5 C VI	−0·52
	D 3	87	7. i. 31	C V 13·1 C VI	−0·46
Ascophyllum nodosum and *Polysiphonia lanosa*	E 1	350	13. v. 30	B II 1·8 B III	−0·52
	E 2	670	14. v. 30	C IV 2·4 C V	+0·40
	E 3	529	2. vii. 30	C VII 4·6 D I	+0·27
	E 4	151	15. vii. 30	C VI 13·7 C VII	+0·67
	E 5	119	15. vii. 30	C V 14·6 C VI	−0·09
	E 6	103	23. vii. 30	C I	−0·30
	E 7	202	25. vii. 30	C I 5·5 C II	+0·37
	E 8	84	28. viii. 30	B II 9·4 B III	−1·00
	E 9	96	5. i. 31	B I 1·8 B II	−0·43
	E 10	84	5. i. 31	B II 9·4 B III	−1·00
	E 11	117	6. i. 31	C VII 8·2 D I	+0·73
	E 12	68	20. iii. 31	C II 0·3 C III	+0·06
Fucus serratus	F 1	364	2. vi. 30	B III 8·2 B IV	−1·49
	F 2	335	11. vi. 30	A I 12·2 A II	−1·31
	F 3	395	13. vi. 30	A III 9·4 A IV	−1·86
	F 4	91	23. vii. 30	C I 1·2 C II	−0·40
	F 5	131	26. vii. 30	A IV 0·7 A V	−1·95
	F 6	82	28. viii. 30	B V 4·3 B VI	−1·37
	F 7	85	28. viii. 30	B V 7·9 B VI	−1·89
	F 8	99	5. i. 31	B I 12·8 B II	−0·58
	F 9	93	5. i. 31	B III 11·8 B IV	−1·83
	F 10	77	3. iv. 31	B VII 0·9	−1·76
Gigartina stellata	G 1	70	26. vii. 30	A IV 0·9 A V	−1·98
	G 2	60	28. viii. 30	B VI 7·9 B VII	−1·64
	G 3	62	7. i. 31	B VII 6·7	−1·89
	G 4	47	3. iv. 31	B VII 0·6	−1·70
Laminaria digitata holdfasts	H 1	17	27. viii. 30	A V	−1·98
	H 2	63	27. viii. 30	A V 1·2	−2·59
	H 3	92	27. viii. 30	B VII +	−2·65
	H 4	25	27. viii. 30	B VII +	−1·86
	H 5	52	7. i. 31	B VII 9·1	−2·77
	H 6	104	3. iv. 31	Near A V	−2·7

includes that of the animals living in it. The weights of the samples ranged from 11 to 670 g., which perhaps merits some explanation. The early samples were large, but were found to take so long to examine thoroughly that a smaller size was adopted, the collecting unit being in most cases a 1 lb. honey-jar. In *Lichina pygmaea*, the fauna proved to be so abundant that the contents of a 3 by 1 in. tube were sufficient for comparison with the other weeds. Each sample of *Laminaria digitata* consisted of one holdfast.

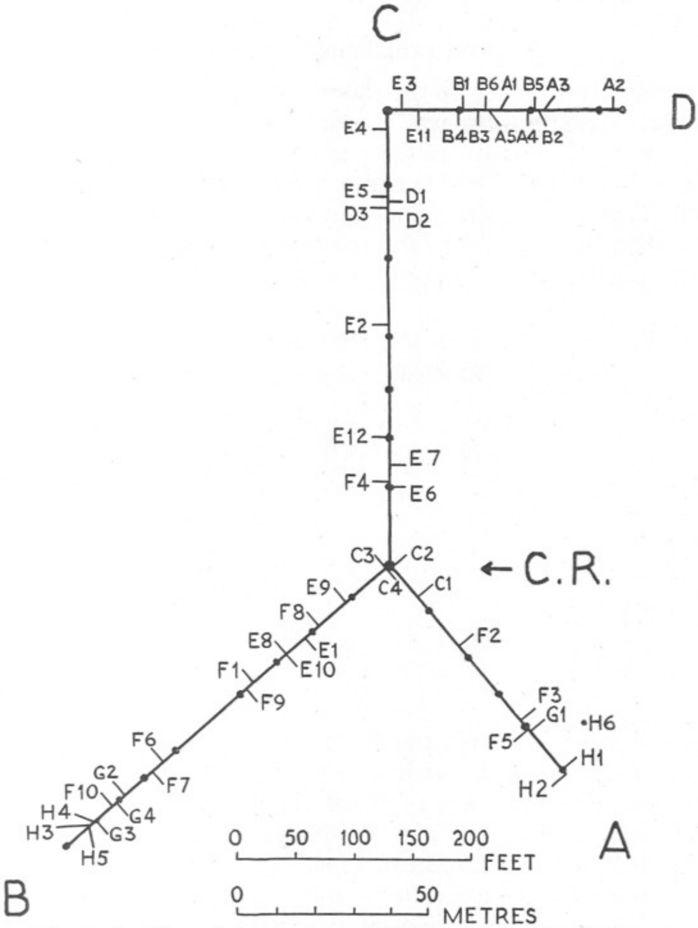

Fig. 3. Position of 50 samples on Traverses A, B, C and D.

THE FAUNAS OF THE SEAWEEDS

The fauna of each weed will now be considered in detail, working roughly from high-water downwards.

Pelvetia canaliculata (Table IV)

This seaweed lives higher up the shore than any other, and supports a very scanty fauna. *Hyale nilssoni* was the only animal that occurred in all five samples, once in fair abundance (48 per 100 g. in A 1). There was one *Ligia oceanica* in A 1 and several in A 2 and A 3, but none in either of the other two samples; *Ligia* was not found among any other algae in this survey. *Pelvetia* lives well outside the ranges of *Littorina littorea* and *L. obtusata*, but *L. saxatilis* was not uncommon. *L. neritoides* was not identified but may form part of the young Littorinidae in A 1 and A 2. There were no copepods or polychaetes. Curiously enough, the lowest sample, A 5 at +1·5 m., contained the smallest number of species, 15 *Hyale nilssoni* making up the whole catch, while the highest sample, A 4 at +2·0 m., gave the smallest total catch, including only two each of *H. nilssoni*, *Lipura maritima* and *Littorina saxatilis*. Sample A 2, though from a level only 0·06 m. lower than that of A 4, contained the largest and most varied fauna found among *Pelvetia*. There is no correlation with height on the shore between these samples, but the very small catches in January and March may indicate a seasonal dearth of animals. The number of insects was remarkably low when compared with those in habitats farther down the shore.

TABLE IV. *PELVETIA CANALICULATA*. ANIMALS INHABITING FIVE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. . .	A 1	A 2	A 3	A 4	A 5
Weight in g. . .	197	52	51	53	97
Date . .	30. vi. 30	10. vii. 30	11. vii. 30	6. i. 31	20. iii. 31
Position in m. . .	D I 11·2 D II	D III 4·6 D IV	D II 2·1 D III	D I 18·3 D II	D I 7·3 D II
Height in m. . .	+1·52	+1·95	+1·76	+2·01	+1·49
Nematoda	. .	17	. .	. .	. .
Oligochaeta	1	. .	. .	. .	. .
Isopoda					
Ligia oceanica	1	38	37	. .	. .
Amphipoda					
Hyale nilssoni	48	6	6	2	15
Insecta					
Lipura maritima	. .	. .	. .	2	. .
Diptera (larvae)	. .	2	. .	. .	. .
Gastropoda					
Littorina saxatilis	. .	17	6	2	. .
Littorinidae (juv.)	5	14	. .	. .	. .
Total	55	94	49	6	15

Fucus spiralis (Table V)

Fucus spiralis occurs on the rocks immediately below *Pelvetia canaliculata*, and occupies a zone around high-water neaps with a vertical range of rather more than 0·6 m. The six samples, B 1 to B 6, cover most of this range. All except B 1 contain faunas similar to each other and to those of *Pelvetia*. *Hyale nilssoni* is again the most abundant animal, varying from 7 to 85 per 100 g. No correlation with tidal levels can be seen in this case; it is true that the lowest sample but one, B 5, contains the fewest *Hyale* and the highest sample, B 2, the most, but B 1 and B 4 from almost exactly the same level as B 5 each contain 70 *Hyale*. The latter sample and B 4 were collected, too, on the same day, which seems to rule out any seasonal difference as regards this species.

TABLE V. *FUCUS SPIRALIS*. ANIMALS INHABITING SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. ..	B 1	B 2	B 3	B 4	B 5	B 6
Weight in g. ..	408	94	80	93	56	77
Date ..	24. vi. 30	10. vii. 30	11. vii. 30	6. i. 31	6. i. 31	20. iii. 31
Position in m. ..	D I 0·9 D II	D II 1·8 D III	D I 5·2 D II	D I 0·3 D II	D II 0·6 D III	D I 7·0 D II
Height in m. ..	+1·18	+1·67	+1·37	+1·15	+1·17	+1·49
Nematoda	6	1	1	..	4	7
Turbellaria or Nemertinea	2	..	..	..	..	..
Polychaeta						
Fabricia sabella	..	1	..	..	4	..
Sabellidae (juv.)	..	1	..	..	..	..
Oligochaeta	1	..	..	..	18	..
Ostracoda	2	1	..	..	..	..
Copepoda Harpacticoida						
Harpacticus chelifer	3	..	..	..	..	..
H. gracilis	6	1	..	..	..	..
H. flexus	12	..	..	..	..	..
Zaus spinatus	15	..	..	..	..	..
Idya furcata	102	..	..	..	..	..
Parathalestris harpacticoides	3	..	..	..	..	..
Westwoodia nobilis	3	..	..	..	..	..
Dactylopusia brevicornis	1	..	..	..	..	..
Laophonte littoralis	..	1	..	..	..	..
Laophonte sp.	1	..	1	..	..	2
Harpacticoida (indet.)	3	..	..	..	..	..
Isopoda						
Idotea granulosa	1	..	..	..	..	..
Naesa bidentata	1	..	..	2	..	..
Amphipoda						
Hyale nilssoni	70	85	25	70	7	18
Decapoda						
Carcinus maenas	1	..	..	..	..	..
Insecta						
Lipura maritima	..	..	..	..	..	1
Aptera (indet.)	1	..	..	..	..	..
Diptera (larvae, indet.)	..	4	..	..	2	..
Acarina	3	5	1	6	2	2
Gastropoda						
Littorina obtusata	1	..	..	1	9	1
L. obtusata spawn	1	2	..	..	..	..
Lacuna sp.	3	3	..	..	..	..
Littorinidae (juv.)	24	9	2	21	..	6
Total	266	114	30	100	46	37

Acarines were always present, though scarce, and these samples also contained occasional nematodes, oligochaetes and young Littorinidae. Still rarer were copepods (except in B 1), ostracods, *Lipura maritima*, and the larvae of diptera.

These remarks apply equally well to sample B 1 except for one group, the copepods, which in this sample alone were quite numerous and were represented by at least ten species. Of 149 per 100 g., 102 were *Idya furcata*, 15 *Zaus spinatus*, 12 *Harpacticus flexus* and 6 *H. gracilis*. A total range in height of only 0·03 m. covered the three samples B 1, B 4 and B 5, and B 1 was only 0·6 m. away from B 4; yet the copepods occurred only in B 1. It is difficult to account for this on a seasonal basis, for B 3 was collected only a fortnight later than B 1 and from a level only 0·2 m. higher on the shore, but contained the smallest numbers both of individuals and species of any of the samples of *Fucus spiralis*. It is true that B 1 was much larger than the other samples, but with the exception of the copepods its contents were very similar to those of the others, indicating that the latter were large enough to give valid results. Had copepods been present in any number in the other samples they could not have been missed.

Lichina pygmaea (Table VI)

The population inhabiting the lichen *Lichina pygmaea* is perhaps the most remarkable on the shore. This lichen grows as small tufts only about 2 cm. in height on rocks between high-water springs and mean sea-level or a little lower. These tufts may grow closely enough together to form a more or less continuous covering of the rock over a few square feet at a time, but the lichen never affords a dense mass of cover such as is provided by the fucoid algae. *L. pygmaea* seems to prefer the more exposed parts of the reef where it receives nearly the full force of the waves, but nevertheless the fauna it supports is by far the most abundant on the shore, at any rate in individuals, not being exceeded even by that of the *Laminaria* holdfasts.

TABLE VI. *LICHINA PYGMAEA*. ANIMALS INHABITING FOUR SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	C 1	C 2	C 3	C 4
Weight in g.	11	12	14	24
Date	5. ix. 30	5. ix .30	7. i. 31	20. iii. 31
Position in m.	C.R. 11·5 A 1	C.R. 0·9 A 1	C.R. 1·8 B 1	C.R. 1·5 B 1
Height in m.	+0·06	+1·34	+1·51	+1·51
Nematoda	9	..	..	..
Oligochaeta				
Lumbricillus pumilio	27	8	7	..
Cirripedia				
Chthamalus stellatus	73	292	293	417
Balanus balanoides	55	..	..	..
Isopoda				
Campecopea hirsuta	3772	2685	2890	2204
Amphipoda				
Hyale nilssoni	46	..	86	8
Insecta				
Lipura maritima	91	..	..	..
Petrobius maritimus	18	..	..	..
Geranomyia unicolor (larvae)	46	175	64	104
Other Diptera (larvae)	109	..	7	29
Acarina	1481	..	179	87
Pelecypoda				
Mytilus edulis (juv.)	91	..	14	21
Lasaea rubra	9418	4550	12140	11575
Gastropoda				
Littorina littorea (juv.)	245	183	129	50
L. obtusata (juv.)	55	40	165	421
L. saxatilis (juv. et ad.)	..	100	86	333
Total	15536	8033	16050	15246

The samples of *Lichina* collected were much smaller than those of the other weeds, being such as would fill a 3 by 1 in. glass tube, whereas the other plants were collected into 1 lb. honey-jars. *Lichina* is a small plant, so in order to fill a honey-jar with it it would be necessary to denude a considerable area of rock. Since *Lichina* grows on rather steep places it would be difficult both to do this and to collect the whole sample from the same height on the shore. The population among *Lichina* is, however, so dense that the small samples collected were quite large enough for comparison with those of other weeds.

Four samples in all were examined, C 1 to C 4, and they contained 1709, 964, 2247 and 3659 animals in actual count, the samples weighing only 11, 12, 14 and 24 g. respectively. The analysis of these samples is shown in Table VI, in numbers per 100 g. of damp lichen. These figures, when compared with those of other weeds on the shore, show how astonishingly numerous are the animals living among *Lichina pygmaea*. By far the most abundant is the small bivalve mollusc *Lasaea rubra*, with 9418, 4550, 12,140 and 11,575 in the four samples. This species is noted in the *Plymouth Marine Fauna* (1931) as "abundant between tide-marks on all rocky shores, in crevices, etc.... rocks below the Hoe, very common among barnacles and the roots of *Fucus*, etc." I have not made comparative counts of *Lasaea rubra* in these different habitats, but they never appear to be so numerous as among *Lichina*; I have found none among the holdfasts of fucoid algae at Wembury, and the species occurred in no other samples in this survey. The density of its population can evidently vary somewhat, being in C 2 less than half what it is in any of the other samples.

The next most numerous animal is the isopod *Campecopea hirsuta*, whose numbers varied from 2204 to 3772 per 100 g. and were thus slightly more regular than those of *Lasaea*. Like *Lasaea rubra*, *Campecopea hirsuta* occurred in no other samples than those of *Lichina pygmaea*. The two species appear to share the same habitats among the lichen and barnacles.

Acarines were very numerous in one sample, C 1, but were either absent or only moderately common in the others. C 1 is about 1·5 m. lower than the other three samples, which seem therefore to be at about the upper limit of distribution of the mites *Rhombognathus pascens* and *R. seahami*, which make up the bulk of the acarine population. This is borne out by the rarity of mites in *Fucus spiralis* from similar levels.

A considerable part of the fauna of this part of the shore consisted of the larvae of diptera. Only one species, *Geranomyia unicolor*, was at all surely identifiable from *Lichina*, but it formed either the whole or a large part of the insect population. It is a fairly large and conspicuous animal about 12 mm. long, and must make up an important part of the animal matter present.

The levels from which these four samples were taken were not chosen very well, being 0·06, 1·34, 1·51 and 1·51 m. respectively above Ordnance Datum. That is to say, while the first sample was from below mean sea-level near the bottom of *Lichina's* range, the other three were all from a little below mean high-water neaps and about 0·6 m. from the top of *Lichina's* range, but none came from intermediate positions. Nevertheless some changes in the faunas due to differences in level are indicated fairly clearly, as has been shown in the mites. Two barnacles are present, *Chthamalus stellatus* and *Balanus* *balanoides*. The former occurred in all four samples, but was much less abundant in the lowest sample, C 1, than in the upper three; although *Chthamalus* can be found on the shore 2 m. below Ordnance Datum, it is most abundant on the higher parts of its range. *B. balanoides* occurred only in the lowest sample; its upper limit on Church Reef varies between +0·76 and +1·31 m., and the other three samples of *Lichina* were all higher than this.

Some of the molluscs also showed the effects of tidal level. Young *Mytilus edulis* were present in fair numbers in the lowest sample, absent from C 2, and scanty in C 3 and C 4. *Littorina saxatilis* occurred in the three high samples, but its lowest recorded limit on Church Reef is +0·43 m. and it was absent from C 1. *L. obtusata* and *L. littorea*, whose ranges on the shore are almost identical, were both present in fair numbers in all four samples, but in very different proportions. In C 1 and C 2 *L. littorea* outnumbered *L. obtusata* by $4\frac{1}{2}$ to 1; in C 3 their numbers were nearly equal, while in C 4 *L. obtusata* outnumbered *L. littorea* by $8\frac{1}{2}$ to 1. These differences cannot be due to altitude, for in C 1 and C 2, with levels 1·3 m. apart, the two species were present in almost identical proportions, and these were collected on the same day. On the other hand samples C 2, C 3 and C 4 were collected from almost the same level but on widely different dates in September, January and March respectively, and showed great changes in the distribution of *L. littorea* and *L. obtusata*. These changes must therefore be seasonal in character.

According to Linke (1933), *L. littorea* at Heligoland lays eggs in the spring and early summer, from January at the earliest till June at the latest; larvae may be present in the plankton until November, but are most abundant during the summer. It is possible then, that the small *L. littorea* in C 1 and C 2 in September had settled during the previous months, and that the decrease in their numbers in January (C 3) and March (C 4) can be accounted for by a natural mortality rate. Linke says also that *L. obtusata* lays spawn most frequently during the summer and that the young forms hatch out during the same season. It is therefore difficult to explain the marked rise in the numbers of this species from 55 and 40 in C 1 and C 2 to 165 in C 3 and 421 in C 4.

Fucus vesiculosus (Table VII)

This seaweed is abundant on some of the rocks in Wembury Bay, but on the traverses surveyed it occurred only as a small patch on Traverse C a little above mean low-water neaps. Three samples, D 1, D 2 and D 3 were taken; their greatest distance apart was only 2·2 m., and 0·12 m. was the greatest difference in level between them, D 1 and D 2 were collected on the same day, July 15, 1930, and contained faunas which were in many ways very like each other, though the population was on the whole less dense in D 1 than in D 2. Thus D 1 contained 6 ostracods, 115 copepods, 20 acarines and 75 young littorinids as compared with 41, 538, 37 and 87 respectively in D 2, and the total populations per 100 g. were 252 and 750; otherwise the catches were remarkably similar. Although the bulk of each fauna consisted of copepods, it was among this group the the greatest differences lay. In D 1, out of 115 copepods, 63 were *Idya furcata*, 17 *Machairopus minutus* and 14 *Harpacticus gracilis*. In D 2 there were almost identical numbers of *Idya furcata* (64) and *H. gracilis* (13), but no *M. minutus*. In addition, however, D 2 contained 187 *Parathalestris clausi*, 109 *P. harpacticoides* and 83 *Thalestris purpurea*, these species being absent from D 1 except for a mere couple of *T. purpurea*. This is a good example of the patchiness of the distribution of so many of the smaller inhabitants of the seaweeds. The sample D 3 came from a position between those of D 1 and D 2, but was collected some six months later, January 7, 1931. Its total number of animals, 374, was more than the 252 of D 1 and less than the 750 of D 2, but was made up almost entirely of 350 acarines, 338 of which were *Rhombognathus pascens* and *R. seahami*.

TABLE VII. *FUCUS VESICULOSUS*. ANIMALS INHABITING THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	D 1	D 2	D 3
Weight in g.	87	78	87
Date	15. vii. 30	15. vii. 30	7. i. 31
Position in m.	C V 13·7 C VI	C V 11·5 C VI	C V 13·1 C VI
Height in m.	−0·40	−0·52	−0·46
Turbellaria and Nemertinea	6	10	..
Nematoda	6	4	..
Oligochaeta	1	..	..
Sipunculoidea			
Phascolosoma minutum	..	6	..
Ostracoda	6	41	1
Copepoda Calanoida			
Pseudocalanus elongatus	1	..	..
Copepoda Harpacticoida			
Ectinosoma melaniceps	..	6	..
Harpacticus chelifer	4	..	..
H. gracilis	14	13	..
H. uniremis	2	..	..
Idya furcata	63	64	2
Thalestris purpurea	2	83	..
Parathalestris clausi	..	187	3
P. harpacticoides	..	109	..
Rhinchothalestris rufocincta	2	6	..
Microthalestris forficula	..	13	..
Westwoodia nobilis	..	6	1
Machairopus minutus	17	..	..
Amphiascus sp.	..	6	..
Laophonte proxima	..	13	..
Laophonte sp.	1	..	..
Harpacticoida (indet.)	9	32	3
Isopoda			
Naesa bidentata	7	4	..
Idotea granulosa	..	1	..
Cryptoniscid (indet.)	1	..	..
Amphipoda			
Pseudoprotella phasma	..	1	..
Amphipoda (indet.)	..	3	..
Acarina			
Rhombognathus pascens and *Rhombognathus seahami*	17	29	338
Acarina (indet.)	3	8	12
Insecta			
Diptera (larvae)	..	5	2
Gastropoda			
Gibbula umbilicalis	..	1	..
Lacuna sp.	6	4	..
Littorina obtusata	9	9	12
Littorinidae (juv.)	75	87	..
Total	252	750	374

There were no young littorinids and only nine copepods. The latter figure may be due to the time of year, for copepods were scarce during the winter in both *Fucus serratus* and in *Ascophyllum*.

Ascophyllum nodosum and Polysiphonia lanosa (Tables VIII–X)

As mentioned in my previous paper (Colman, 1933) these two algae are treated as a unit, since they always seem to occur together on Church Reef, the *Polysiphonia* living as an epiphyte on the *Ascophyllum*. *P. lanosa* grows as dense tufts of dichotomously branching twigs, whose ends are curved and interlock intimately. It provides a favourite harbouring place for many small animals, in particular ostracods, copepods and mites, the last two of which usually die *in situ* with the legs clasped right round the *Polysiphonia* stems. This makes them difficult to see and to dislodge, a fact which was not at first realized.

Twelve samples of *Ascophyllum* were collected, E 1 to E 12, and the first three were much larger than the others, weighing 350, 670 and 529 g. respectively. The first two were the first samples of any weed examined in this survey, and far fewer small animals are recorded from them than from any of the other samples of *Ascophyllum*; they have only been included in order to illustrate the points now under discussion. These samples were merely divided into small portions and washed vigorously in bowls; animals such as oligochaetes, isopods, amphipods and gastropods, which on dying do not clasp the weed and in any case are fairly large and conspicuous, appeared in similar numbers to those in other samples and were probably collected satisfactorily, but the ostracods, copepods, acarines and perhaps the nematodes were mostly left behind among the weed and so were missed. When this was realized, the next sample, E 3, was examined completely, and every twig of *Polysiphonia* was teased out from every other with needles under a dissecting microscope and the animals carefully picked off. This entailed the handling one by one of 3926 animals, with subsequent sorting and counting, not to mention the identification of many of them, and it took so long that the smaller size of weed sample used in the rest of the survey was decided on. The samples in general are admittedly too small to be quite satisfactory, but they are as large as it is practicable for one person to examine thoroughly, and in all the samples except E 1 and E 2 I counted all the animals.

Ignoring for the moment those two samples, four groups stand out as the most abundant among *Ascophyllum*, namely ostracods, copepods, acarines and gastropods. The ostracods were often extraordinarily numerous, with 1480 per 100 g. in E 6. Their numbers seem to vary widely at the same season on different parts of the reef. The six samples E 3 to E 8 inclusive were all collected during July and August, but the numbers varied from 90 to 1480; the poorer of these catches all came from the landward end of Traverse C, while the others were from nearer the middle of the reef (see Map, Fig. 3).

There is apparently no correlation between abundance of ostracods and height on the shore, at any rate within the range of *Ascophyllum nodosum*.

The catches of ostracods were rather perplexing as regards seasonal abundance. On August 28 E 8 contained 805, while the number dropped to 24 and 11 in E 9 and E 10 which were both collected on January 5, E 10 being from exactly the same place as E 8. It would be tempting to conclude from these figures that there is a winter minimum for intertidal ostracods, but sample E 11, collected next day, contained 201, although it came from the landward end of Traverse C where the numbers were smaller than elsewhere during the summer. These results might be due to seasonal migration, but it is idle to speculate on this until the species inhabiting *Ascophyllum* have been worked out. I found myself unable to identify ostracods with any confidence, and unfortunately my collection of them was destroyed. Recently (April 1939) I collected some from Church Reef which Mr A. G. Lowndes was kind enough to examine; he found that they were all *Xestoleberis aurantia* (Baird). They were not abundant, however, and during the summer there is certainly more than one species present.

The copepods (Tables IX and X) were identified fairly completely with the exception of young stages, and the results show, as in *Fucus vesiculosus*, that the *total numbers* of copepods have only a limited significance. Twenty-three species were identified from *Ascophyllum*, but only one species, *Westwoodia nobilis*, occurred with any regularity and was, indeed, absent from only one sample, E 5. In the samples in which it was found its numbers varied from 2 in E 9 (January) to 203 in E 6 (July). The next largest catch of *W. nobilis* was 104 in E 12 collected in March, after three poor catches in January. This seems to indicate a winter minimum for the species, but the summer figures are too irregular to show any definite seasonal maximum. While E 6 with 203, and E 7 with 93, were both collected in the fourth week in July, E 5 collected on July 15 contained no *W. nobilis* at all, and the numbers were small in the other two July samples. Another species of the same genus, *Westwoodia pygmaea*, was present in quite large numbers (136) in E 12, but was not represented in any other sample.

The other species of Harpacticoida appeared only sporadically, though several of them were occasionally numerous. The samples E 3, E 4 and E 5, all collected in the first half of July, were the richest in species, and several families here make practically their only appearance in these catches of *Ascophyllum*. *Harpacticus gracilis* was quite abundant with 129, 165 and 33 in these three samples, and there were 16 *H. uniremis* in E 5. The only other species of the family Harpacticidae was represented by a solitary *H. chelifer* in E 10 in January. Of the Idyidae, there were 373 *Idya furcata* in E 5, which was the largest number of one species of copepod in any sample of *Ascophyllum*, and 61 in E 4; no adult Idyids appeared after mid-July. Apart from the two species of *Westwoodia* already mentioned, various Thalestridae were found from time to time of which three were occasionally abundant; there

TABLE VIII. *ASCOPHYLLUM NODOSUM* AND *POLYSIPHONIA LANOSA*. ANIMALS INHABITING TWELVE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	E 1	E 2	E 3	E 4	E 5	E 6	E 7	E 8	E 9	E 10	E 11	E 12
Weight in g.	350	670	529	151	119	103	202	84	96	84	117	68
Date	13. v. 30	14. v. 30	2. vii. 30	15. vii. 30	15. vii. 30	23. vii. 30	25. vii. 30	28. viii. 30	5. i. 31	5. i. 31	6. i. 31	20. iii. 31
Position in m.	B II 1·8 B III	C IV 2·4 C V	C VII 4·6 D I	C VI 13·7 C VII	C V 14·6 C VI	C I	C I 5·5 C II	B II 9·4 B III	B I 1·8 B II	B II 9·4 B III	C VII 8·2 D I	C II 0·3 C III
Height in m.	−0·52	+0·40	+0·27	+0·67	−0·09	−0·30	+0·37	−1·00	−0·43	−1·00	+0·73	+0·06
Coelenterata												
Clava squamata (polyps)	..	+	+	..	..	..	..	..	..	..	33	..
Laomedea flexuosa	..	..	..	..	..	+	+	..	..	..	..	..
Dynamena pumila	common	..	+	..	..	..	+	..	+	+	..	+
Sertulariidae (indet.)	..	..	..	..	..	+	..	..	..	..	..	..
Stauromedusae (juv.)	..	..	..	..	..	..	1	..	..	..	..	..
Turbellaria and Nemertinea	1	3	19	47	39	82	56	94	28	86	187	121
Nematoda	17	13	61	126	60	49	72	61	44	46	211	153
Polychaeta												
Nereidae (indet.)	..	..	..	..	..	..	..	..	..	..	..	2
*Sabellidae	..	..	5	40	..	..	..	..	1	6	744*	60*
Spirorbis borealis	..	..	..	13	..	..	..	..	..	..	..	..
Oligochaeta												
Lumbricillus scoticus	11	82	20	20	4	..	..	3	14	17	3	2
L. pumilio			45	26	4	17	1	7	10	6	19	40
L. spp. (juv.)	..	..	..	..	..	..	..	..	..	..	53	66
Ostracoda	4	2	90	232	351	1480	815	805	24	11	201	225
Copepoda (see Table IX)	2	5	279	570	731	358	613	168	49	56	62	372
Tanaidacea												
Tanais cavolini	..	..	..	..	..	..	1	..	..	..	2	..
Isopoda												
Naesa bidentata	2	1	1	..	3	26	2	26	4	2	..	18
Idotea granulosa	10	10	1	6	..	1	2	13	54	75	97	10
Amphipoda												
Astacilla longicornis	..	1	..	..	..	..	..	..	..	..	..	..
Apherusa jurinei	..	..	..	..	..	..	1	..	..	..	2	..
Melita sp.	..	..	..	..	..	..	..	..	..	..	1	..
Gammarus marinus	..	..	..	..	..	..	..	..	..	..	1	..
Hyale nilssoni	28	13	17	18	..	53	26	63	84	86	73	96
Amphithöe rubricata	..	1	..	..	4	..	..	..	2	..	..	3
Amphipoda (juv., indet.)	..	..	..	..	5	..	..	..	..	..	..	..

Decapoda												
Carcinus maenas (megalopa)	..	..	..	..	1	..	..	..	..	..	..	..
Xantho incisus (juv.)	..	..	..	1	..	..	..	..	..	..	..	..
Pycnogonida												
Ammothea echinata	..	..	..	..	..	..	..	..	..	..	1	..
Pycnogonid (indet.)	..	..	..	..	..	1	..	..	..	..	..	..
Acarina												
Rhombognathus pascens and *Rhombognathus seahami*	..	..	36	278	42	62	173	148	195	251	248	678
Acarina (indet.)	9	9	19	30	73	31	13	46	9	24	227	68
Insecta												
Lipura maritima	..	..	..	40	..	..	..	..	..	..	7	..
Collembola (indet.)	..	..	..	..	..	..	..	..	..	..	..	1
Thalassomyia frauenfeldi and *Clunio marinus* (larvae)	..	..	73	73	140	134	15	..	..	..	171	28
Ephydridae (pupa)	..	..	..	..	..	..	..	..	..	..	..	2
Diptera (larvae, indet.)	1	..	..	..	..	..	..	..	2	6	..	..
Diptera (adults, indet.)	..	..	..	..	..	..	..	..	..	..	..	3
Coleoptera (indet.)	..	..	..	..	..	..	..	..	..	..	..	2
Insecta (pupae, indet.)	..	..	..	..	..	..	..	..	..	..	..	3
Pelecypoda												
Mytilus edulis (juv.)	1	1	..	..	..	..	..	..	..	..	..	..
Pelecypoda (indet.)	1	..	..	..	4	17	8	43	15	36	13	40
Gastropoda												
Lacuna sp.	..	..	5	2	2	..	..	..	..	..	..	..
Littorina obtusata	3	2	4	2	1	..	..	..	..	..	2	5
L. obtusata (spawn)	..	1	..	1	..	..	..	..	..	..	..	1
†Littorinidae (juv.)	19	32	67	72	55	487	92	252	75	160	355	260
Bryozoa												
Flustrella hispida	..	..	..	..	..	..	..	..	..	1	1	..
Total	109	176	742+	1597	1519	2798+	1891+	1729	610+	869+	2714	2259+

* Mainly *Fabricia sabella*. † Mainly *Littorina obtusata*

TABLE IX. *ASCOPHYLLUM NODOSUM* AND *POLYSIPHONIA LANOSA*. COPEPODA IN SAMPLES E 3 TO E 12. IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	..	E 3	E 4	E 5	E 6	E 7	E 8	E 9	E 10	E 11	E 12
Weight in g.	..	529	151	119	103	202	84	96	84	117	68
Date	..	2. vii. 30	15. vii. 30	15. vii. 30	23. vii. 30	25. vii. 30	28. viii. 30	5. i. 31	5. i. 31	6. i. 31	20. iii. 31
Position in m.	..	C VII 4·6 D I	C VI 13·7 C VII	C V 14·6 C VI	C I	C I 5·5 C II	B II 9·4 B III	B I 1·8 B II	B II 9·4 B III	C VII 8·2 D I	C II 0·3 C III
Height in m.	..	+0·27	+0·67	−0·09	−0·30	+0·37	−1·00	−0·43	−1·00	+0·73	+0·06
Harpacticidae											
Harpacticus chelifer		..	..	..	..	..	..	..	1	..	..
H. gracilis		129	165	33	..	..	..	..	..	..	..
H. uniremis		..	..	16	..	..	..	..	..	..	..
Zaus spinatus		1	..	..	..	..	..	..	..	..	..
Idyidae											
Idya furcata		20	61	373	..	..	..	..	..	..	..
I. gracilis		1	..	..	..	..	..	..	..	..	..
Idyidae (indet.)		..	..	8	..	..	..	..	..	..	..
Thalestridae											
Thalestris longimana		..	..	..	..	..	..	..	4	..	21
T. purpurea		..	40	30	..	..	..	..	..	..	..
T. sp. (indet.)		4	..	..	37	..	..	..	..	..	..
Parathalestris clausi		..	13	3	..	..	..	11	..	..	9
P. harpacticoides		7	..	..	..	280	..	..	..	..	..
Microthalestris forficula		4	..	..	..	..	..	..	..	..	..
Dactylopusia tisboides		..	146	..	..	..	..	..	..	..	..
D. vulgaris		6	..	..	117	..	17	..	..	..	..
D. brevicornis		..	..	..	..	..	..	1	..	..	..
Westwoodia nobilis		14	46	..	203	93	48	2	24	30	104
W. pygmaea		..	..	..	..	..	..	..	..	..	136
Diosaccidae											
Amphiascus minutus		1	46	..	..	..	..	..	..	..	..
Canthocamptidae											
Nitocra typica		..	13	..	..	..	..	..	..	..	..
Mesochra pygmaea		22	..	..	..	..	..	..	..	..	..
Ameira tenuicornis		..	..	156	..	..	..	..	..	..	..
Laophontidae											
Laophonte cornuta		..	..	..	..	..	..	..	..	..	1
L. brevirostris		..	20	..	..	..	..	..	..	..	..
L. littoralis		..	20	..	..	..	..	..	..	..	..
L. spp. (indet.)		55	..	96	1	..	..	..	..	..	27
Cletodidae (indet.)		1	..	..	..	..	..	..	..	..	..
Harpacticoida (juv., indet.)		14	..	16	..	240	103	35	27	32	74
	Total	279	570	731	358	613	168	49	56	62	372

were 280 *Parathalestris harpacticoides* in E 7, 146 *Dactylopusia tisboides* in E 4, and 117 *D. vulgaris* in E 6. Several species of other families occurred in fair numbers once or twice, such as 46 *Amphiascus minutus* in E 4, 156 *Ameira tenuicornis* in E 5 and 96 *Laophonte* spp. in E 5. This genus *Laophonte* is perhaps the most easily recognized of all the harpacticoid genera, but it is also one of the hardest in which to determine the species; *L. brevirostris* and *L. littoralis* were both identified for me by Dr R. Gurney.

TABLE X. *ASCOPHYLLUM NODOSUM* AND *POLYSIPHONIA LANOSA*. FAMILIES OF COPEPODA HARPACTICOIDA IN SAMPLES E 3 TO E 12, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. ..	E 3	E 4	E 5	E 6	E 7
Weight in g. ..	529	151	119	103	202
Date ..	2. vii. 30	15. vii. 30	15. vii. 30	23. vii. 30	25. vii. 30
Position in m. ..	C VII 4·6 D I	C VI 13·7 C VII	C V 14·6 C VI	C I	C I 5·5 C II
Height in m. ..	+0·27	+0·67	−0·09	−0·30	+0·37
Harpacticidae	130	226	49	..	..
Idyidae	21	..	381	..	..
Thalestridae	35	245	33	357	373
Diosaccidae	1	46	..	..	..
Canthocamptidae	22	13	156	..	..
Laophontidae	55	40	96	1	..
Cletodidae	1	..	..	..	..
(Juv., indet.)	14	..	16	..	240
Total	279	570	731	358	613

Sample no. ..	E 8	E 9	E 10	E 11	E 12
Weight in g. ..	84	96	84	117	68
Date ..	28. viii. 30	5. i. 31	5. i. 31	6. i. 31	20. iii. 31
Position in m. ..	B II 9·4 B III	B I 1·8 B II	B II 9·4 B III	C VII 8·2 D I	C II 0·3 C III
Height in m. ..	−1·00	−0·43	−1·00	+0·73	+0·06
Harpacticidae	..	..	1	..	..
Idyidae	..	..	..	..	..
Thalestridae	65	14	28	30	270
Diosaccidae	..	..	..	..	..
Canthocamptidae	..	..	..	..	..
Laophontidae	..	..	..	..	28
Cletodidae	..	..	..	..	..
(Juv., indet.)	103	35	27	32	74
Total	168	49	56	62	372

These copepods have been discussed at some length in order to bring out the patchiness of their distribution. Only one species out of 23 or more occurred regularly, though seven were present in one sample or another in numbers exceeding 100 each. Infrequency of occurrence is here at any rate no true measure of rarity. Many young forms were found in samples E 7 to E 12. They may have been young stages whose adults were not represented, or those of the species present in these samples; they were mostly less than 0·5 mm. in length, which made their dissection difficult and their determination a matter of great uncertainty.

Table X shows the occurrence of the seven families of copepods found in *Ascophyllum*. It emphasizes the importance of the Thalestridae, and shows that adults of other families were not present in any number after the middle of July.

The other two groups generally present in large numbers were acarines and the Littorinidae. The numbers of acarines, leaving out of consideration samples E 1 and E 2, varied from 55 in E 3 to 746 in E 12. No good correlation with either seasons or heights on the shore is apparent, though on the whole they appear to be most plentiful in the winter and early spring. The most abundant catch, 746 in E 12, was in March, the next most abundant, 475 in E 11, was in January, and the third, 308 in E 4, in July; the other July catches, however, were among the poorest. Then again E 12 was at +0·06 m., E 11 a good deal higher at + 0·73 m., and E 4 almost as high at +0·67 m., while E 10 down at −1·00 m. was almost as rich as E 4. Most of these mites were *Rhombognathus pascens* and *R. seahami*; other species were present, including *Halacarus basteri* and *Hydrogamasus littoralis*, and were on some occasions quite numerous, as in E 5 and E 11. These mites were identified for me by Mr J. N. Halbert.

The Littorinidae include several individuals of a species of *Lacuna* which were too young to be determined, several *Littorina obtusata*, and large numbers of young stages which appear to be mostly *L. obtusata*. The adults of this latter species, though apparently so numerous in the field, are in reality not nearly so abundant as many of the smaller animals, and it seems to be a matter of chance whether or not a sample of 100 g. or so will contain any *L. obtusata* large enough to be recognizable. The young Littorinidae, however, were always present in fair or large numbers, from 67 in E 3 to 487 in E 6. Here again no correlation can be shown with either season, height or position on the reef. It is surprising that the spawn of *L. obtusata*, which often seems so common, appeared only three times, on May 14, July 15 and March 20.

The several other groups can now be considered, taking them in their zoological order. Three species of hydroid were identified, *Clava squamata*, *Laomedea flexuosa* and *Dynamena pumila*. They were not counted, except for a rather straggling colony of *Clava* in E 11 in which there were 33 polyps. *Dynamena pumila* is the only hydroid which was common, but it is restricted to the *Ascophyllum* holdfasts and the proximal portions of the plant. This part was not studied as closely as the distal portions with their epiphytic tufts of *Polysiphonia*, and this omission probably causes a considerable gap in the collection of the fauna inhabiting *Ascophyllum*. There was one young stauromedusan in sample E 7, which is noteworthy on account of the height of this sample on the shore, 0·37 m. above Ordnance Datum, or about mean sea-level.

Turbellaria and Nemertinea (lumped together throughout this paper) occurred in moderate numbers, fluctuating fairly widely without correlation with either season, height or position. The same applies to the nematodes. This last group has not been worked out sample by sample, but a batch from *Ascophyllum* was determined for me by Dr Baylis and contained the following species: *Anticoma limalis* (numerous), *Oncholaimus brachycercus* (numerous), *Enoplus communis*, *Symplocostoma longicolle*, and *Thoracostoma figuratum*.

Polychaetes were on the whole few or absent. Two small nereids appear in E 12, and 13 *Spirorbis borealis* in E 4. Small sabellids occurred more frequently, and on one occasion were really numerous, 744 in E 11; these were mainly, if not entirely, *Fabricia sabella*, a worm about 3 mm. long, but the tube containing them was unfortunately destroyed before they could be examined completely. This was unlucky because this sample was the highest of all the *Ascophyllum* samples, at 0·73 m., and *F. sabella* did not appear again in large numbers until the laminarian zone was reached some 3 m. lower down the shore.

Two species of oligochaete were usually present and sometimes quite numerous. These were *Lumbricillus scoticus* and *L. pumilio*, identified for me by the late Dr J. Stephenson (1932). *L. pumilio* is so far the only new species identified from these collections. *L. scoticus* is about 5 mm. long and *L. pumilio* about 3 mm. Both are orange in colour in contrast with the dark-red *Polysiphonia* among which they live, and they are easy to see in the field as they are often on the move, writhing round each other and the twigs of the alga. It is surprising that they have not been previously recorded from Plymouth. They were most numerous in May and early July (E 2, E 3 and E 4) and in January and March (E 11 and E 12). In the last two samples most of them were so small that the species could not be separated; this perhaps indicates that the young worms appear in mid-winter, reach adult size in late spring, and then gradually become fewer during the summer, the survivors giving rise to next year's brood.

The specimens of *Tanais cavolini* from E 7 and E 11 were the only tanaids collected from other than the laminarian zone, but this species did not occur elsewhere than in these two samples of *Ascophyllum*.

Of the isopods, *Astacilla longicornis* occurred once, in E 2 at +0·4 m. This is a sublittoral species and is found at 40 fathoms off the Eddystone. Perhaps this individual was washed loose from its normal habitat by wave action, carried up the reef in the surf and entangled in the weed as the tide fell. This would explain the presence of individuals of a number of species which are not normally found between tide-marks. The isopods *Naesa bidentata* and *Idotea granulosa*, both widely distributed intertidal species, occurred in nearly all the samples. *I. granulosa* was quite abundant in January, but otherwise was not numerous; these January forms were mostly young.

The amphipods include five species, of which only *Hyale nilssoni* was either numerous or of regular occurrence; it was most abundant in January and March, but not markedly so. A noteworthy feature of these samples is the great rarity of the genus *Gammarus*, which is indeed represented only by a single *G. marinus* in E 11. This emphasizes the difference between the fauna inhabiting seaweeds and that living below stones at the same level, for in the latter habitat *G. marinus* and *G. locusta* are everywhere abundant. *Amphithöe rubricata* is an amphipod which makes a nest, and two of these were found in broken nodes of *Ascophyllum*, in samples E 5 (July 15) and E 9 (January 5). These nests measure only about 12 by 6 mm., but may contain quite a rich fauna. The one in E 5 included 11 turbellarians or nemertines, 25 nematodes, 100 copepods (made up of 11 *Idya furcata*, 16 *Thalestris purpurea*, 3 *Parathalestris clausi*, 46 *Ameira tenuicornis* and 24 *Laophonte* spp.), and 4 acarines, giving a total of 140. The nest in E 9 was less remarkable and contained only 26 copepods, of which 7 were *Parathalestris clausi*. A female of *Amphithöe rubricata* in E 2, May 14, ejected 32 young on being killed.

The crabs *Carcinus maenas* and *Xantho incisus*, like *Gammarus marinus* and *G. locusta*, are common under stones when the tide is out, but evidently avoid the seaweed; they are represented only by a *Carcinas maenas* megalopa in E 5 and a young *Xantho incisus* in E 4, both collected on July 15.

It was surprising that of the two pycnogons captured one should be an *Ammothea echinata* found in E 11, for this is not usually an intertidal species and E 11 is the highest *Ascophyllum* sample. It may be another stray washed up by the surf and trapped in the weed.

Insects, and in particular the larvae of diptera, form an important ingredient of the fauna around mean sea-level. The collembolan *Lipura maritima* was found only in two samples, but it is notoriously patchy in its distribution; it is probably much more abundant on *Ascophyllum* than these figures would suggest. Chironomid larvae, belonging probably (according to Dr Edwards) to the two species *Clunio marinus* and *Thalassomyia frauenfeldi*, were sometimes common, particularly in the samples from high up on the shore. The lowest level at which these species occurred was 0·3 m. below Ordnance Datum, and they were found in all samples collected above this level except for E 2 at +0·4 m. (This sample was examined somewhat cursorily as regards the smaller forms, as already mentioned, but I would not have missed any animals as large as these chironomid larvae, for they are not only bigger than *Lumbricillus scoticus* but also let go on being killed and are less liable than some other species to get tangled up in the weed.) They were most abundant in E 11, the highest sample, in January, with 171; next came E 5 on July 15 with 140 at −0·09 m., but there were still 134 in E 6 on July 23 at −0·3 m., the lowest sample in which they occurred; the March sample, E 12, contained 28. The fact that these larvae were found in January, March and July seems to mean either that there are several broods in the year or that these two species have an unusually prolonged larval life. Besides the two species mentioned above, other dipteran larvae were occasionally found, one in E 1 at −0.52 m., two in E 9 at −0·43 m. and six in E 10 at −1·0 m., three of the four lowest samples of *Ascophyllum*. The catch in E 12 at +0·06 m. included ephydrid and other insect pupae, adult diptera and coleoptera, and a collembolan which was certainly not *Lipura maritima*.

The samples E 10 and E 11, January 5 and 6, each contained one colony of the bryozoan *Flustrella hispida*, at −1·0 and +0·73 m. respectively. No other bryozoan was taken higher than −1·64 m., so that the occurrence of *F. hispida* as high as +0·73 m., or a little below high-water neaps, is remarkable.

Fucus serratus (Table XI)

Fucus serratus is widely distributed on Church Reef, but it does not cover so great an area as *Ascophyllum nodosum*. The range of the latter, from 0·9 m. above to 1·2 m. below Ordnance Datum, includes many wide, level stretches of the reef on which it can grow abundantly; *Fucus serratus* extends from 0·4 m. above to 2·75 m. below Ordnance Datum, a vertical range of more than 3 m., but much of this coincides with the sloping edges of the reef. On Church Reef *F. serratus* is on the whole more exposed to wave action than is *A. nodosum*. Ten samples, F 1 to F 10, were collected, ranging in height from −0·40 m. down to −1·95 m. Samples F 4 and F 8 (−0·40 m. and −0·58 m.) were higher than the two lowest samples of *Ascophyllum*; F 1, F 2 and F 6 (−1·49, −1·31 and −1·37 m.) were from about the middle of the range of *F. serratus*, while F 3, F 5, F 7, F 9 and F 10 (from −1·76 to −1·95 m.) were from similar levels to those of the four samples of *Gigartina stellata* and just above the laminarian zone.

On the whole, *Fucus serratus* has a poorer fauna than either its higher neighbour *Ascophyllum* or its lower neighbour *Gigartina*, which is, I think, largely due to the differences in growth form of these algae. The fauna of *Ascophyllum* is mainly contained in the tufts of *Polysiphonia*, while the fronds of *Gigartina stellata* are covered with warty protuberances to which many small animals can cling; *Fucus serratus*, on the other hand, is usually rather smooth and affords poor holding ground for copepods, mites and so on. Occasionally, however, it carries epiphytic growths of a brown, filamentous alga, *Elachistea fucicola*, which grows in small tufts along the edges of the frond and is a favourite haunt of various small arthropods. The sample F 3 had a fair growth of *Elachistea* and contained 1189 animals per 100 g.; F 5 had a slight growth and contained 465, while the other eight samples were free of the epiphyte and the numbers of their faunas ranged from 311 down to only 61. The increase in the populations of F 3 and F 5 was made up largely of copepods.

Coelenterates were remarkably scarce on *Fucus serratus*, one colony of *Dynamena pumila* on each of F 1 and F 2 being the sum total. This affords a striking contrast with *Gigartina stellata* from the same levels, on which hydroids are numerous.

Turbellarians and nemertines hardly appear at all though there were many of them on *Ascophyllum*; and nematodes, though usually present, were numerous in only one sample, F 3, which was infested with *Elachistea*. Most of the nematodes in this sample (identified by Dr Baylis) were young *Pontonema* (*Paroncholäimus*) *?ditlevseni*, with a few *Enoplus communis* and *Symplocostoma longicolle*. Polychaetes, oligochaetes and sipunculids appeared occasionally, but usually only one at a time.

Ostracods were surprisingly rare when compared with those in *Ascophyllum* at similar levels. For example, *Ascophyllum*, sample E 6, from a height of

Table XI. *Fucus serratus*. Animals Inhabiting Ten Samples, in numbers per 100 g. of Damp Weed

Sample no. ..	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 9	F 10
Weight in g. ..	364	335	395	91	131	82	85	99	93	77
Date ..	2. vi. 30	11. vi. 30	13. vi. 30	23. vii. 30	26. vii. 30	28. viii. 30	28. viii. 30	5. i. 31	5. i. 31	3. iv. 31
Position in m. ..	B III 8·2 B IV	A I 12·2 A II	A III 9·4 A IV	C I 1·2 C II	A IV 0·7 A V	B V 4·3 B VI	B V 7·9 B VI	B I 12·8 B II	B III 11·8 B IV	B VII 0·9
Height in m. ..	−1·49	−1·31	−1·86	−0·40	−1·95	−1·37	−1·89	−0·58	−1·83	−1·76
Coelenterata										
Dynamena pumila (colonies)	1	1	..	..	..	..	..	..	..	..
Turbellaria and Nemertinea	..	..	1	..	..	..	1	3	..	..
Nematoda	10	..	163	3	13	2	..	10	10	1
Polychaeta										
Nereidae (indet.)	..	..	1	..	..	..	..	..	..	..
Fabricia sabella	..	..	1	..	..	..	1	4	..	..
Oligochaeta (indet.)	1	1	..	..	..	..	..	..	..	..
Sipunculoidea										
Phascolosoma minutum	..	1	2	..	..	..	..	..	..	..
Ostracoda	1	..	8	7	8	..	..	5	..	1
Copepoda Harpacticoida										
Harpacticus chelifer	53	32	404	2	27	8	1	..	..	..
Zaus spinatus	19	10	247	..	5	..	3	..	..	..
Porcellidium fimbriatum	..	..	10	..	..	..	..	..	..	..
Idya furcata	50	114	13	7	..	1	3	..	..	..
Aspidiscus fasciatus	..	..	7	..	..	..	..	..	..	..
A. littoralis	1	..	..	..	239	..	159	..	..	27
Parathalestris clausi	60	7	47	..	52	4	3	..	..	..
P. harpacticoides	15	2	17	..	32	..	..	..	..	..
Dactylopusia tisboides	..	..	14	..	..	..	..	..	..	..
D. vulgaris	7	2	..	..	..	..	..	..	..	..
Canthocamptidae (indet.)	..	2	..	..	..	..	..	..	..	..
Laophonte sp. (indet.)	..	..	3	2	3	..	..	..	..	..
Harpacticoida (indet.)	7	3	13	..	2	..	..	3	43	26
Isopoda										
Naesa bidentata	5	9	1	12	1	1	..	6	4	..
Idotea baltica	..	..	..	..	..	..	..	1	..	..
I. neglecta	..	..	..	..	..	..	..	1	..	..
I. granulosa	2	1	6	..	2	5	1	20	..	3

Amphipoda										
Apherusa jurinei	2	1	..	3	..	..	..	2	..	..
Hyale nilssoni	..	..	..	..	..	..	..	12	2	..
Amphithöe rubricata	1	1	..	..	..	..	..	..	..	..
Pleonexes gammaroides	..	..	2	..	..	..	..	..	..	..
Biancolina cuniculus	1	..	..	..	..	..	..	..	..	..
Pseudoprotella phasma	..	..	..	..	1	..	..	..	..	..
Amphipoda (juv., indet.)	3	..	3	..	4	..	..	6	1	..
Decapoda										
Carcinus maenas (megalopa)	..	..	1	..	..	..	..	..	..	..
Acarina										
Rhombognathus pascens and *Rhombognathus seahami*	37	34	114	42	46	21	31	198	194	18
Acarina (indet.)	..	..	..	..	4	12	..	2	1	..
Insecta										
Diptera (larvae, indet.)	1	..	11	..	5	1	..	2	..	..
Pelecypoda (juv., indet.)	..	..	3	..	2	..	..	3	..	..
Gastropoda										
Patina pellucida	1	1	12	..	2	4	15	..	..	1
Gibbula cineraria	..	..	..	2	..	..	..	..	..	..
G. umbilicalis	..	..	..	1	..	..	..	1	..	..
Lacuna sp.	..	..	..	1	..	..	..	..	..	..
Littorina obtusata	1	3	1	7	1	1	..	6	..	..
L. obtusata (spawn)	1	1	1	1	..	..	..	..	..	..
L. littorea	..	..	..	1	..	..	..	..	..	..
Littorinidae (juv.)	23	8	80	22	..	1	3	26	2	..
Gastropoda (juv., indet.)	1	..	3	..	..	..	..	..	..	..
Bryozoa										
Membranipora pilosa	..	..	..	..	5	..	22	..	..	9
Flustrella hispida	..	..	..	..	11	..	13	..	..	1
Total	304	234	1189	113	465	61	256	311	257	87

−0·30 m. contained 1480 ostracods, whereas *Fucus serratus* sample F 4 from −0·40 m. contained only 7. These two samples had a difference in height of only 0·1 m., were from places on the reef only 1·2 m. apart, and were collected on the same day, July 23 1930.

There were twelve species of copepod in the samples of *F. serratus*, and the total number of this group varied from 3 to 775. On the whole they were rarest in January and April, most abundant in June, and erratic in August, but there were not enough samples to make clear any marked seasonal variations. Only four species found in *F. serratus* were not found also in *Ascophyllum*, namely *Porcellidium fimbriatum*, *Aspidiscus fasciatus*, *A. littoralis* and an unidentified canthocamptid. In spite of this, however, the two populations were not alike in general make-up, since the species common to the two are present in very different proportions. In addition there are several species, occasionally common in *Ascophyllum*, which are absent from *Fucus serratus*, such as *Harpacticus gracilis*, *Thalestris purpurea*, *Westwoodia nobilis*, *W. pygmaea*, *Amphiascus minutus* and *Ameira tenuicornis*. In *Fucus serratus* six species appeared in fair or large numbers. *Harpacticus chelifer* was present in all the June, July and August samples and was commonest in June. In F 3 at −1·86 m. it was really numerous (404), making up more than half the copepods present; it was the second most abundant in F 1 (53) and in F 2 (32). (Only a single specimen of this species was found in *Ascophyllum*.) *Zaus spinatus* occurred in five samples but was common only once, with 247 in F 3. *Idya furcata*, found on six occasions, led the rest with 114 in F 2, came third with 50 in F 1, but was not numerous in its other samples. *Aspidiscus littoralis*, a relatively large harpacticoid, was abundant in F 5 (239) and in F 7 (159); these are both low samples (−1·95 and −1·89 m.) and it was not found above −1·5 m.; in F 7 it formed all but 10 of the copepod population. This species was also the only one identified from the January and April samples, at which time there were present a number of immature forms, as in *Ascophyllum*. *Parathalestris harpacticoides* and *P. clausi* were not uncommon and generally occurred together.

The isopods *Naesa bidentata* and *Idotea granulosa* were widely but not abundantly distributed; they occurred sparingly in nearly all the samples, as in *Ascophyllum*.

Amphipods were rather scarce, but were none the less represented by six species. *Hyale nilssoni*, so plentiful in *Ascophyllum* and other weeds higher up on the shore, was found in only two samples of *Fucus serratus*; there were 12 in F 8 from −0·58 m., well within the range occupied by *Ascophyllum*, and 2 in F 9 from −1·83 m. at the top of the laminarian zone, which must be very near the lower limit for *Hyale nilssoni* (see also the reference to this species in the section on *Gigartina stellata*).

The acarines occurred more steadily than any other group, and in five of the seven summer samples their numbers varied only from 31 to 42. The other two of the seven, F 3 and F 5, have already been mentioned as supporting growths of *Elachistea fucicola*; F 3 carried a fairly heavy epiphytic growth and 114 mites, while on F 5 there was a slight growth and only 50 mites. The acarines were much more numerous in the two January samples (200 and 195), but there were only 18 of them in F 10 in April. Nearly all the acarines belonged to *Rhombognathus pascens* and *R. seahami*, but Mr J. N. Halbert also found *Halacarus basteri* in a batch from F 3.

A few larvae of diptera were to be found in five samples. There were 5 even in F 5 which was the lowest sample of *Fucus serratus*, from −1·95 m. or about mean low-water springs; two occurred in mid-winter, in the January sample F 8. No insects or their larvae were found among *Gigartina* from similar levels.

Among the molluscs, young specimens of *Patina pellucida* appeared in samples as high as −1·31 m., though the adults are not found above the laminarian zone 0·6 m. further down. *Littorina obtusata* was the only other gastropod which occurred at all regularly, and its spawn was found in the four samples between June 2 and July 23, but not in any others. The number of young littorinids varied from none to 80.

Three of the lowest samples, F 5 at −1·95 m., F 7 at − 1·89 m. and F 10 at −1·76 m., supported several colonies of the bryozoa *Membranipora pilosa* and *Flustrella hispida*. These were never so abundant as on the neighbouring *Gigartina stellata*, and *Alcyonidium hirsutum*, which is fairly common on the latter weed, was not found at all on *Fucus serratus*.

Gigartina stellata (Table XII)

This red alga is abundant from above mean low-water springs down to below tide-marks. The highest position recorded was 1·5 m. below Ordnance Datum, and the four samples G 1 to G 4 came from −1·98, −1·64, −1·89 and −1·70 m., with a range in level of only 0·34 m. in all. In spite of the fact that they came from similar heights, however, the fauna of each sample differed in several important respects from the others, though they also show some features in common. G 1 and G 2 were collected at the height of summer in July and August, G 3 in January and G 4 at the beginning of April, yet none of the differences between these faunas can be set down as seasonal.

Certain animals were present in all four catches with fair regularity, such as *Idotea granulosa*, young *Mytilus edulis* and *Patina pellucida*, and the bryozoa *Membranipora pilosa*, *Alcyonidium hirsutum* and *Flustrella hispida*. Of these animals only *Idotea granulosa* and *Mytilus edulis* are found farther up the shore, the others all belonging to the sublittoral fauna, some members of which can live as far up as low-water neaps but as a rule no higher.

Polychaetes, copepods and amphipods were, as a rule, represented by a few individuals of several species which are more common in other zones; the species of copepod are usually more numerous farther up the shore, especially among *Ascophyllum*, while the polychaetes belong to the laminarian zone. A point of interest is the overlap in G 4 of the closely related amphipods *Hyale nilssoni* and *H. pontica*. The former is ubiquitous and often abundant from the *Pelvetia* zone down to around low-water neaps, while the latter species is normally sublittoral and is only occasionally to be met with between tide-marks.

Apart from the animals so far considered from *Gigartina*, from 50 to 90% of each catch was made up of one or two groups present in quite exceptional

TABLE XII. *GIGARTINA STELLATA*. ANIMALS INHABITING FOUR SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no. ..	G 1	G 2	G 3	G 4
Weight in g. ..	70	60	62	47
Date ..	26. vii. 30	28. viii. 30	7. i. 31	3. iv. 31
Position in m. ..	A IV 0·9 A V	B VI 7·9 B VII	B VII 6·7	B VII 0·6
Height in m. ..	−1·98	−1·64	−1·89	−1·70
Coelenterata				
Halyclistus auricula	7	..	..	..
Dynamena pumila (branches)	17	601	127	111
Turbellaria and Nemertinea	9	..	2	..
Nematoda	4	47	2	13
Polychaeta				
Odontosyllis ctenostoma	..	..	3	..
Eusyllis lamelligera	..	..	..	2
Nereidae (indet.)	..	..	..	4
Polydora ciliata	..	2	..	..
Amphiglena mediterranea	..	2	2	11
Fabricia sabella	14	..	2	11
Oridia armandi	..	..	3	9
Spirorbis borealis	19	47	164	..
Polychaeta (indet.)	..	..	..	2
Sipunculoidea				
Phascolosoma minutum	43	..	..	..
Ostracoda	..	..	2	..
Copepoda Harpacticoida				
Harpacticus chelifer	86	2	..	..
Zaus spinatus	..	2	2	2
Psamathe longicauda	1985	..	32	9
Aspidiscus littoralis	585	2	6	32
Idyidae (nauplii)	3930	..	..	..
Parathalestris clausi	..	..	..	13
P. harpacticoides	..	..	3	..
Dactylopusia tisboides	..	..	..	11
Harpacticoida (indet.)	..	..	..	4
Cirripedia				
Verruca stroemia	..	..	3	..
Balanus balanoides	..	..	..	2
Isopoda				
Naesa bidentata	4	3	..	2
Idotea granulosa	56	37	16	9
Cryptoniscidae (indet.)	..	..	..	2
Amphipoda				
Apherusa jurinei	5	..	5	..
Hyale nilssoni	..	38	..	2
H. pontica	..	..	2	2
Pleonexes gammaroides	..	8	..	..
Jassa falcata	248	2	6	11
Amphipoda (indet.)	..	..	5	..
Acarina				
Rhombognathus pascens and *Rhombognathus seahami*	117	1273	422	1209
Acarina (indet.)	14	..	2	..
Pelecypoda				
Mytilus edulis (juv.)	21	115	13	19
Gastropoda				
Patina pellucida	17	18	3	13
Lacuna sp.	7	..	3	..
Littorinidae (juv.)	35	155	..	19
Gastropoda (juv., indet.)	..	5	2	11
Bryozoa				
Membranipora pilosa	40	25	37	115
Alcyonidium hirsutum	35	52	42	6
Flustrella hispida	43	21	86	132
Total	7341	2457	997	1785

numbers. In G 1, out of a total of 7341 no fewer than 6586 consisted of the two copepods *Psamathe longicauda* and *Aspidiscus littoralis* and their nauplii. These species are closely related; both are broad, powerful forms, flat ventrally and stream-lined dorsally and apparently well adapted to withstand wave action. The nauplii are interesting for they are not free-swimming; they crawl over the surface of the weed, and those of *Psamathe longicauda* can cling on very tightly by means of a ventral sucker (Gurney, 1933). Other noteworthy animals in G 1 were 43 of the sipunculid *Phascolosoma minutum*, 86 of the copepod *Harpacticus chelifer* and 248 of the amphipod *Jassa falcata*. None of these was present in any quantity in the other samples of *Gigartina*.

In G 2, half the catch consisted of the mites *Rhombognathus pascens* and *R. seahami* (1273), and half the remainder was made up of branches of the hydroid *Dynamena pumila* (601). *Hyale nilssoni*, *Mytilus edulis* and young littorinidae were present in fair numbers, but the most noticeable feature otherwise was the dearth of copepods, which were more than 1000 times as few as in G 1.

In G 3 the total numbers were much less than in the other catches, but here again half the total consisted of the acarines *Rhombognathus pascens* and *R. seahami* (424). *Dynamena pumila* (127 branches) was fairly abundant, and there were many more of the polychaete *Spirorbis borealis* (164) than usual, but otherwise the fauna though varied was not numerous.

Much the same is true of G 4, where the same two species of mite form over two-thirds of the total. Here again there is considerable variety of species, but few of them are present in any number. It was only in this sample that *Hyale nilssoni* and *H. pontica* were found together.

The most distinctive feature of the *Gigartina* fauna as a whole is the large number of the acarines *Rhombognathus pascens* and *R. seahami*. These two species make up almost the entire acarine population in most of the weeds above the laminarian zone; only in *Ascophyllum* are other species at all common, and even then only occasionally.

Laminaria digitata holdfasts* (Tables XIII–XVIII)

Laminaria digitata is predominantly a sublittoral alga, and does not live higher (except in tide-pools) than low-water springs; most of the animals living among its holdfasts are also distributed mainly below tide-marks. This fauna, as is well known, is extremely numerous and contains a great variety of species, particularly of polychaetes, of which there were found over forty different kinds in this survey. The form of the rhizoids making up the holdfast, which intertwine closely round each other, does not leave much space

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* I have not studied at all thoroughly the animals living on the fronds of *Laminaria digitata*. They do not appear to be numerous or of many species. On 5. iv. 39 I examined one frond and stalk of average size, and on it I could find only the following: 71 copepods, made up of 3 *Aspidiscus littoralis*, 38 *Zaus spinatus*, 28 *Parathalestris clausi*, and 2 not determined; in addition there were a number of acarines, but nothing else.

between them, and such room as there is appears to be filled with fine and coarse sand, small stones, broken bits of shell and so on. Nevertheless, it is among this detritus that most of the extensive fauna is to be found, though some animals live on the surface of the holdfast such as barnacles, hydroids and bryozoa, while a few polychaetes and gastropods bore into the tissues of the *Laminaria*. In addition there is a hard veneer, 1 or 2 mm. thick, between the *Laminaria* holdfast and the rock. This veneer is a calcareous, encrusting alga, kindly identified for me by Dr Margery Knight as *Lithophyllum incrustans* (Philippi). It appears to extend under all the holdfasts, but does not always cover the surface of the rock between them; I have therefore considered it to be, from an ecological point of view, part of the *Laminaria*. It is riddled with wormholes, probably made by *Polydora*, but which may contain many other forms such as nematodes, the small sabellid *Fabricia sabella* and so on. I have not attempted to analyse in detail the different parts of a *Laminaria* holdfast, but it is evident that each one contains a number of more or less separate habitats, each with its own association of animals; such habitats are the general surface, the deep interstices between the rhizoids, the tissues of the *Laminaria* itself, and finally the encrusting alga beneath the whole.

Some instructions for collectors state that the fauna of a *Laminaria* holdfast can be examined by placing the holdfast in a jar of sea water and leaving it overnight, after which the contained animals will have emerged and will be found on the walls of the jar. I have tried this method, but found it grossly misleading and of no value. Some of the syllids come out, it is true, but all the syllids together make up only about one-tenth of the total polychaete population. Most of the animals remain in their burrows and die there, and will be partially decomposed and unfit for identification by the time they can be examined; it is astonishing how quickly amphipods, in particular, rot and fall to pieces. There is, in fact, no short cut to the estimation of the fauna of a *Laminaria* holdfast. The whole must be preserved, broken up, and picked to pieces with needles under a dissecting microscope, leaving no piece with a greater diameter than about 3 mm.; then the detritus must be gone through grain by grain and the animals removed. In the case of the large holdfast H 6 this dissection, with the sorting, counting and identification of species, took more than two months.

Six individual holdfasts were examined, samples H 1 to H 6. The two smallest, H 1 and H 4, which weighed 17 and 25 g., came from the top of the laminarian zone or about low-water springs; the others were all collected from as low as possible during very good tides, which on occasions fall 0·5 m. or more below the official level of low-water of ordinary springs. H 6 was as large a holdfast as could be found and weighed 104 g. The total number of animals per 100 g. varied from 1653 in H 1 to 5662 in H 4. It was curious to find the densest population in the highest holdfast of all, considering that most of the animals were sublittoral forms.

Table XIII shows the laminarian population. Certain groups which contain a good many species each are not analysed fully here, but are dealt with in separate tables below; these groups are Polychaeta, Copepoda, Tanaidacea, Isopoda, Amphipoda, Bryozoa and Tunicata.

TABLE XIII. *LAMINARIA DIGITATA* HOLDFASTS. ANIMALS INHIBITING SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 1	H 2	H 3	H 4	H 5	H 6
Weight in g.	17	63	92	25	52	104
Date	27. viii. 30	27. viii. 30	27. viii. 30	27. viii. 30	7. i. 31	3. iv. 31
Position in m.	A V	A V 1·2	B VII +	B VII +	B VII 9·1	Near A V
Height in m.	−1·98	−2·59	−2·65	−1·86	−2·77	−2·7
Porifera						
Leucoselenia sp.	..	3	..	..	..	..
Halichondria panicea	..	+	..	20	+	..
Haliclona macandrewii	..	..	..	..	..	4
Porifera (indet.)	+	..	1	..	..	..
Coelenterata						
**Sertularella polyzonias*	..	..	..	..	..	+
**Kirchenpaueria pinnata*	+	+	7	4	+	+
**Dynamena pumila*	+	+	+	76	+	2
Actiniaria (juv., indet.)	..	3	1	4	..	..
Turbellaria and Nemertinea	12	3	167	32	13	14
Nematoda	82	189	410	640	38	128
Polychaeta (see Tables XVII and XVIII)	1259	1924	2275	3992	1280	1606
Oligochaeta (indet.)	..	5	15	48	..	2
Sipunculoidea						
Phascolosoma minutum	..	..	3	4	..	2
Ostracoda (indet.)	..	8	..	12	25	..
Copepoda (see Table XIV)	53	78	27	36	65	65
Cirripedia						
Verruca stroemia	29	29	19	172	?	5
Balanus crenatus	..	..	1	..	..	..
Tanaidacea (see Table XV)	18	19	8	28	4	5
Isopoda (see Table XV)	..	5	3	16	2	12
Amphipoda (see Table XV)	129	76	129	148	175	95
Decapoda						
Pilumnus hirtellus	..	..	1	16	2	2
Brachyura (juv., indet.)	..	3	..	..	..	..
Pycnogonida						
Ammothea echinata	18	3	1	..	..	..
Acarina (indet.)	..	11	10	8	8	7
Pelecypoda						
Mytilus edulis (juv.)	12	14	85	148	123	1
Anomia ephippium (juv.)	17	8	2	4	8	13
Musculus marmoratus (juv.)	..	..	1	..	..	..
Hiatella arctica (juv.)	..	5	1	4	..	1
Pelecypoda (juv., indet.)	6	16	..	64	40	4
Gastropoda						
Patina pellucida	6	2	15	40	8	1
Gastropoda (juv., indet.)	6	8	4	4	9	13
Gastropod egg	..	..	1	..	..	..
†Bryozoa (see Table XVI)	+	32	95	132	+	35
†Tunicata (see Table XVI)	6	14	20	..	6	..
Total	1653 +	2458 +	3302 +	5662	1806 +	2017 +

* Counted by branches. † Counted by colonies.

Sponges occur on *Laminaria* but were not found elsewhere in this survey; there were three species, of which the commonest was *Halichondria panicea*. They were not so abundant or conspicuous here as under shaded, overhanging rocks at higher levels on the shore. Perhaps there is too much fine sand to suit them.

Coelenterates, also, were not very well represented, though two species, *Kirchenpaueria pinnata* and *Dynamena pumila*, were always present. They appeared to be more or less smothered in detritus and worm tubes. Occasional small anemones were found, but none large enough for identification.

Flatworms or nemertines were generally present in small numbers, and were quite numerous (167) in sample H 3, but these forms were very small. It was rather surprising to find no nemertines large enough to be recognizable.

Polychaetes were extremely abundant, making up from two-thirds to four-fifths of the total, their numbers varying from 1259 to 3992. They will be discussed by themselves after the less abundant animals.

Oligochaetes were not common and have not been identified. They did not include either *Lumbricillus scoticus* or *L. pumilio*. The small sipunculid *Phascolosoma minutum* occurred sparingly in three samples, as did the few ostracods present.

TABLE XIV. *LAMINARIA DIGITATA* HOLDFASTS. COPEPODA HARPACTICOIDA IN SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 1	H 2	H 3	H 4	H 5	H 6
Weight in g.	17	63	92	25	52	104
Date	27. viii. 30	27. viii. 30	27. viii. 30	27. viii. 30	7. i. 31	3. iv. 31
Position in m.	A V	A V 1·2	B VII +	B VII +	B VII 9·1	Near A V
Height in m.	−1·98	−2·59	−2·65	−1·86	−2·77	−2·7
Ectinosoma sp.	..	..	..	..	..	2
Zaus spinatus	..	..	..	..	..	6
Alteutha depressa	..	..	..	..	2	1
Alteutha sp.	..	..	1	..	..	..
Idya furcata	..	..	..	..	..	5
I. minor	..	..	..	..	..	13
I. ensifera	..	..	1	..	..	6
Psamathe longicauda	6	..	..	..	..	..
Aspidiscus fasciatus	..	..	..	..	..	2
A. littoralis	6	..	..	..	13	..
Idyidae (indet.)	..	..	..	..	12	5
Parathalestris harpacticoides	..	..	4	12	13	1
Rhinchothalestris rufocincta	..	5	..	..	6	..
Dactylopusia tisboides	..	..	..	..	..	2
D. brevicornis	..	..	..	..	..	1
Thalestridae (indet.)	6	..	..	..	..	..
Amphiascus sp.	..	..	2	..	..	2
Laophonte cornuta	18	49	19	36	13	13
Laophonte spp. (indet.)	17	24	..	..	6	4
Harpacticoida (indet.)	..	..	..	..	..	2
Total	53	78	27	48	65	65

There were at least fifteen species of copepod (see Table XIV), but the total numbers of the group were small, varying from 27 to 78. *Alteutha depressa*, *Idya minor* and *I. ensifera* were found only in *Laminaria* but were not common, while the other species all occurred in one or more other weeds. *Laophonte cornuta* is the only species which occurred in all six samples and was also the most numerous; only one individual of it was taken in another alga, in *Ascophyllum* sample E 12 where it was probably a wave-washed stray. It is remarkable that this copepod, so constantly present among *Laminaria* holdfasts, should not have been found on either *Gigartina* or *Fucus serratus* collected from the same level as the highest *Laminaria*. *Parathalestris harpacticoides* occurred in four samples, but the other species in only one or two samples each.

The barnacle *Verruca stroemia* seems to inhabit all *Laminaria digitata* holdfasts, but in these samples the density of its population varied widely from 5 to 172 per 100 g. (None were recorded from H 5, but since I did not specifically note at the time that they were absent, it is more likely that they were omitted by mistake.) *Verruca stroemia* does not live on the rock itself higher than about −2·5 m.; when associated with *Laminaria* it extends its range some 0·7 m. higher. One other barnacle was recorded, a single small individual of *Balanus crenatus* in H 3 from −2·65 m. *B. crenatus* is a common sublittoral species which is hardly ever found between tide-marks, and indeed this sample was from below low-water of ordinary springs (−2·51 m.).

TABLE XV. *LAMINARIA DIGITATA* HOLDFASTS. TANAIDACEA, ISOPODA, AND AMPHIPODA IN SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 1	H 2	H 3	H 4	H 5	H 6
Weight in g.	17	63	92	25	52	104
Date	27. viii. 30	27. viii. 30	27. viii. 30	27. viii. 30	7. i. 31	3. iv. 31
Position in m.	A V	A V 1·2	B VII +	B VII +	B VII 9·1	Near A V
Height in m.	−1·98	−2·59	−2·65	−1·86	−2·77	−2·7
Tanaidacea						
Apseudes latreillei	..	..	1	8	..	..
Heterotanais oerstedi	..	..	4	16	..	1
Paratanais batei	18	19	2	4	4	4
Tanaidacea (indet.)	..	..	1	..	..	..
Total	18	19	8	28	4	5
Isopoda						
Anthura gracilis	..	..	1	..	..	..
Gnathia maxillaris	..	..	..	..	..	2
G. dentata	..	..	..	16	..	..
Gnathia sp. (juv., indet.)	..	3	..	..	..	..
Idotea granulosa	..	..	..	..	..	1
Janira maculosa	..	..	1	..	..	5
Janiridae (indet.)	..	2	..	..	2	..
Munna kröyeri	..	..	1	..	..	4
Total	..	5	3	16	2	12
Amphipoda						
Leucothöe incisa	..	..	..	..	..	2
Stenothöe monoculoides	..	..	1	..	..	2
Apherusa jurinei	..	..	13	..	20	7
Elasmopus rapax	..	3	23	8	8	2
Tritaeta gibbosa	..	..	..	..	..	2
Microdeutopus damnoniensis	..	..	2	20	..	9
Microdeutopus chelifer	..	..	6	..	..	..
Lembos websteri	..	..	..	12	..	2
Eurystheus maculatus	..	..	17	..	2	6
Amphithöe rubricata	..	..	1	..	..	..
Jassa falcata	..	..	..	..	6	4
J. dentex	..	..	3	32	..	..
Microjassa cumbrensis	19	..	..	..	..	..
Podocerus variegatus	..	..	26	..	..	7
Caprella acanthifera	..	..	2	..	..	..
C. linearis	..	2	..	..	..	..
Amphipoda (juv., indet.)	110	71	35	76	139	52
Total	129	76	129	148	175	95

The Tanaidacea (see Table XV) produced three species, *Apseudes latreillei* in two samples, *Heterotanais oerstedi* in three, and *Paratanais batei* in all six; even the last, however, was never numerous, 19 in H 2 being the largest catch of it. These were the only tanaids collected, except for one or two *Tanais cavolini* in *Ascophyllum*.

Although six species of isopod were identified (see Table XV), there were never more than 16 individuals present per 100 g. The single specimen of *Idotea granulosa* in H 6 is worth noting; this sample was one of the lowest,

−2·7 m., but this species also occurs as high up on the shore as +1·2 m., just below mean high-water neaps, which is an unusually extensive range for an intertidal animal.

The amphipods (see Table XV) were more numerous, and form quite an important part of the laminarian fauna. Their numbers varied from 76 to 175, and there were always a considerable number of young forms present which were not identified. The proportion of these young individuals varied from 35 out of 129 in H 3 to 71 out of 76 in H 2. Sixteen species were identified from *Laminaria*; seven of these occurred in only one sample each, five species occurred twice, three species three times, and one species, *Elasmopus rapax*, five times. None was found in all six samples. Thirteen of these species were found only on *Laminaria* holdfasts, while three occurred elsewhere, namely *Apherusa jurinei* (on *Fucus serratus*, *Gigartina stellata* and *Ascophyllum*), *Amphithöe rubricata* (on *F. serratus and Ascophyllum*), and *Jassa falcata* (on *Gigartina*).

Other arthropods were not numerous. There are usually one or two of the crab *Pilumnus hirtellus* in a *Laminaria* holdfast; in these samples it was absent from only H 1 and H 2. *Pilumnus hirtellus* often seems to take shelter in the pits excavated by the limpet *Patina pellucida*. There were a few of the pycnogon *Ammothea echinata* in the first three samples. Acarines were usually to be found, but in small numbers only, from 7 to 11 mites being present in all the samples (except H 1 where there were none); none of them belonged to the genus *Rhombognathus*. The poverty of acarines and copepods on *Laminaria* holdfasts is remarkable, and in strong contrast with the situation on neighbouring weeds such as *Gigartina*. No insects were found on *Laminaria*.

Pelecypods were fairly numerous, but most or all of them were young. *Mytilus edulis* and *Anomia ephippium* appeared in all six samples, the former being as a rule the commoner. There were occasional specimens of *Hiatella arctica*, and in H 3 a solitary young *Musculus marmoratus*; this last species usually lives in the test of tunicates. It is difficult to know how to treat a group like this, where the animals are fixed and where there are apparently no adults. It seems that the young stages on *Laminaria* are more tolerant both of sedimentation and of overcrowding by other species than are the adults; this is rather surprising if one considers the density of population of a mussel bed. It can hardly be exposure that prevents these young *Mytilus* from growing up, for they are uncovered only on exceptionally low tides, and even then will be kept wet by the waves unless the low-tide coincides with a glass calm.

Patina pellucida, ubiquitous on *Laminaria* stems and holdfasts, was the only gastropod identified, though a few young individuals of other species were always present.

There is a considerable growth of bryozoa (see Table XVI) on the holdfasts; they are mostly encrusting, though there are usually several tuft-like colonies present also. The encrusting bryozoa are difficult to count. They are very thin and fragile and are usually covered with worm-tubes and sand; even when they are clean it is not easy to see where one colony ends and another begins. In the samples H 1, H 2 and H 5 they were not examined in detail. Holdfasts H 3, H 4 and H 6, however, were worked up in the British Museum (Nat. Hist.) where the help of experts could be obtained. Each of these samples was carefully cleaned, and a small piece broken off each bryozoan before the holdfast was cut up. These fragments were then very kindly identified by Dr Hastings. Nine species in all were present (see Table XVI). *Schizoporella hyalina* and *Cellepora costazii* occurred in all three samples, and the former was on the whole the most abundant species, though outnumbered (58 to 30) in H 3 by *Membranipora lineata*. Six species were found on H 3, six on H 4 and four on H 6, but each sample contained one or two species not found on either of the others. It would be necessary to examine more *Laminaria* holdfasts to obtain an accurate estimate of the bryozoan population.

TABLE XVI. *LAMINARIA DIGITATA* HOLDFASTS. BRYOZOA AND TUNICATA IN THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 3	H 4	H 6
Weight in g.	92	25	104
Date	27. viii. 30	27. viii. 30	3. iv. 31
Position in m.	B VII +	B VII +	Near A V
Height in m.	−2·65	−1·86	−2·7
Bryozoa			
Membranipora lineata	58	4	..
Microporella ciliata	..	4	4
Umbonula verrucosa	..	16	..
Mucronella coccinea	..	..	2
Schizoporella hyalina	30	48	27
S. unicornis	1	..	..
Cellepora costazii	3	36	2
C. pumicosa	1	24	..
Tubulipora plumosa	2	..	..
Total	94	132	35
Tunicata			
Botrylloides leachi	8	..	..
Sidnyum turbinatum	2	..	..
Aplidium pallidum	4	..	..
Diplosoma listerianum	5	..	..
Didemnidae (indet.)	1	..	..
Total	20	..	..

Of the three samples just considered, only H 3 supported any tunicates (see Table XVI). These numbered 20 per 100 g. and were also identified by Dr Hastings. They were divided among four species as follows: 8 *Botrylloides leachi*, 5 *Diplosoma listerianum*, 4 *Aplidium pallidum* and 2 *Sidnyum turbinatum*, with the addition of a very young didemnid. Of these species *Botrylloides leachi* and *Sidnyum turbinatum* are elsewhere found between tide-marks and in shallow water, while *Diplosoma listerianum* and *Aplidium pallidum* are common sublittoral forms.

Laminaria digitata holdfasts: Polychaeta.

The polychaetes in *Laminaria* holdfasts (see Tables XVII and XVIII) were extremely numerous, running from 1259 to 3992 per 100 g. In each of the six samples the total number was counted accurately, but only in samples

H 3, H 4 and H 6 were the species determined at all completely. These three holdfasts were worked up at the British Museum (Nat. Hist.) where I could avail myself of the advice and criticism of Mr C. C. A. Monro. Samples H 1, H 2 and H 5 were examined when I was out of reach of specialists, and in them I have recorded only those species about whose identity I was in no doubt.

There are at least 43 species of polychaete in these catches from *Laminaria* holdfasts, divided among thirteen families. Few species occurred in all samples, but there were at least 26 in each of H 3 and H 6, 17 in H 2 and H 5, 16 in H 4, and 6 in H 1.

TABLE XVII. *LAMINARIA DIGITATA* HOLDFASTS. FAMILIES OF POLYCHAETA IN THREE SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 3	H 4	H 6
Weight in g.	92	25	104
Date	27. viii. 30	27. viii. 30	3. iv. 31
Position in m.	B VII +	B VII +	near A V
Height in m.	−2·65	−1·86	−2·7
Aphroditidae	1	..	3
Phyllodocidae	3	4	3
Syllidae	236	412	241
Nereidae	45	40	140*
Eunicidae	..	..	..
Spionidae	760	24	59
Cirratulidae	3	..	4
Capitellidae	6	108	7
Maldanidae	48	260	160
Sabellariidae	..	4	..
Terebellidae	1	..	1
Sabellidae	1083	3084	935
Serpulidae	89	32	53
Indet.	..	24	..
Total	2275	3992	1606

* Including 85 larval Nereidae from one tube.

Before the individual species are considered, it is worth while examining briefly the distribution of families in H 3, H 4 and H 6, as set forth in Table XVII. In each of these samples the sabellids are the most numerous, and form from almost a half to more than three-quarters of the total, or on an average about two-thirds. A long way after the sabellids come the syllids, the spionids and the maldanids. Except in H 3 the syllids were the second most numerous family, but were always outnumbered by the sabellids by from four to seven times. The 760 spionids in H 3 made up one-third of the total number of polychaetes in that sample, but there were only 24 and 59 of them in the other two. On a preliminary examination of a holdfast, the serpulids appear to be more numerous relatively than they are in fact, owing to their conspicuous white shells. The remaining families are not, as such, sufficiently numerous to call for comment.

With the exception of the syllids and one or two very small species such as *Micromaldane ornithochaeta*, *Fabricia sabella* and *Spirorbis borealis*, most of the species of polychaete in *Laminaria* holdfasts are smaller than normal, usually about one-half of the sizes given by Fauvel (1923, 1927).

TABLE XVIII. *LAMINARIA DIGITATA* HOLDFASTS. POLYCHAETA IN SIX SAMPLES, IN NUMBERS PER 100 G. OF DAMP WEED

Sample no.	H 1	H 2	H 3	H 4	H 5	H 6
Weight in g.	17	63	92	25	52	104
Date	27. viii. 30	27. viii. 30	27. viii. 30	27. viii. 30	7. i. 31	3. iv. 31
Position in m.	A V	A V 1·2	B VII +	B VII +	B VII 9·1	Near A V
Height in m.	−1·98	−2·59	−2·65	−1·86	−2·77	−2·7
Aphroditidae						
Lagisca extenuata	..	..	..	..	..	1
Pholöe minuta	..	3	1	..	6	2
Phyllodocidae						
Eulalia bilineata	..	1	..	..	..	..
Eulalia sp. (indet.)	..	..	..	..	4	..
Eteone picta	..	..	..	4	..	..
Phyllodocidae (indet.)	..	..	3	..	..	3
Syllidae						
Syllis gracilis	36	14	4	16	6	5
S. (Typosyllis) prolifera	..	..	9	..	..	..
S. (Typosyllis) variegata	..	..	..	12	..	..
S. (Typosyllis) armillaris	..	..	..	12	..	..
S. (Ehlersia) ferrugina	..	..	..	..	..	1
Trypanosyllis zebra	6	5	..	..	8	10
Odontosyllis ctenostoma	..	..	2	4	2	..
Pionosyllis sp. (indet.)	..	..	1	..	..	..
Grubea limbata	..	..	1	..	4	..
Sphaerosyllis ovigera	..	3	..	..	6	..
S. erinaceus	30	17	87	332	8	12
Exogone gemmifera	..	..	..	..	6	7
E. brevipes	..	..	..	..	..	1
E. verrugera	..	1	..	..	..	..
Autolytus sp. (indet.)	..	..	3	..	2	..
Syllidae (indet.)	..	..	129	36	..	205
Nereidae						
Perinereis cultrifera	..	5	..	..	..	..
Platynereis dumerili	..	..	..	..	12	..
Nereidae (indet.)	..	12	45	40	40	140*
Eunicidae						
Lumbriconereis sp. (indet.)	..	3	..	..	..	..
Spionidae						
Polydora ciliata	..	..	45	4	..	1
P. caeca	..	..	28	..	..	..
P. hoplura	..	..	1	..	..	..
P. giardi	..	..	399	20	..	53
Polydora spp. (indet.)	..	12	287	..	4	4
Spionidae (indet.)	..	..	..	..	..	1
Cirratulidae						
Heterocirrus alatus	..	..	..	..	..	1
Dodecaceria concharum	..	5	3	..	..	3
Capitellidae						
Capitellides giardi	..	..	4	108	..	..
Capitellidae (juv., indet.)	..	..	2	..	..	7
Maldanidae						
Micromaldane ornithochaeta	..	..	47	260	..	160
Maldanidae (juv., indet.)	..	..	1	..	..	..
Sabellariidae						
Sabellaria spinulosa	..	..	..	4	..	..
Terebellidae						
Polycirrus caliendrum	..	..	1	..	..	1
Sabellidae						
Potamilla reniformis	..	..	..	..	..	6
P. torelli	..	..	..	..	..	5
Dasychone bombyx	..	..	1	..	..	1
Amphiglena mediterranea	..	57	24	708	32	7
Fabricia sabella	106	62	998	2328	44	750
Oridia armandi	..	9	60	48	44	163
Jasmineira elegans	..	..	..	..	..	1
Sabellidae (indet.)	..	..	..	..	..	2
Serpulidae						
Hydroides norvegicus	..	1	..	..	..	..
Pomatoceros triqueter	18	11	7	..	6	..
Spirorbis borealis	48	82	82	32	34	53
Polychaeta (indet.)	1015	1621	..	24	1012	..
Total	1259	1924	2275	3992	1280	1606

* Including 85 larval Nereidae from one tube.

APHRODITIDAE. (From now on, see Table XVIII.) *Lagisca extenuata* occurred once and *Pholöe minuta* in four samples, but only in small numbers.

PHYLLODOCIDAE. *Eulalia bilineata* and *Eteone picta* each occurred in one sample, and there were occasionally other members of this family.

SYLLIDAE. At least 16 species of this family were found (including species of *Pionosyllis* and *Autolytus* which were not determined further than the genus), but only two of them occurred in all six samples, namely *Syllis gracilis* and *Sphaerosyllis erinaceus*. The former species is relatively large and, for a syllid, easy to identify; probably all those present were found and counted, so that although it occurred in all the holdfasts it cannot be considered abundant, for its numbers ranged only from 5 to 36. *S. erinaceus*, on the other hand, is minute, and determinable only if well preserved. These holdfasts were pickled whole, and evidently in some the formalin took some time to penetrate and thus gave some of the smaller and more delicate animals time to decompose sufficiently to become unfit for identification. There were probably a good many *S. erinaceus* among the unidentified syllids in H 3, H 4 and H 6, and among the unidentified polychaetes in the other three samples. *Trypanosyllis zebra* is a readily recognizable species which occurred sparingly in four samples.

NEREIDAE. This family includes many of the larger polychaetes, but those found on *Laminaria* holdfasts did not exceed about 2 or 3 cm. in length and were usually even smaller. The identification of nereids depends largely on the arrangement of the paragnaths in the pharynx, so that unless the pharynx is extruded the fore-part has to be dissected. This was not practicable on such small worms as these. A few *Perinereis cultrifera* in H 2 and some *Platynereis dumerili* in H 5 died with the pharynx protruded and were identified, but the majority were not determinable. At first I thought that all these small nereids were young ones which would later on migrate to other habitats, but the presence of at any rate some adults is shown by a tough and leathery tube in H 6. This tube, which was about 2 cm. long and closed at both ends, was entirely filled by 85 very young nereids each about 2 mm. in length and bright yellow in colour. It must have been used by a mature worm to lay eggs in, if not also to inhabit. Mr Monro was unable to say to what species either tube or young worms belonged.

EUNICIDAE. This family was represented only by three *Lumbiconereis* sp. in H 2.

SPIONIDAE. All but one of these consisted of species of the genus *Polydora*, nearly all of which were *P. giardi*, which is somewhat surprisingly not included in the *Plymouth Marine Fauna* (1931). *P. giardi* was abundant in H 3; some 400 per 100 g. were identified, and probably the bulk of the 287 unidentified *Polydora* belonged to this species. The same sample also contained 45 *P. ciliata*, 29 *P. caeca*, and a solitary *P. hoplura*. These *Polydora* riddle with their tubes the calcareous alga, *Lithophyllum incrustans* (Philippi), which cements the *Laminaria* to the rock. In samples H 4 and H 6 there were very few *Polydora* present, but the *Lithophyllum* was in each case extensively tunnelled with burrows which I attribute to this genus. In these samples the tunnels were occupied by sabellids, syllids and other worms.

CIRRATULIDAE. There was a single specimen of *Heterocirrus alatus* in H 6, and a few of the boring worm *Dodecaceria concharum* in H 2, H 3 and H 6 (but none in H 4).

CAPITELLIDAE. The minute species *Capitellides giardi* was quite common (108) in H 4, and there were 4 specimens of it in H 3. The occasional young capitellids in H 3 and H 6 were not of this species. *C. giardi* is not given in the *Plymouth Marine Fauna* (1931).

MALDANIDAE. This family included one common species, *Micromaldane ornithochaeta*, and one young individual in H 3 of another species. *M. ornithochaeta* is evidently one of the commonest polychaetes in *Laminaria* holdfasts, for there were 47 in H 3, 260 in H 4, and 160 in H 6. It is not an easy animal to find as it is colourless and very small, measuring only about 1·5 mm. by 0·1 mm., and is hardly visible to the naked eye.

SABELLARIIDAE. *Sabellaria spinulosa* occurred once, in H 4.

TEREBELLIDAE. There was a single specimen of *Polycirrus caliendrum* in each of the two samples H 3 and H 6.

SABELLIDAE. There were seven species of this family, including the commonest polychaete on the shore, *Fabricia sabella*, a small and active worm about 3 mm. long. *Oridia armandi*, about the same size and difficult to distinguish from *Fabricia sabella*, was always present but in smaller numbers. *Amphiglena mediterranea*, which measures about 1 cm., was very common (708) in H 4, but less numerous in the other samples, for 57 in H 2 was the next largest catch. The abundance of *Fabricia sabella* is quite extraordinary; it is found mainly in the fine detritus near the surface of the holdfast, but also occurs in interstices in the deeper parts. Although it is so small, it is sufficiently numerous to make up a considerable part of the total animal material present. The other sabellids only occurred in ones and twos in H 6, with the addition of a single *Dasychone bombyx* in H 3. The specimens of *D. bombyx*, *Potamilla reniformis* and *P. torelli* were all less than half the sizes given by Fauvel (1927).

SERPULIDAE. *Spirorbis borealis* was always present and in fair numbers, varying from 32 to 82; as has been mentioned, special search was made for other species of *Spirorbis*, but without success. *Pomatoceros triqueter* is not common or even always present on *Laminaria* holdfasts, though abundant on stones nearby; it was missing from H 4 and H 6, but occurred in small numbers on the other four samples. There was also, on H 2, a single *Hydroides norvegicus*, a species which might be expected to occur more frequently in such a habitat.

SUMMARY AND COMPARISON OF THESE FAUNAS

The faunas of these various seaweeds can now be compared as a whole. The species inhabiting the different plants have been dealt with in the foregoing sections.

In Table XIX the distribution of the various groups is shown in all fifty samples, and it can be used as a summary of Tables IV–XVIII in the previous sections. Table XX shows the average number of each group per 100 g. of each weed, and summarizes Table XIX.

Pelvetia canaliculata is the highest marine alga on the shore at Wembury, and supports the most meagre fauna which averages only 43·8. The dominant animals are the isopod *Ligia oceanica*, the amphipod *Hyale nilssoni*, and young Littorinidae most of which are probably *Littorina saxatilis*. Notable absentees are polychaetes, ostracods, copepods and acarines.

The fauna of *Fucus spiralis* is more varied and somewhat more abundant, averaging 98·8. *Ligia oceanica*, which lives mainly above high-water mark, no longer makes its appearance, but acarines and copepods are now found in most samples in small numbers; in one sample, B 1, the copepods were numerous. *Hyale nilssoni* is the dominant species, and on an average makes up almost half of the population.

The faunas of the fucoid algae all have certain features in common and grade into one another to some extent, but the population of *Lichina pygmaea* is unlike any other on the shore. The lichen does not contain a particularly large number of species, but is nevertheless from 10 to 100 times richer in individuals than are algae from similar levels, and its animal population averages no less than 13,716 per 100 g. More than nine-tenths of these animals consist of two species, the pelecypod *Lasaea rubra* and the isopod *Campecopea hirsuta*, neither of which was found elsewhere; the larvae of the fly *Geranomyia unicolor* were also confined to *Lichina*. Nematodes, ostracods and copepods were either very scarce or altogether absent, in strong contrast with the neighbouring fucoids.

The three samples of *Fucus vesiculosus* came from levels corresponding with about the middle of the *Ascophyllum nodosum* zone, and many species are common to the two algae. In two of the *F. vesiculosus* samples the numbers of copepods and young Littorinidae were similar to those in *Ascophyllum*, and in the third sample there were many acarines. Otherwise, however, the fauna in *F. vesiculosus* was much the more scanty, with an average of 458·5.

In *Ascophyllum nodosum* both species and individuals are numerous, due in large part to the popularity of the tufts of *Polysiphonia lanosa* as a habitat; the average population numbers 1417·7. Ostracods, copepods, acarines and young Littorinidae are all abundant, and several other groups appear in numbers greater than 20 per 100 g. instead of in twos and threes as in the

TABLE XIX. VARIOUS GROUPS OF ANIMALS IN EIGHT SPECIES OF WEED, IN NUMBERS PER 100 G. OF DAMP WEED

Seaweed	Sample no.	Weight in g.	Date	Height relative to O.D. in m.	Porifera	Coelenterata	Turbellaria and Nemertinea	Nematoda	Polychaeta	Oligochaeta	Sipunculoidea	Ostracoda	Copepoda	Cirripedia	Tanaidacea	Isopoda	Amphipoda	Decapoda	Pycnogonida	Acarina	Insecta	Pelecypoda	Gastropoda	Bryozoa	Tunicata	Total
Pelvetia canaliculata	A 1	197	30. vi. 30	+1·52	..	..	..	..	..	1	..	..	..	..	..	1	48	..	..	..	..	..	5	..	..	55
	A 2	52	10. vii. 30	+1·95	..	..	..	17	..	..	..	..	..	..	..	38	6	..	..	..	2	..	31	..	..	94
	A 3	51	11. vii. 30	+1·76	..	..	..	..	..	..	..	..	..	..	..	37	6	..	..	..	..	..	6	..	..	49
	A 4	53	6. i. 31	+2·01	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	2	..	2	..	..	6
	A 5	97	20. iii. 31	+1·49	..	..	..	..	..	..	..	..	..	..	..	..	15	..	..	..	..	..	..	..	..	15
Fucus spiralis	B 1	408	24. vi. 30	+1·18	..	..	2	6	..	1	..	2	150	..	..	1	71	1	..	3	1	..	27	..	..	266
	B 2	94	10. vii. 30	+1·67	..	..	..	1	1	..	..	1	2	..	..	..	86	..	..	5	4	..	14	..	..	114
	B 3	80	11. vii. 30	+1·37	..	..	..	1	..	..	..	..	1	..	..	..	25	..	..	1	..	..	2	..	..	30
	B 4	93	6. i. 31	+1·15	..	..	..	..	..	..	..	..	..	..	..	2	70	..	..	6	..	..	22	..	..	100
	B 5	56	6. i. 31	+1·17	..	..	..	4	4	18	..	..	..	..	..	..	7	..	..	2	2	..	9	..	..	46
	B 6	77	20. iii. 31	+1·49	..	..	..	7	..	..	..	..	2	..	..	..	18	..	..	2	1	..	7	..	..	37
Lichina pygmaea	C 1	11	5. ix. 30	+0·06	..	..	..	9	..	27	..	..	..	137	..	3770	45	..	..	1480	264	9505	300	..	..	15536
	C 2	12	5. ix. 30	+1·34	..	..	..	..	..	8	..	..	..	292	..	2683	..	..	..	..	175	4550	325	..	..	8033
	C 3	14	7. i. 31	+1·51	..	..	..	..	..	7	..	..	..	293	..	2886	86	..	..	178	71	12150	379	..	..	16050
	C 4	24	20. iii. 31	+1·51	..	..	..	..	..	..	..	..	..	417	..	2205	8	..	..	87	137	11584	808	..	..	15246
Fucus vesiculosus	D 1	87	15. vii. 30	−0·40	..	..	6	6	..	1	..	6	115	..	..	8	..	..	..	20	..	..	90	..	..	252
	D 2	78	15. vii. 30	−0·52	..	..	10	4	..	..	6	41	538	..	..	5	4	..	..	37	5	..	100	..	..	750
	D 3	87	7. i. 31	−0·46	..	..	..	..	..	..	..	1	10	..	..	..	..	..	..	350	2	..	11	..	..	374
Ascophyllum nodosum and *Polysiphonia lanosa*	E 1	350	13. v. 30	−0·52	..	+	1	17	..	11	..	4	2	..	..	12	28	..	..	9	1	1	23	..	..	109 +
	E 2	670	14. v. 30	+0·40	..	1	3	13	..	83	..	2	5	..	..	10	14	..	..	9	..	1	35	..	..	176 +
	E 3	529	2. vii. 30	+0·27	..	1	19	61	5	64	..	90	279	..	..	1	17	..	..	55	73	..	76	..	..	742 +
	E 4	151	15. vii. 30	+0·67	..	..	47	126	53	46	..	232	570	..	..	6	18	1	..	308	113	..	77	..	..	1597
	E 5	119	15. vii. 30	−0·09	..	..	39	60	..	8	..	351	731	..	..	3	9	1	..	115	140	4	58	..	..	1519
	E 6	103	23. vii. 30	−0·30	..	+	82	49	..	17	..	1480	358	..	..	27	53	..	1	93	134	17	487	..	..	2798 +
	E 7	202	25. vii. 30	+0·37	..	1 +	56	72	..	1	..	815	613	..	1	4	27	..	..	186	15	8	92	..	..	1891 +
	E 8	84	28. viii. 30	−1·00	..	..	94	61	..	10	..	805	168	..	..	39	63	..	..	194	..	43	252	..	..	1729
	E 9	96	5. i. 31	−0·43	..	+	28	44	1	24	..	24	49	..	..	58	86	..	..	204	2	15	75	..	..	610 +
	E 10	84	5. i. 31	−1·00	..	+	86	46	6	23	..	11	56	..	..	77	86	..	..	275	6	36	160	1	..	869 +
	E 11	117	6. i. 31	+0·73	..	33	187	211	744	75	..	201	62	..	2	97	77	..	1	475	178	13	357	1	..	2714
	E 12	68	20. iii. 31	+0·06	..	+	121	153	62	109	..	225	372	..	..	26	99	..	..	746	38	40	268	..	..	2259 +
Fucus serratus	F 1	364	2. vi. 30	−1·49	..	1	..	10	..	1	..	1	212	..	..	7	7	..	..	37	1	..	27	..	..	304
	F 2	335	11. vi. 30	−1·31	..	1	..	..	..	1	1	..	172	..	..	10	2	..	..	34	..	..	13	..	..	234
	F 3	395	13. vi. 30	−1·86	..	..	1	163	1	..	2	8	775	..	..	7	5	1	..	114	11	3	97	..	..	1188
	F 4	91	23. vii. 30	−0·40	..	..	..	3	..	..	..	7	11	..	..	12	3	..	..	42	..	..	35	..	..	113
	F 5	131	26. vii. 30	−1·95	..	..	..	13	..	..	..	8	360	..	..	3	5	..	..	50	5	2	3	16	..	465
	F 6	82	28. viii. 30	−1·37	..	..	..	2	..	..	..	..	13	..	..	6	..	..	..	33	1	..	6	..	..	61
	F 7	85	28. viii. 30	−1·89	..	..	1	..	1	..	..	..	169	..	..	1	..	..	..	31	..	..	18	35	..	256
	F 8	99	5. i. 31	−0·58	..	..	..	3	..	..	..	5	3	..	..	28	20	..	..	200	2	3	33	..	..	311
	F 9	93	5. i. 31	−1·83	..	..	..	10	..	..	..	..	43	..	..	4	3	..	..	195	..	..	2	..	..	257
	F 10	77	3. iv. 31	−1·76	..	..	..	1	..	..	..	1	53	..	..	3	..	..	..	18	..	..	1	10	..	87
Gigartina stellata	G 1	70	26. vii. 30	−1·98	..	24	9	4	33	..	43	..	6586	..	..	60	254	..	..	129	..	21	60	118	..	7341
	G 2	60	28. viii. 30	−1·64	..	602	..	47	50	..	..	..	5	..	..	40	48	..	..	1274	..	115	178	98	..	2457
	G 3	62	7. i. 31	−1·89	..	127	2	2	174	..	..	2	44	3	..	16	18	..	..	424	..	13	8	164	..	997
	G 4	47	3. iv. 31	−1·70	..	111	..	13	38	..	..	..	70	2	..	13	15	..	..	1208	..	19	43	253	..	1785
Laminaria digitata holdfasts	H 1	17	27. viii. 30	−1·98	+	+	12	82	1259	..	..	..	53	29	18	..	129	..	18	..	..	35	12	+	6	1653 +
	H 2	63	27. viii. 30	−2·59	3 +	3	3	189	1924	5	..	8	78	29	19	5	76	3	3	11	..	43	10	32	14	2458 +
	H 3	92	27. viii. 30	−2·65	1	8	167	410	2275	15	3	..	27	20	8	3	129	1	1	10	..	89	20	95	20	3302
	H 4	25	27. viii. 30	−1·86	20	84	32	640	3992	36	4	12	48	172	28	16	148	16	..	8	..	220	44	132	..	5662
	H 5	52	7. i. 31	−2·77	+	+	13	38	1280	..	..	25	65	+	4	2	175	2	..	8	..	171	17	+	6	1806 +
	H 6	104	3. iv. 31	−2·7	4	2 +	14	128	1606	2	2	..	65	5	5	12	95	2	..	7	..	19	14	35	..	2017 +

other fucoids. Of all the groups listed in Tables XIX and XX, only Porifera, Sipunculoidea, Cirripedia and Tunicata are unrepresented in *Ascophyllum*. Many of its species are true intertidal forms which are not found except between high- and low-water marks.

The population of *Fucus serratus* resembles that of *F. vesiculosus* in many ways. The average total numbers are 324·6 and 458·5 respectively, in each of them copepods and acarines form the bulk of the fauna, and ostracods are very rare when compared with *Ascophyllum*. Although individuals are in many cases scarce in *Fucus serratus*, the number of species represented by them is large.

TABLE XX. AVERAGE POPULATIONS OF EIGHT SEAWEEDS, IN NUMBERS PER 100 G.

	Pelvetia canaliculata	*Fucus spiralis*	*Lichina pygmaea*	*Fucus vesiculosus*	*Ascophyllum nodosum* and *Polysiphonia lanosa*	*Fucus serratus*	*Gigartina stellata*	*Laminaria digitata* holdfasts
Porifera	..	..	..	..	..	..	..	8·3
Coelenterata	..	..	..	..	3·0	0·2	216·0	31·0
Turbellaria and Nemertinea	..	0·3	..	5·3	63·6	0·5	2·8	40·2
Nematoda	3·4	3·2	..	3·3	76·1	21·2	16·5	247·8
Polychaeta	..	0·8	..	..	72·6	0·6	73·8	2056·0
Oligochaeta	0·2	3·2	11·0	0·3	39·2	0·2	..	9·7
Sipunculoidea	..	..	..	2·0	..	0·3	10·8	1·5
Ostracoda	..	0·5	..	16·0	353·3	3·0	0·5	7·5
Copepoda	..	25·8	..	221·0	272·2	178·1	1676·2	54·0
Cirripedia	..	..	287·0	..	..	..	1·2	51·0
Tanaidacea	..	..	..	..	0·2	..	..	13·7
Isopoda	15·2	0·5	2886·0	4·3	30·0	8·1	32·2	6·3
Amphipoda	15·4	46·3	35·0	1·3	48·1	4·3	83·8	125·3
Decapoda	..	0·2	..	..	0·2	0·1	..	4·0
Pycnogonida	..	..	..	..	0·2	..	..	3·7
Acarina	..	3·2	436·0	135·7	222·4	75·6	758·8	7·3
Insecta	0·8	1·3	161·0	2·3	58·3	2·0	..	..
Pelecypoda	..	..	9447·0	..	14·8	0·8	42·0	96·2
Gastropoda	8·8	13·5	453·0	67·0	163·3	23·5	72·2	19·5
Bryozoa	..	..	..	..	0·2	6·1	158·2	73·5
Tunicata	..	..	..	..	..	..	..	7·8
Total	43·8	98·8	13,716·0	458·5	1417·7	324·6	3145·0	2864·3

In *Gigartina stellata* the acarines are more abundant than they are anywhere else, and average 758·8 out of a total population of 3145. In one sample the copepods reached the very large number of 6586 per 100 g., but were rare in the other three samples. Thanks to the one rich catch, however, their average in the four samples of *Gigartina* is some six times as high as in *Ascophyllum*. Otherwise *Gigartina* is distinguished from the other weeds mainly by the larger numbers of hydroids and encrusting bryozoa, by the presence of small numbers of several species which belong more properly to the sublittoral region, and by the complete absence of oligochaetes and insect larvae.

In *Laminaria digitata* holdfasts there is a very great increase in the number of species present. Polychaetes are the dominant group, and on an average make up more than two-thirds of the population (2056 out of 2864·3); by far the most abundant worm is *Fabricia sabella*. Sponges and tunicates were found only on *Laminaria*, while insects were the only group missing. Nematodes, tanaids and amphipods all occurred in larger numbers than on any other weeds, but copepods and acarines were notably scarce. Speaking generally, it can be stated that on the levels around mean sea-level and mean low-water neaps the most abundant groups are ostracods, copepods, acarines and young littorinids, and that in the holdfasts of *Laminaria* their place is taken by polychaetes.

So far, in this paper, the densities of the various populations have been expressed only in relation to a given mass of weed, 100 g. In comparing the numbers of animals in different weeds I have to some extent implied that 100 g. of one weed represents the same amount of environment as 100 g. of another. This implication, while not accurate, is by no means grossly misleading. It is true that, on the whole, samples collected near low-water mark will contain relatively more water than those from higher up the shore which have been exposed to the drying power of the air for some hours; nevertheless it is remarkable how quickly a weed such as *Gigartina stellata*, growing in separate tufts, loses any superficial water and becomes quite dry outside, and also how wet all but the most superficial layers of a densely growing plant like *Ascophyllum nodosum* remain on even the hottest day. On the whole, I do not think that it is seriously wrong to compare the populations of the weeds by numbers per 100 g.

Another matter is the estimation of the fauna of each weed over a given area of rock; this can be done from the figures given for 100 g. if the weight of each weed per sq. m. is known. I have measured this very roughly by the use of a simple piece of apparatus consisting of a band of galvanized iron 10 cm. wide and 115 cm. long. Allowing for an overlap of 3 cm. for rivetting the ends together, this can be bent to form a circle with a circumference of 112 cm., which encloses an area of 0·1 sq. m. The circular shape is maintained by means of two wooden pieces set at right angles and each 35·7 cm. in length. In use, the gear was placed firmly on the seaweed and a knife was run round the outside as deep as the underlying rock; then the weed inside the sampler was all cut away from the rock and weighed. This weighing was done in a bucket with a spring-balance, a method which, though crude, should give comparable results from weed to weed. I weighed from 4 to 7 samples of 0·1 sq. m. of each weed except for *Lichina pygmaea*, of which I weighed 4 samples each covering only 0·01 sq. m. The weights of the weeds in kg. per sq. m. are shown in Table XXI; these figures are admittedly rough.

TABLE XXI

Seaweed	Wt. per sq. m. in kg.
Pelvetia canaliculata	5·5
Fucus spiralis	5·7
Lichina pygmaea	2·0
Fucus vesiculosus	10·0
Ascophyllum nodosum and *Polysiphonia lanosa*	14·3
Fucus serratus	8·2
Gigartina stellata	2·7
Laminaria digitata (holdfasts only)	2·5

Since in the foregoing sections the numbers of animals were given per 100 g. or 0·1 kg., the numbers per sq. m. can be obtained by multiplying those in each weed by 10 times the weight in kg. per sq. m. The result is shown in Table XXII, and this can now be compared with Table XX, where the numbers are given per 100 g.

TABLE XXII. AVERAGE POPULATIONS OF EIGHT SEAWEEDS, IN NUMBERS PER SQ. M. OF ROCK SURFACE

	Pelvetia canaliculata	*Fucus spiralis*	*Lichina pygmaea*	*Fucus vesiculosus*	*Ascophyllum nodosum* and *Polysiphonia lanosa*	*Fucus serratus*	*Gigartina stellata*	*Laminaria digitata* holdfasts
Porifera	..	..	..	..	..	..	..	208
Coelenterata	..	..	..	..	429	16	5833	775
Turbellaria and Nemertinea	..	17	..	530	9095	41	76	1005
Nematoda	187	182	..	330	10880	1738	445	6195
Polychaeta	..	46	..	..	10380	49	1993	51400
Oligochaeta	11	182	220	30	5606	16	..	242
Sipunculoidea	..	..	..	200	..	25	292	38
Ostracoda	..	28	..	1600	50530	246	13	188
Copepoda	..	1471	..	22100	38920	14600	45240	1350
Cirripedia	..	..	5740	..	..	..	32	1275
Tanaidacea	..	..	..	..	29	..	..	342
Isopoda	836	28	57720	430	4290	664	870	158
Amphipoda	847	2639	700	130	6877	353	2262	3132
Decapoda	..	11	..	..	29	8	..	100
Pycnogonida	..	..	..	..	29	..	..	92
Acarina	..	182	8720	13570	31810	6189	20490	182
Insecta	44	74	3220	230	8337	164	..	..
Pelecypoda	..	..	188940	..	2115	66	1134	2405
Gastropoda	484	770	9060	6700	23350	1927	1949	488
Bryozoa	..	..	..	..	29	500	4273	1838
Tunicata	..	..	..	..	..	..	..	195
Total	2409	5630	274,320	45,850	202,735	26,621	84,902	71,608

The largest population is still that of *Lichina pygmaea*, with over a quarter of a million per sq. m., but it is now closely followed by *Ascophyllum* with over 200,000, owing to the much greater bulk of this alga. The other weeds come in the same order as before. This table brings out again the numerical importance over wide ranges of the shore of copepods, acarines and young gastropods, and emphasizes the exceptional abundance of ostracods among *Ascophyllum*. The figures for the holdfasts of *Laminaria* are minimal; at the levels exposed by the tide at the time that these measurements were made there were only 78 holdfasts per sq. m., but there are probably two or three times as many immediately below low-water of ordinary springs, and these would have been exposed had the tide reached the predicted level.

No fewer than eight large groups of animals reach their maximum in *Ascophyllum*, namely Turbellaria and Nemertinea (9095), Nematoda (10,880), Oligochaeta (5606), Ostracoda (50,530), Amphipoda (6877), Acarina (31,810), Insecta (8337) and Gastropoda (23,350). Cirripedia (5740), Isopoda (i.e. *Campecopea hirsuta* (57,720)) and Pelecypoda (i.e. *Lasaea rubra* (188,940)) are most abundant among *Lichina pygmaea*; Coelenterata (5833), Sipunculoidea (292), Copepoda (45,240) and Bryozoa (4273 colonies) among *Gigartina stellata*; and Porifera (208), Polychaeta (51,400), Tanaidacea (342), Decapoda (100), Pycnogonida (92) and Tunicata (195 colonies) on *Laminaria digitata* holdfasts. These figures once again emphasize the general importance of *Ascophyllum nodosum* and *Polysiphonia lanosa* as a habitat for intertidal invertebrates on Church Reef.

COMPARISON WITH POPULATIONS OF SOIL, ETC.

These intertidal numbers are large, and I have collected a few other examples of big populations of small animals for comparison. The population of the soil is frequently cited as an example of exceptional abundance (e.g. Elton, 1927, p. 107) and in Table XXIII there are shown the populations of eight types of soil and of the tussocks of a grass. In the original reports they were mostly given in numbers per acre, but when necessary I have reduced them to numbers per sq. m. so that these figures are directly comparable with those in Table XXII.

TABLE XXIII. THE POPULATIONS OF NINE TYPES OF SOIL, ETC., IN NUMBERS PER SQ. M., FOR COMPARISON WITH TABLE XXII

	Cameron, 1917		Morris, 1920	Morris, 1922		Ford, 1935	Ford, 1937	Baweja, 1939	
	Ungrazed	Grazed		Manured	Not manured			Normal soil	Sterilized soil
Turbellaria	..	..	..	..	..	7	..	..	..
Nematoda	..	..	..	891	196	592	..	200	14
Oligochaeta						..	..	350	55
Enchytraeidae						811	..	..	..
Lumbricidae	..	..	..	249	113	656	..	..	..
Isopoda	..	..	..	..	..	692	..	90	48
Myriapoda	..	..	..	..	..	538	..	2515	545
Diplopoda	..	..	..	338	147	..	..	..	..
Chilopoda	..	..	..	..	53	..	..	..	..
Arachnida	..	..	..	..	..	..	..	1685	1176
Acarina	..	..	..	131	53	2431	3985	..	..
Araneidae	..	..	..	..	..	100	..	..	..
Opiliones	..	..	..	..	..	25	..	..	..
Gastropoda	..	..	..	..	..	161	..	42	4
Other species	..	..	..	..	..	..	205	..	..
Insecta									
Protura	..	..	..	..	..	..	..	1	..
Collembola	..	..	140	590	171	59640	6766	7427	14100
Thysanura	..	..	..	27	11	86	..	45	29
Orthoptera	..	..	..	3	3	..	..	7	1
Hemiptera	..	..	4	3	2	25	..	258	678
Psocoptera	..	..	..	..	..	..	..	25	8
Thysanoptera	..	..	11	5	6	25	543	18	31
Lepidoptera	..	..	4	7	12	..	..	10	48
Coleoptera	..	..	184	196	93	789	..	607	615
Hymenoptera	..	..	2	732	176	57	..	181	28
Diptera	..	..	542	350	135	61	..	2317	9173
Indet.	..	..	..	..	..	51	..	..	..
Total Insecta	207	380	885	1908	611	60734	..	10900	24711
Total other Invertebrata	..	..	..	1821	612	6013	..	5000	1842
Grand Total	..	..	..	3729	1223	66,747	11,499	15,900	25,553

The survey of Cameron (1917) went to a depth of 1 ft. (0·3 m.) in an ungrazed meadow and in alluvial pasture at Holmes Chapel, Cheshire. Morris (1920) worked to the same depth in permanent pasture in the same locality. Morris (1922) examined manured and unmanured soils down to 9 in. (0·23 m.) at Rothamsted. Ford (1935) surveyed the soil and surface populations in a meadow at Botley, near Oxford; the surface population was much the smaller, and in Table XXIII I have added it to the soil fauna. Ford (1937) investigated the tussocks of a grass, *Brometum*, at Headington, also near Oxford. Finally, Baweja (1939) compared at Rothamsted the population of untreated soil under grass with that of soil which had been previously sterilized.

It will be at once apparent that the populations of soil are, on the whole, very much smaller than those of intertidal algae, with the exception of one group, the Collembola, which are really abundant in some soils (e.g. Ford, 1935). The larvae of Diptera are usually an important component of the soil fauna, but even so they rarely approach the numbers present in *Ascophyllum* (over 8000). Only in previously sterilized soil (Baweja, 1939) was this figure exceeded, for in this soil there were 9173 fly larvae per sq. m. Ford (1938) compares the population of grass tussocks (Ford, 1937) with that of human communities. He concludes that, allowing for the difference in size between the animals concerned, "the population of the Brometum, at its greatest density, is rather less crowded than are the inhabitants of Belgium".

Two other examples of the enormous numbers of animals to be met with between tide-marks may be mentioned. On rocks exposed to wave-action barnacles may become extremely numerous, and may occupy all the available space. Moore (1935, p. 305) mentions several examples where the population of *Balanus balanoides* exceeds 100,000 per sq. m.; small, first-year barnacles may even reach 200,000 if no space is already occupied by older and larger individuals. Secondly, Mr P. R. Crimp (personal communication) is finding nematodes to the number of upwards of a million per sq. m. in intertidal muds in the Tamar estuary.

Distribution of the Animals on the Shore

This account will conclude with a list of species found during the survey, which are new to the *Plymouth Fauna*, with their habitats, but first it is necessary to mention the distribution of the main groups of animals, since in some of them the species have been worked out in part only or not at all. The basis of the following section is Tables XX and XXII.

Porifera. Sponges were found only on the holdfasts of *Laminaria*, and it was not easy to count them because they grow round each other and the branches of the holdfast; this makes it difficult to see where one sponge ends and the other begins, when two or more neighbouring sponges belong to the same species. At least three species were present, and the average number of sponges, 8·3 per 100 g., can probably be taken as below the true figure.

Coelenterata. Five species of hydroid were found, but none above +0·73 m., the highest sample of *Ascophyllum*. They were never really common on *Ascophyllum*, they were scarce on *Fucus serratus* (though they were more plentiful on the stalks of these algae than on the fronds which were the parts examined), and absent from all the other fucoid algae. There was a fair quantity of *Dynamena pumila* on *Gigartina*, and hydroids were not uncommon on *Laminaria*. In this last habitat they appear to be more or less smothered by fine sand and worm-tubes. The sessile stauromedusa *Haliclystus auricula* was found on *Gigartina*, and one young stauromedusa on *Ascophyllum*. There were occasional very small anemones on *Laminaria*.

TURBELLARIA AND NEMERTINEA. These two phyla have perforce been grouped together, though at times they were not rare. They consisted in the main of very small worms about 2 mm. long, which shrivelled up on being killed. This made them impossible to recognize without cutting sections of each. There were a few in occasional samples of *Fucus spiralis*, *F. vesiculosus*, *F. serratus* and *Gigartina stellata*, an average of 63·6 in *Ascophyllum nodosum*, and of 40·2 in *Laminaria*. They never formed a dominant part of the fauna.

NEMATODA. Nematodes are widely distributed on the shore and were found in all the weeds except *Lichina*. Dr Baylis has identified six species and two other genera. Nematodes were present in all samples of *Ascophyllum*, *Gigartina* and *Laminaria*, and were common in the last-named with an average of 247·8. Very few of them were longer than 1 cm.

POLYCHAETA. With the exception of one sample of *Ascophyllum*, E 11, which contained 744, polychaetes were not abundant until the *Laminaria* holdfasts were reached, where they were extremely numerous. They were not very rare in *Gigartina*, but otherwise they were found only in occasional samples, and were absent altogether from *Pelvetia*, *Lichina* and *Fucus vesiculosus*. There were at least 43 species of this group.

OLIGOCHAETA. This group occurred only sporadically in most weeds, and was not found at all on *Gigartina*. On *Ascophyllum* two species of *Lumbricillus* were not uncommon, *L. scoticus* which was originally described from a similar habitat at Millport, and *L. pumilio* which was a new species. These two were the only oligochaetes identified (by the late Dr J. Stephenson), but there were certainly two or three other species on the *Laminaria* holdfasts.

SIPUNCULOIDEA. Only one species was found, *Phascolosoma minutum*, which occurred in seven samples distributed among *Fucus vesiculosus*, *F. serratus*, *Gigartina* and *Laminaria*. It was never common, 43 in G 4 being the largest catch.

OSTRACODA. Ostracods were found in all weeds except *Pelvetia* and *Lichina*, but were quite scarce except in *Ascophyllum*. Here they were the most numerous group, with an average of 353·3 and a maximum of 1480 per 100 g. Those collected in 1930 and 1931 were not identified, but in April 1939 I collected about 150 from *Ascophyllum* which were examined by Mr A. G. Lowndes; they were all *Xestoleberis aurantia*.

COPEPODA. Like the ostracods, copepods were not found in either *Pelvetia* or *Lichina*, but except in *Ascophyllum* they were by far the more abundant of the two groups in the other weeds. They constituted the largest group in *Fucus vesiculosus*, *F. serratus* and *Gigartina*, and the second largest in *Fucus spiralis* and *Ascophyllum*. They form a dominant part of the fauna over a wide range in height, from +0·7 m. or a little below high-water neaps down to

−2 m. which is about mean low-water springs. Altogether 36 species of copepod have been identified.

CIRRIPEDIA. Since this survey was made chiefly on the weeds themselves, rock-dwelling barnacles were not generally collected. They were scraped off in fair numbers with *Lichina*, however, and *Verruca stroemia* is quite common on *Laminaria* holdfasts, and occasional on *Gigartina*. 4 species were found.

TANAIDACEA. There were four species of this small group, of which *Tanais cavolini* was found in two samples of *Ascophyllum* and the others on *Laminaria*. None were found anywhere else and they were never at all common.

ISOPODA. The isopods were more numerous and were found in all the weeds. There were 12 species, but the specific make-up differed widely on different parts of the shore; the dominant species were: *Ligia oceanica* on *Pelvetia*; *Campecopea hirsuta* on *Lichina*; and *Naesa bidentata* and *Idotea granulosa* on *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus* and *Gigartina*. *Campecopea hirsuta* was the only abundant isopod, but it was confined to *Lichina* where its average number was no less than 2886.

AMPHIPODA. 23 species of amphipod were found, of which only one, *Hyale nilssoni*, was at all common above the level occupied by *Gigartina*. *Hyale nilssoni* was a conspicuous member of the populations of *Pelvetia*, *Fucus spiralis* and *Ascophyllum*, in which it occurred in all samples and where it was often the only amphipod present. It was less numerous in *Fucus serratus* and was not found below *Gigartina*. *Hyale nilssoni* has an unusually extensive range for an intertidal animal, from below mean high-water springs down to about mean low-water springs; on Church Reef this represents a vertical range of more than 3·5 m. *Apherusa jurinei* and *Amphithöe rubricata* are widely distributed below mean sea-level and also live below tide-marks. *Jassa falcata*, found on *Gigartina* and *Laminaria*, was abundant in one sample (248 in G 1), and several species, notably *Elasmopus rapax*, are not infrequent on *Laminaria* holdfasts but are not found higher up the shore. On the average, amphipods were most numerous on *Laminaria* (125·3), followed by *Gigartina* (83·8), *Ascophyllum* (48·1), *Fucus spiralis* (46·3) and *Lichina* (35).

DECAPODA. Decapod crustacea were not common. There was an occasional young crab or megalopa of *Carcinus maenas* and *Xantho incisus* on the fucoid algae, and several *Pilumnus hirtellus* on *Laminaria*.

PYCNOGONIDA. These were equally scarce. Only one species, *Ammothea echinata*, was identified, which occurred occasionally on *Ascophyllum* and *Laminaria*.

ACARINA. This is a very numerous intertidal group which has not yet been properly examined at Plymouth. Mr J. N. Halbert has identified 4 species from samples of *Ascophyllum* and *Fucus serratus*, but there are certainly more species than this; those found on *Laminaria* holdfasts appear to be all different from those found higher up. There were no acarines in *Pelvetia* and but few in *Fucus spiralis*, though they occurred in all the samples of the latter. In *Lichina*, *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus* and *Gigartina* they were usually or at any rate sometimes abundant. The largest single catch was in *Lichina* (1480) in C 1, but on an average they were most plentiful in *Gigartina* (758·8); next came *Lichina* with an average of 436, *Ascophyllum* (222·4), *Fucus vesiculosus* (135·7) and *F. serratus* (75·6). There is a very marked drop in these numbers to only 7·3 on reaching the *Laminaria* holdfasts. The great majority of them belong to two truly intertidal species, *Rhombognathus pascens* and *R. seahami*; *Halacarus basteri* is not uncommon in *Ascophyllum*.

INSECTA. Insects of one kind or another were found on all the weeds except *Gigartina* and *Laminaria*, and at all levels between +2·01 m. and −1·95 m. or from below mean high-water springs down to about mean low-water springs. The collembolan *Lipura maritima* and the thysanuran *Petrobius maritimus* were found occasionally above mean sea-level, and in one sample of *Ascophyllum* (E 12) there were one or two pupae and adults of beetles and flies. The great bulk of the insect collection, however, consisted of the larvae of diptera; these were found at all times at which collections were made, but were common only on *Lichina* and *Ascophyllum*. On the former weed the dominant species was *Geranomyia unicolor*, a large, brown larva 12 mm. long, which makes a rather tenuous tube, and on *Ascophyllum* the majority were (probably) *Clunio marinus* and *Thalassomyia frauenfeldi*. Although the larvae were always to be seen I have not found any of their pupae among the weeds examined.

PELECYPODA. No bivalves were found on *Pelvetia*, *Fucus spiralis* or *F. vesiculosus*, and they were very scarce on *F. serratus*. Young specimens of *Mytilus edulis* were found above high-water neaps, and were sometimes common on *Lichina*, *Gigartina* and *Laminaria*, while *Anomia ephippium* and *Hiatella arctica* were usually both to be found in rather small numbers on the holdfasts of *Laminaria*. The only really numerous bivalve was *Lasaea rubra*, which occurs in such astonishing numbers on *Lichina*.

GASTROPODA. As shown in Table XIX, gastropods were found in every sample except A 5 (*Pelvetia*), and were often numerous especially on *Lichina* and *Ascophyllum*. Below low-water neaps there were *Patina pellucida*, *Gibbula cineraria*, *G. umbilicalis* and the young forms of other species, but for the most part the gastropods consisted of the young of littorinids.

BRYOZOA. 12 species of bryozoa were identified, of which 9 were found only on *Laminaria* holdfasts. The other three species, *Membranipora pilosa*, *Alcyonidium hirsutum* and *Flustrella hispida*, did not occur on any *Laminaria* holdfasts but were all common on *Gigartina*. *Alcyonidium hirsutum* was found only on *Gigartina*, *Membranipora pilosa* was not uncommon on the lowest samples of *Fucus serratus* as well, while *Flustrella hispida* was found twice on *Ascophyllum*, even as high as +0·73 m., or just below high-water neaps; this last species is perhaps confined between tide-marks, but the others are also sublittoral.

TUNICATA. Colonial tunicates are not uncommon on some *Laminaria* holdfasts, though they are by no means present on all of them. Four species were found on one holdfast, and a few very small simple ascidians were sometimes present. The group did not occur elsewhere.

LIST OF SPECIES, FOUND AMONG INTERTIDAL SEAWEEDS, NOT RECORDED IN THE *PLYMOUTH MARINE FAUNA*

The following is a list of those species recorded in this paper whose names are not in the *Plymouth Marine Fauna*, 2nd edition, 1931. This does not imply that they have not already been recorded at Plymouth by other workers since 1931. The number in brackets after each sample number is the number of animals found. A reference to a good description is given for each species.

PORIFERA

Haliclona macandrewii Bowerbank [1866, p. 284].

On *Laminaria*. H6 (4). Dr Burton thinks that this species may be identical with *Chalina cinerea* (Grant) in the *Plymouth Marine Fauna* (1931).

NEMATHELMINTHA

Anticoma limalis Bastian [Stekhoven, 1935].
On *Ascophyllum*. E3 (2). May be numerous.

Leptosomatum sp.
On *Laminaria*. H6. (Immature.)

?Linhomoeus sp.
On *Laminaria*. H3.

Oncholaimus brachycercus de Man [Stekhoven, 1935].
On *Ascophyllum*. E3. May be numerous.

Pontonema (Paroncholaimus) ?ditlevseni de Connick & Stekhoven [Ditlevsen, 1928, p. 224].
On *Fucus serratus*. F3 (immature, numerous).

Symplocostoma longicolle Bastian [Stekhoven, 1935].
On *Ascophyllum*, *Fucus serratus* and *Laminaria*. F3 (few), H6 (1).

Thoracostoma figuratum (Bastian) [Stekhoven, 1935].
On *Ascophyllum* and *Laminaria*. H3, H6.

ANNELIDA

POLYCHAETA

Syllis (Ehlersia) ferrugina Langerhans [Fauvel, 1923, p. 269].
On *Laminaria*. H6 (1).

Eusyllis lamelligera Marion & Bobretsky [Fauvel, 1923, p. 294].
On *Gigartina*. G4 (2).

Exogone brevipes (Claparède) [Fauvel, 1923, p. 306].
On *Laminaria*. H6 (1).

Exogone verrugera (Claparède) [Fauvel, 1923, p. 307].
On *Laminaria*. H2 (1).

Polydora giardi Mesnil [Fauvel, 1927, p. 50].

On *Laminaria*. H3 (399), H4 (20), H6 (53). This appears to be the commonest species of *Polydora* in *Laminaria* holdfasts; the worms bore into the calcareous alga *Lithophyllum incrustans* which cements the holdfast to the rock.

Heterocirrus alatus (Southern) [Fauvel, 1927, p. 99].
On *Laminaria*. H6 (1).

Capitellides giardi Mesnil [Fauvel, 1927, p. 157].
Occasionally common on *Laminaria*. H3 (4), H4 (108).

OLIGOCHAETA

Lumbricillus scoticus Elmhirst & Stephenson [1926, p. 469].

Fairly common on *Ascophyllum*, particularly among tufts of *Polysiphonia*, associated with *Lumbricillus pumilio*. E1, E2, E3 (20), E4 (20), E5 (4), E8 (3), E9 (14), E10 (17), E11 (3), E12 (2).

Lumbricillus pumilio Stephenson [1932, p. 902].

On *Lichina*, and in association with *Lumbricillus scoticus* on *Ascophyllum* and *Polysiphonia*. C1 (27), C2 (8), C3 (7). E1, E2, E3 (45), E4 (26), E5 (4), E6 (17), E7 (1), E8 (7), E9 (10), E10 (6), E11 (19), E12 (40).

CRUSTACEA

COPEPODA

HARPACTICOIDA

Harpacticus uniremis Kröyer [Sars, 1911, v, p. 51].

On *Fucus vesiculosus* and *Ascophyllum*. D1 (2). E5 (16), rather above mean low-water neaps.

Idya ensifera (Fischer) [Sars, 1911, v, p. 90]
On *Laminaria*. H3 (1), H6 (6).

Idya gracilis Scott [Sars, 1911, v, p. 94].
On *Ascophyllum*. E3 (1).

Aspidiscus littoralis G. O. Sars [1911, v, p. 79].

On *Fucus serratus*, *Gigartina* and *Laminaria*. F1 (1), F5 (239), F7 (159), F10 (27). G1 (585), G2 (2), G3 (6), G4 (32). H1 (6), H5 (13). In F5, 26. vii. 30 and F7, 28. viii. 30, four-fifths were young stages. In G1, 26. v. 30, there were also 3930 nauplii of this species and of *Psamathe longicauda*. There were 3 *Aspidiscus littoralis* on frond of *Laminaria*, 5. iv. 39.

Machairopus minutus G. O. Sars [1911, v, p. 86].
On *Fucus vesiculosus*. D1 (17).

Thalestris purpurea G. O. Sars [1911, v, p. 109].
On *Fucus vesiculosus* and *Ascophyllum*. D 1 (2), D 2 (83).

Ameira tenuicornis Scott [Sars, 1911, v, p. 217].
On *Ascophyllum*. E 5 (156).

Laophonte brevirostris (Claus) [Sars, 1911, v, p. 256].
On *Ascophyllum*. E 4 (20).

Laophonte littoralis Scott [Sars, 1911, v, p. 255].
On *Fucus spiralis* and *Ascophyllum*. B 2 (1). E 4 (20). The sample B 2 was just below mean high-water neaps, E 4 just above mean sea-level.

TANAIDACEA

Heterotanais oerstedi Kröyer [Sars, 1899, II, p. 14].
On *Laminaria*. H 3 (4), H 4 (16), H 6 (1).

ISOPODA

Gnathia dentata G. O. Sars [Monod, 1926, p. 516; Sars, 1899, II, p. 54].
On *Laminaria*. H 4 (16). Male, female and young stages all present, 27. viii. 30.

Idotea granulosa Rathke [Collinge, 1917, p. 742; Sars, 1899, II, p. 82].
On *Fucus spiralis*, *F. vesiculosus*, *Ascophyllum*, *Fucus serratus*, *Gigartina* and *Laminaria*. B 1 (1). D 2 (1). E 1 (10), E 2 (10), E 3 (1), E 4 (6), E 6 (1), E 7 (2), E 8 (13), E 9 (54), E 10 (75), E 11 (97), E 12 (10). F 1 (2), F 2 (1), F 3 (6), F 5 (2), F 6 (5), F 7 (1), F 8 (20), F 10 (3). G 1 (56), G 2 (37), G 3 (16), G 4 (9). H 6 (1). This is the only common idoteid living among algae on Church Reef. Its distribution is almost identical with that of *Naesa bidentata*, with the addition of an individual in H 6 from −2·7 m. or below low-water springs. The January samples of *Ascophyllum*, E 9, E 10 and E 11, contained many young forms.

AMPHIPODA

Leucothöe incisa D. Robertson [Chevreux & Fage, 1925, p. 123].
On *Laminaria*. H 6 (2).

Biancolina cuniculus (Stebbing) [Chevreux & Fage, 1925, p. 342].
On *Fucus serratus*. F 1 (1).

ARACHNIDA

ACARINA

Hydrogamasus littoralis (G. and R. Canestrini) [Halbert, 1920, p. 120].
On *Ascophyllum*. E 4, E 5. Not common.

Rhombognathus pascens (Lohmann) [Viets, 1927*a*, p. 106; 1927*b*, p. 11].
Apparently always associated with *R. seahami* (q.v.).

Rhombognathus seahami (Hodge) [Viets, 1927*a*, p. 107; 1927*b*, p. 12].

Apparently always associated with *R. pascens*. These two species are common or abundant in most samples from just above mean sea-level down to low-water springs. They were scarce in *Fucus spiralis* and the three higher samples of *Lichina*, absent from *Pelvetia* and *Laminaria*, common or abundant in *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus* and especially in *Gigartina*; apparently least abundant during the summer but there were 1273 in G2 on 28. viii. 30. C1 (1481). D1 (17), D2 (29), D3 (338). E3 (36), E4 (278), E5 (42), E6 (62), E7 (173), E8 (148), E9 (195), E10 (251), E11 (248), E12 (678). F4 (42), F5 (46), F6 (21), F7 (31), F8 (198), F9 (194), F10 (18). G1 (117), G2 (1273), G3 (422), G4 (1209).

Halacarus basteri (Johnston) [Viets, 1927*b*, p. 18].

On *Fucus serratus* and *Ascophyllum*; not uncommon on the latter, where it appears to make up about one-tenth of the mite population.

INSECTA

DIPTERA (Larvae)

Thalassomyia frauenfeldi Schin. [Chevrel, 1903, as *Scopelodromus isemerinus*, larvae on pp. 16–23. Edwards, 1926, p. 786, considers this to be identical with *Thalassomyia frauenfeldi*.]

Larvae (probably this species) common on *Ascophyllum*, associated with those of *Clunio marinus*.

Geranomyia unicolor Hal.

Larvae common on *Lichina* in January, March and September. C1 (46), C2 (175), C3 (64), C4 (104).

ACKNOWLEDGEMENTS

In a work involving the taxonomy of such diverse groups of animals the list of acknowledgements is bound to be somewhat long. My original optimistic intention was to identify all the animals myself; as far as possible I did so, but with several species discretion had to prevail. I am indebted to the following specialists for their help:

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Mr C. C. A. Monro	(Polychaeta)
The late Dr J. Stephenson	(Oligochaeta)
Mr A. G. Lowndes	(Ostracoda)
Dr R. Gurney	(Copepoda)
Dr I. Gordon	(Crustacea)
Mr J. N. Halbert	(Acarina)
Dr F. W. Edwards	(Diptera)
Mr J. R. le B. Tomlin	(Pelecypoda)
Dr A. B. Hastings	(Bryozoa, Tunicata)
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SUMMARY

This paper gives an account of a survey of the invertebrate populations (omitting Protozoa) of eight species of seaweeds on Church Reef, Wembury Bay, extending over the entire intertidal range.

Above high-water neaps the faunas are poor, except for that in *Lichina pygmaea* which is the richest in individuals on the shore.

Between high-water neaps and low-water springs the most numerous groups are copepods, acarines, young littorinids and (in *Ascophyllum* only) ostracods.

In the holdfasts of *Laminaria digitata* polychaetes are very abundant and make up the majority of the population.

The intertidal faunas are compared with those in the soil on land, and prove to be far more abundant. Even the most plentiful group in the soil, the insects, is rarely as numerous as it is in *Ascophyllum* around mean sea-level.

Altogether 177 species are recorded, of which 35 are not in the *Plymouth Marine Fauna* (1931).

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NOTE

The lengths of whole traverses given in metres in Table I are conversions of the total lengths in feet, and not the sum of the component sections in metres. There is inevitably a slight error involved in converting from one scale to another, and this error may be quite large when accumulated from one section to another.

In the later tables, the total numbers of animals per 100 g. are converted directly from the total numbers per sample, and are therefore not necessarily the same as the sum of the component numbers.

A PRELIMINARY STUDY OF THE ECOLOGY OF A MUD-FLAT

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(Text-figs. 1–4)

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INTRODUCTION

In addition to a plankton investigation in the Cardiff area (Rees, 1939) an ecological investigation of a mud-flat was begun. Owing to certain circumstances the work was abruptly terminated, thus restricting the scope and intensity of the work, but as it touches upon certain sections of the Tamar survey (Hartley & Spooner, 1938), now in progress, it appears desirable to present the available data, however restricted, from another area for comparative purposes. This report is limited to the period August and the beginning of September 1937. Winter work on the lines performed in this period would be impracticable owing to the softness of the mud in the upper levels for, even in the summer, it was not unusual to sink to one's knees in unexpected patches.

Ten stations, from high water to low water, were taken along a traverse at a position shown in Fig. 1. This position may profitably be compared with that of the plankton station by referring to Fig. 1 in Rees (1939). The sewage outfall about 150 m. down-channel from the traverse is also noted as it appears to have an important influence on the fauna. The tidal levels above Ordnance Datum have been calculated, and the distance between adjacent stations measured (Table I). The values for the tidal levels are, of necessity, quite approximate and are calculated on the basis of a spring rise of 11·50 m. and a neap rise of 8·46 m. These are the values at Cardiff, which is not a standard port, and no allowance has been made for the higher values occurring at the mud-flat. The vertically exaggerated cross-section of the traverse, shown in Fig. 2, is derived from Table I.

TABLE I. DATA RELATING TO THE STATIONS

All the values are given in metres.

Station	1	2	3	4	5	6	7	8	9	10
Tidal level	10·97	10·67	10·21	9·90	9·45	8·08	5·79	3·81	1·07	0
Distance from preceding station		170	90	120	84	120	110	90	160	200

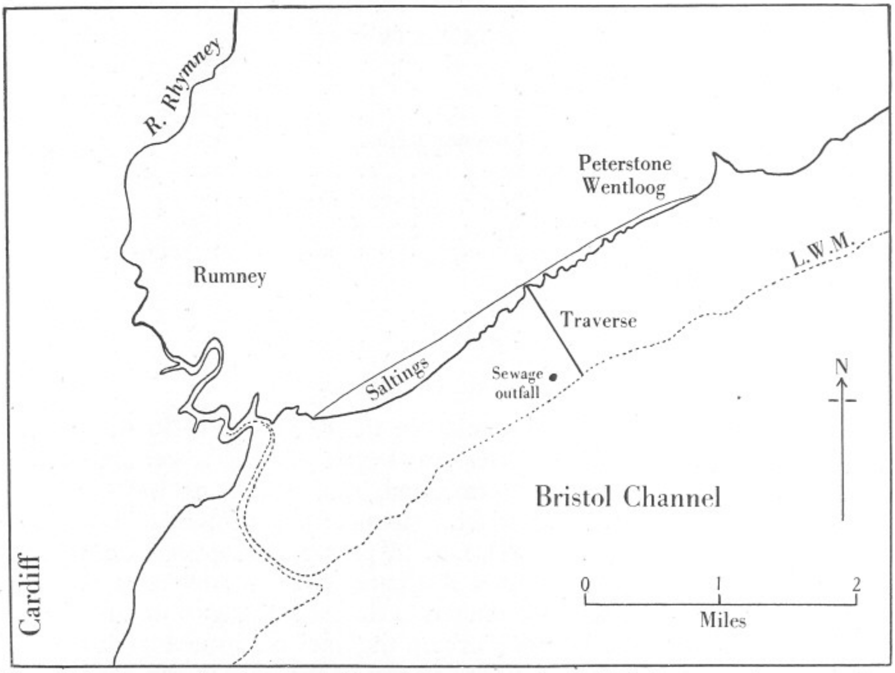

Fig. 1. Sketch-map showing the position of the traverse along which the ten stations were taken.

On the coast side the flat is terminated by saltings about 5 ft. in height with the top 1½–2 ft. humified and containing a large number of *Scrobicularia plana* shells. Beneath this humified layer hard clay extends to the flat level. Numbers of dead *Scrobicularia* occur along the fringe of the flat.

St. 1, placed about 130 m. from the fringe, was situated in a hard deposit, which, during the summer, became dry and tessellated at the neap-tide period. A little way beyond St. 1 *Salicornia dolichostachys** formed a zone stretching in the direction of the traverse for about 200 m. with St. 2 situated in a mud patch in the middle of this zone. The deposit at this station was also fairly hard but, though uncovered at neap tide, was never seen as dry and tessellated.

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* I am obliged to Prof. R. C. McLean for this identification.

St. 3 was just outside the *Salicornia* zone and the following stations up to St. 6 had an increasingly softer, grey deposit with St. 5 in the softest area. At St. 6 the deposit was firmer and at St. 7, at mid-water mark, the change from the loose grey deposit of the higher levels to the hard, yellowish deposit of the lower levels was clearly marked. At the remaining stations the deposit was hard and yellow, and the surface, in contrast to the smooth surface of the grey deposit, rough.

The extent and development of black mud followed the same sequence, the mud being quite black and beginning near the surface at Sts. 2–6, and then becoming greyer and more deeply placed at the following stations.

A brown diatom scum developed on the surface in the summer months. This was mainly, if not wholly, confined to the region of St. 1 during the spring-tide period when the deposit was moist, its restriction in area being probably due to the greater stability of the mud here.

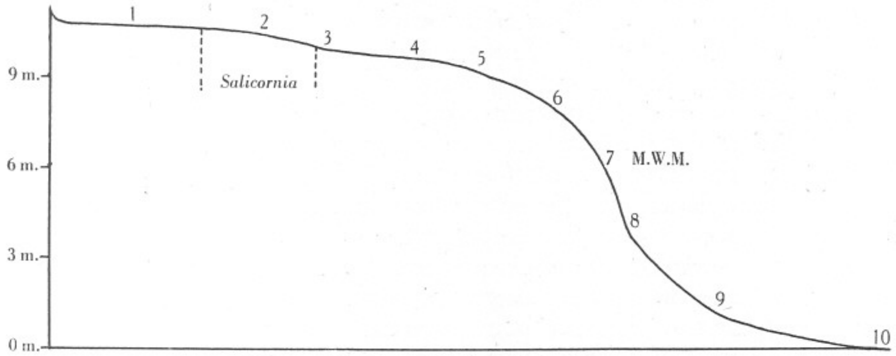

Fig. 2. The cross-section of the traverse.

Information given by an intelligent workman, who laid the sewage pipes, points to a series of humified layers at various depths. This has not been personally investigated, but from the measurements given by him it seems probable that the uppermost layer extends to the edge of the *Salicornia* zone. The second layer would appear to extend to the neighbourhood of St. 6 and the third layer between Sts. 6 and 7. All these layers extend inland for a considerable distance. The form of the traverse (Fig. 2) may be partly accounted for by these layers and partly by the action of the strong tidal stream. One small point of interest is a slight increase in gradient between Sts. 2 and 3 due to the effect of the *Salicornia* in raising the level of the flat.

The flat is broken up by a series of deep runnels directed seawards and into these run a number of smaller subsidiary runnels. The upper edges of the deep runnels are generally raised slightly above the mud-flat level and in many places are bound by a growth of *Vaucheria*.

The erosion of the saltings and the encroachment of the mud-flat inland takes place irregularly along the coast, but there is good evidence for believing that in places the rate is over 1 ft. per year.

METHODS

Four samples were brought back to the laboratory from each station.

(*a*) The sample required for the analysis of the macrofauna consisted of the mud within an area of $\frac{1}{16}$ sq. m. and a depth of 18 cm. In the laboratory this sample was sieved and the animals removed, identified, and counted.

Owing to the clayey character of the samples, sieving presented some difficulty. A sheet of copper gauze about 1 ft. square and with perforations of approximately 0·2 mm. was bent into a hemispherical form and slung by its corners under a water tap to which was attached a piece of rubber tubing. This tubing served to decrease the exit opening and so increased the water pressure over unit area, and by its manipulation the stream of water could be directed on any part of the gauze. A handful of the mud was placed on the gauze and the tap turned full on. Practically all the mud could be removed.

When a large number of *Hydrobia ulvae* was present the fraction of the whole sample which had not passed through the gauze was resieved through sieves with perforations of 0·5 and 1·0 mm. diameter. This process made the separation of *Hydrobia* from other material considerably easier.

(*b*) A brass tube, open at both ends, was forced vertically into the mud, removed with a column of mud inside, and corked at both ends. In the laboratory this column was forced out from the bottom and 1 cm. blocks cut off from the surface downwards. Each block was made into a suspension with a little sea water, the suspension placed in portions on a marked slide, and the animals counted as quickly as possible. This was made all the easier by the movements of the nematodes and oligochaetes. Some of the copepods and other forms were counted 2 or 3 times in the process but as each, when moving in the suspension, left a track behind them, correction was easily made. When the number of animals in a group, particularly the nematodes, was high, a $\frac{1}{2}$ or $\frac{1}{4}$ portion of the suspension was used in counting these and the group neglected in the remainder of the sample, the number obtained being increased by a factor.

The same tube was used for all stations. It had an internal diameter of 1·8 cm. giving an area of 2·546 sq. cm.

(*c*) A similar sample to (*b*) was cut into 2 cm. blocks, a total of 5 blocks being obtained for each sample. Each block was weighed wet, dried at 105° C., and reweighed dry. From the weights the percentage weight of water in the wet mud was obtained.

(*d*) A third brass tube was used to obtain material for mechanical analysis and the top 3 cm. of mud, in which the microfauna mainly lived, was dried and analysed at leisure.

The method adopted for grade analysis was experimental. The results have proved unsatisfactory and it is unfortunate that, as analysis was performed after I had left the district, the samples have proved irreplaceable. The method of soil analysis as agreed upon by the International Society of Soil Science

(1930), using the Atterburg scale, was adopted. This scale recognizes the following fractions.

(1) Stones (over 2·0 mm.).
(2) Coarse sand (2·0–0·2 mm.).
(3) Fine sand (0·2–0·02 mm.).
(4) Silt (0·02–0·002 mm.).
(5) Clay (less than 0·002 mm.).

In analysis the organic matter in the mud was first oxidized by H_2O_2, afterwards treated with HCl, and thoroughly washed with distilled water. The material was then stirred with 10 % ammonia and made up to the 10 cm. mark with distilled water. The liquid was poured off from the sedimented material after 8 hr. The material still suspended in the liquid consisted of the clay fraction. This process was repeated until all the clay was removed, the bulk of liquid obtained then evaporated to dryness at 105° C., and the clay fraction weighed dry. The residue was again made up to 10 cm. with distilled water and poured off after 4 min. 48 sec. Repetition of this process brought out the whole of the silt fraction which was filtered off, dried and weighed. The residue consisted of fine sand—there being no coarse sand fraction. Each fraction was rigidly examined microscopically before being passed as the material dealt with by this method was of an unusual nature.

Sea-water samples were analysed for salinity by titration with silver nitrate, and for *p*H by Maclendon's method with cresol red as indicator.

Some Chemical and Physical Factors

The sea water. No series of water samples have been taken through the year but sufficient have been analysed to show that the salinity was about 3 °/₀₀ less than at the plankton station for which a series of readings are available (Rees, 1939). The salinity during the period of work reported here varied from 24·5 °/₀₀ at the beginning to 25·5 °/₀₀ at the end but earlier in the year the monthly average salinity had been less than 20 °/₀₀.

As a general rule there was very little change in salinity between high and low water. The amount depended on the height of the tide, i.e. on the amount of movement of the water mass further out in the channel. On occasions when the height of the tide was low no salinity change occurred with the state of the tide, but with high spring tides there was a difference of about 1 °/₀₀.

The *p*H was high and varied about *p*H 8·00 during this period.

Water content of mud. Table II gives the percentage of water in the wet mud at different levels for each station.

The water content of the mud is dependent on at least three factors, (*a*) period of exposure between tides, (*b*) the distribution of particle size and (*c*) the efficiency in packing.

Interpretation of the values in Table II is complicated by the fact that the samples were not taken at the same time but each was taken when that particular station was visited. Climatic conditions between the visits therefore affects the sequence but the deeper sections are less affected by these conditions than are the surface ones.

If particle size and efficiency in packing were constant over the area then the water content would increase towards low water, with the maximum content at St. 10. This is not so. From 0 to 4 cm. the maximum content occurred at St. 5 and from 6 to 10 cm. at St. 6. It has already been mentioned that the texture and colour of the mud changed from a loose, grey deposit at the upper stations to a hard, yellowish deposit at the lower stations. At the least there is a change in the efficiency in packing and it is probably this that counteracts, to some extent, the tendency towards increase in water content at the low-water stations.

TABLE II. PERCENTAGE WATER CONTENT OF THE MUD

Stations ...	1	2	3	4	5	6	7	8	9	10
0–2 cm.	37·8	44·9	50·6	49·1	**63·8**	52·6	56·3	52·6	44·4	47·6
2–4 cm.	29·4	36·6	41·0	41·1	**55·8**	42·8	52·0	46·0	38·1	41·5
4–6 cm.	30·5	34·2	38·2	36·8	42·1	37·8	46·3	**47·0**	39·0	42·9
6–8 cm.	28·8	35·9	38·4	41·6	43·5	**44·4**	43·2	42·3	43·5	44·1
8–10 cm.	32·8	34·9	37·4	37·6	43·3	**43·6**	37·5	42·4	38·3	42·3

Grade analysis. The available results are given in Table III and there is here shown a tendency towards an increase in clay content towards low water. This agrees with the appearance of the samples and is not inconsistent with the water content, if this is due, as suggested, to a greater efficiency in packing.

TABLE III. GRADE ANALYSIS OF THE SURFACE MUD

Values given as percentages by weight.

Station	Clay	Silt	Fine sand	Loss in weight
1	22·4	34·9	27·0	15·7
3	17·8	50·3	13·1	18·8
5	28·0	46·5	9·4	16·1
6	30·5	34·5	14·2	20·9
7	33·1	31·3	17·6	18·0

It is noticeable that there was a considerable loss in weight. This was especially due to the treatment of the sample with H_2O_2, HCl and water. The sea salt in the dry sample was washed away by the distilled water. This accounts for a loss of about 2 %, and with the other reagents there was a loss of organic matter, calcium ion, carbonate ion, mixed sesquioxides of iron, and some silica. Dr Gregg, who kindly analysed one sample, estimated a loss of 4–5 % of iron and a rather lesser value for silica. Incineration of a sample gave a loss of 12 % which may be taken as an estimate of organic matter although this value includes the additional loss of carbonate and the constitutional water of the clay (this water is included in the dry weight of mud). These figures for loss of constituents must be taken with reserve as they serve merely as indications.

MUD-DWELLING SPECIES

Reference is made in this section only to those forms which may be regarded as living in the mud during the intertidal period. *Hydrobia ulvae* is included since a large proportion of the individuals was found below the immediate surface of the mud. The fauna is divided into macrofauna and microfauna purely on the basis of the method of quantitative analysis employed in their estimation.

MACROFAUNA

Nereis diversicolor O.F.M.
Nereis succinea (Leuckart)
Nephthys sp.
Diastylis rathkei Kröyer
Sphaeroma rugicauda Leach
Corophium volutator Pallas
Hydrobia ulvae Pennant
Macoma balthica (L.)
Scrobicularia plana (da Costa)
Muscid larvae*
Tipulid larvae*

MICROFAUNA

Polydora ciliata (Johnston)
Other polychaetes
Stenhelia palustris (Brady)
Nannopus palustris Brady
Platychelipus littoralis Brady
Leptocythere castanea (G. O. Sars)
Nematodes
Oligochaetes
Nemertines
Insect larvae
Foraminifera
Nauplii

* These were identified with reservations by Dr F. W. Edwards to whom I am obliged.

The Macrofauna

In Table IV are given the numbers, to the nearest 10 or 100, of the animals per sq. m. at each station. Only three species were of importance, these being *Nereis diversicolor*, *Hydrobia ulvae* and *Macoma balthica*. The zonation of these species is given in Fig. 3 in which the stations are placed according to their distances from one another and not according to tidal level.

TABLE IV. NUMBERS PER SQUARE METRE OF THE MACROFAUNA

Station...	1	2	3	4	5	6	7	8	9	10
Nereis diversicolor	240	600	2000	1700	800	1100	720	260	30	..
Nereis succinea	..	..	..	..	..	..	..	..	..	+
Nephthys sp.	..	..	..	..	..	..	..	..	..	+
Diastylis rathkei	..	..	..	..	..	..	..	..	..	10
Sphaeroma rugicauda	..	..	..	..	..	..	..	..	+	..
Corophium volutator	..	..	..	..	..	..	..	..	..	2400
Hydrobia ulvae	..	1200	2500	1100	2600	1200	5600	10,100	18,100	50
Macoma balthica	..	..	320	140	290	500	800	500	690	190
Scrobicularia plana	..	..	..	+	..	..	..	..	..	..

Nereis diversicolor. This species was especially abundant, the highest number of 2000 per sq. m. being obtained at St. 3. It extended down to St. 9, a level lower than it generally extends elsewhere. For comparison the numbers obtained by Nicol (1935) at the Aberlady salt-marsh may be used. The average of five pools gives the equivalent of 330 per sq. m. and in one exceptional pool, not in the five, she found the equivalent of 96,000 young *Nereis* per sq. m. The numbers obtained in the present mud-flat were, however, consistently high.

An analysis showed that the intestines were empty in the large majority of specimens, and that mud was to be found in the remainder. It is generally agreed (Hunt, 1925) that a high frequency of empty intestines indicates a mainly carnivorous diet. This result agrees with Thamdrup (1935) who places

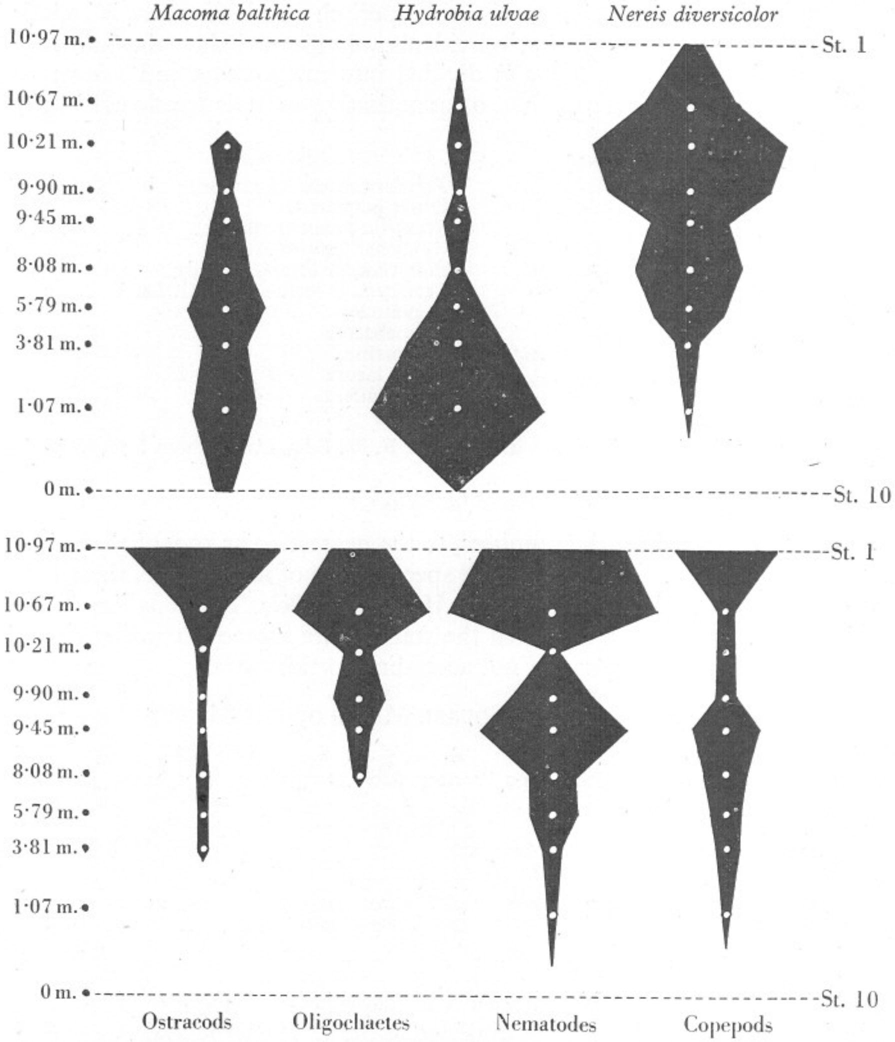

Fig. 3. The distribution of some of the macrofauna species and microfauna groups. The stations are plotted according to their distances from one another and not according to the tidal levels which are otherwise indicated in the figure.

Nereis diversicolor as a transition between the general deposit feeders and those that select organisms, either plant or animal.

Hydrobia ulvae. The numbers are, again, very high but the greater frequency of this species towards low water is of some interest. Wohlenberg (1937) found it mainly in the upper third of the beach and this is its more general distribution. This feature is probably largely dependent on the nature of the substratum, for Nicol (1935) found it occurring in pools with a firm substratum, while in pools with the mud in a semi-liquid condition—an extreme form of the soft mud in the upper levels of the present mud-flat—only a few specimens were found. Further, Fraser (1932) found it fairly thickly over parts of "thick mud" while it appeared to be absent on "thin mud".

As to numbers comparison may again be made with Nicol (1935). In sandy pools 6400 per sq. m. were found, and on bare mud a number, presumably exceptional, of 32,500 per sq. m.

Macoma balthica. Like *Hydrobia* this species also occurred with greatest frequency below mid-water mark, unlike the results of Stephen (1929) who generally found *Macoma* in the upper half of the beach. Stephen (1931) considers 150–200 per sq. m. in the muddy sand at Aberlady as relatively abundant and Petersen (1918) gives 20 per sq. m. as typical of a *Macoma* community. Fraser (1932), on the other hand, found 6000 per sq. m. in "thick mud" at Dingle Beach and none in the "thin mud". The "thick mud" of Dingle Beach agrees with the deposit in the lower levels of the present area only in firmness and stability. The "thick mud" consists of considerably coarser particles. Bassindale (1938) states that *Macoma* does not tolerate soft mud or clayey mud in the Mersey estuary. The clayey mud in the lower levels of this flat appears to be quite favourable to *Macoma* and possibly more favourable than the soft mud.

A number of specimens were below 0·3 cm. in length (spat), and the average was about 0·5 cm.

Corophium volutator. An unusual distribution appeared for this species. While it was observed in very small numbers in the runnels of the *Salicornia* zone and near St. 5, it was obtained in large numbers only at St. 10. This station was rarely visited and no note on the persistence of the species can be given, though there is good reason to believe that its appearance was only temporary. Sars (1894) dredged it from a depth of 5 fm. in the Christiania Fjord, and Wohlenberg (1937) found it distributed towards low water under certain conditions, but usually found it, as it occurs elsewhere, towards high water.

The absence of *Corophium* in the higher levels may be due to the high organic content as indicated by the black mud (Hart, 1930).

Scrobicularia plana. In spite of the number of shells at the edge of the flat only a single specimen was obtained. This does not necessarily mean that the species has virtually died out as it is possible that the samples were not taken from a sufficient depth.

The Microfauna

Attention was particularly directed in this section to the quantitative work and the systematic aspect was only briefly considered. Furthermore, all the microfauna groups were not dealt with and such forms as the Infusoria and flagellates were neglected. The results are given in Table V as the numbers in the various groups at each station in each 1 cm. layer with an area of 10 sq. cm., the numbers being given to the nearest 10 or 100.

TABLE V. OCCURRENCE OF THE MICROFAUNA AT THE STATIONS

Numbers given for an area of 10 sq. cm.

Station ...	... ...	1	2	3	4	5	6	7	8	9	10
Copepods	0–1 cm.	500	50	90	110	310	240	160	140	50	..
	1–2 cm.	..	30	..	..	30	..	..	..	..	..
	2–3 cm.	..	..	..	..	+	..	..	..	..	..
Total		500	80	90	110	340	240	160	140	50	..
Nematodes	0–1 cm.	7300	7900	770	4100	6700	1600	2200	970	270	70
	1–2 cm.	530	1600	160	40	660	80	120	110	60	..
	2–3 cm.	50	440	..	..	160	..	..	..	..	..
	3–4 cm.	..	480	..	..	..	..	..	..	..	..
	4–5 cm.	..	20	..	..	..	..	..	..	..	..
Total		7880	10,440	930	4140	7520	1680	2320	1080	330	70
Oligochaetes	0–1 cm.	120	460	80	220	60	50	..	..	..	..
	1–2 cm.	80	220	70	60	30	20	..	..	..	..
	2–3 cm.	120	50	..	?	10	..	..	..	..	..
	3–4 cm.	..	50	..	..	..	..	..	..	..	..
Total		320	780	150	280	100	70	..	..	..	..
Ostracods	0–1 cm.	740	240	60	30	30	60	20	30	..	..
	1–2 cm.	50	..	10	..	..	..	+	..	..	..
	2–3 cm.	..	..	..	..	..	..	..	..	..	..
	3–4 cm.	..	+	..	..	..	..	..	..	..	..
	4–5 cm.	..	+	..	..	..	..	..	..	..	..
Total		790	240	70	30	30	60	20	30	..	..
Foraminifera	0–1 cm.	50	20	..	..	..	..	+	..	+	..
	1–2 cm.	140	30	..	..	..	..	..	..	..	..
	2–3 cm.	90	+	..	..	..	..	..	..	..	..
	3–4 cm.	..	..	..	..	..	..	..	..	..	..
	4–5 cm.	..	20	..	..	..	..	..	..	..	..
Total		280	70	..	..	..	..	+	..	+	..
Nauplii	0–1 cm.	410	80	..	..	..	80	..	..	..	..
	1–2 cm.	10	..	..	..	..	..	..	..	..	..
Total		420	80	..	..	..	80	..	..	..	..
Polychaetes	0–1 cm.	..	50	..	..	..	..	..	..	240	20
	1–2 cm.	..	30	..	..	..	..	..	..	..	..
	2–3 cm.	..	50	..	..	..	..	..	..	..	..
	3–4 cm.	..	+	..	..	..	..	..	..	..	..
Total		..	130	..	..	..	..	..	..	240	20
Nemertines	0–1 cm.	..	..	..	+	..	..	30	+	+	..
Rotifers	0–1 cm.	..	..	..	..	..	60	..	..	..	..
Insect larvae	0–1 cm.	..	..	10	..	..	..	..	..	..	..

In order to assess the density of the organisms comparison is made in Table VI between the numbers obtained by Moore (1931) at the Loch Head station, this being his richest station, and the highest numbers from the present area, both sets being equivalent to an area of 100 sq. cm.

TABLE VI. COMPARISON OF NUMBERS IN DIFFERENT AREAS

Numbers refer to surface area of 100 sq. cm.

	Nematodes	Polychaetes	Ostracods	Copepods
Loch Head	2515	34	125	697
Bristol Channel	104,000	2400	7900	5000

The values for the Bristol Channel reveal an abundant microfauna. Nematodes, present to the extent of over 10 million per sq. m. at St. 2, were always dominant numerically but were not always so by volume. A rough calculation gives the volume of nematodes in the top cm. layer at St. 2 as 0·3 % and of oligochaetes nearly 0·5 %. An estimate of 1 % by volume of living organisms in the particular layer would be a reasonable approximation.

It is clear from Table V that the main mass of the fauna was in the surface layer, and that numbers decreased towards the lower levels until there were very few specimens at a depth of 3–4 cm.

Fig. 3 also gives the horizontal distribution of some of the microfauna groups and shows that the highest numbers were present in the upper part of the intertidal zone. Copepods and ostracods were present in highest numbers at St. 1. This sample was taken during the spring-tide period when the deposit was moist, but the presence of such numbers at a position which becomes arid for several days is a matter of considerable interest.

Note may be made of some systematic results. *Leptocythere castanea* appeared to be the only ostracod present. There were at least two species of oligochaetes, one of which appeared to select diatoms for food while the other contained mud in its intestines, and two species of nematodes. I am unable to say what polychaete species was present at the low-water stations, but *Polydora ciliata* was present at St. 2. The three species of copepods are of interest in that, though belonging to different families, they agree in having natatory first legs, relatively small fifth legs, and a strong development of spines. The data do not reveal an obvious differential zoning of these three species.

OTHER SPECIES

In the *Salicornia* zone there is a pile of stones poorly covered by a growth of *Ascophyllum nodosum*. Here were found *Carcinus maenas*, *Sphaeroma rugicauda*, *Clitellio arenarius*, *Lineus* sp., *Membranipora* sp., and mites. On one of the stones, usually covered by the water in a deep runnel, occurred a pile-like mass of the diatom *Melosira Borreri* amongst which was *Obelia dichotoma* bearing another diatom, *Lycmophora Lyngbyi*, and *Zoothamnion* sp.

Some of the stones near low water supported *Diadume luciae* and *Balanus improvisus*. *B. improvisus* and *Obelia dichotoma* were found on the piles towards low water.

Underneath the *Vaucheria*, on a bed of black, humified mud, were found enormous numbers, considering the available space, of the spring-tail *Archistoma besselsi*.* These insects occasionally spread out over the water in the runnels.

Crangon vulgaris was sometimes common in the runnels and *Tachidius discipes* was found here though not in the mud.

DISCUSSION

Until the Tamar survey (Hartley & Spooner, 1938) results are available it would be premature to do more than define some of the environmental factors which appear to be of importance.

There are several indications that the traverse crossed two very different areas. The intermediate zone between these is comparatively narrow and may be taken as occurring about St. 6. Above the station the deposit is loose and the gradient low, below the station the deposit is hard and clayey and the gradient steeper. This difference is due to the fact that the sources of the deposits are entirely different. In the higher levels the deposit was, and is, derived by sedimentation from the overlying sea water at high tide, while in the lower levels the speed of the tidal stream (see Rees, 1939) prevents any sedimentation, or at least any deposition is purely temporary and is removed when the stream starts again. The tidal streams exert a scouring action on what was previously a land deposit so that the clay bed is exposed and partially removed.

The gradient, as shown in Fig. 2, is essentially of the form to be expected from the action of the tidal streams, which decrease in speed as the coast-line is reached, and from the previous history of the area as revealed by the humified layers at different depths.

The absence of a marked difference between the salinities at high and low water indicates that the salinity is not such as to differentiate the area into salinity zones. While there is no such effective difference it is of considerable importance that the salinity changes in the course of the year. During the period of investigation more particularly referred to in this report the salinity was about 25 °/₀₀ but in the period January–March was below 20 °/₀₀.

Another factor, which is common to all intertidal areas, refers to the periods of exposure between tides at different tidal levels, leading to a zonation in the fauna.

While it has not been fully substantiated by direct observation it can be assumed that the diatom content of the mud is greatest in the higher levels and is probably very low towards low water. Opacity of the sea water prevents

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* I am indebted to Mr J. M. Brown for this identification.

any considerable photosynthesis when the mud is covered by a deep layer of water. Diatoms must photosynthesize far more effectively in the upper levels where such a deep layer of water does not occur. In view of the importance of the diatom supply as a source of food this factor acquires some importance.

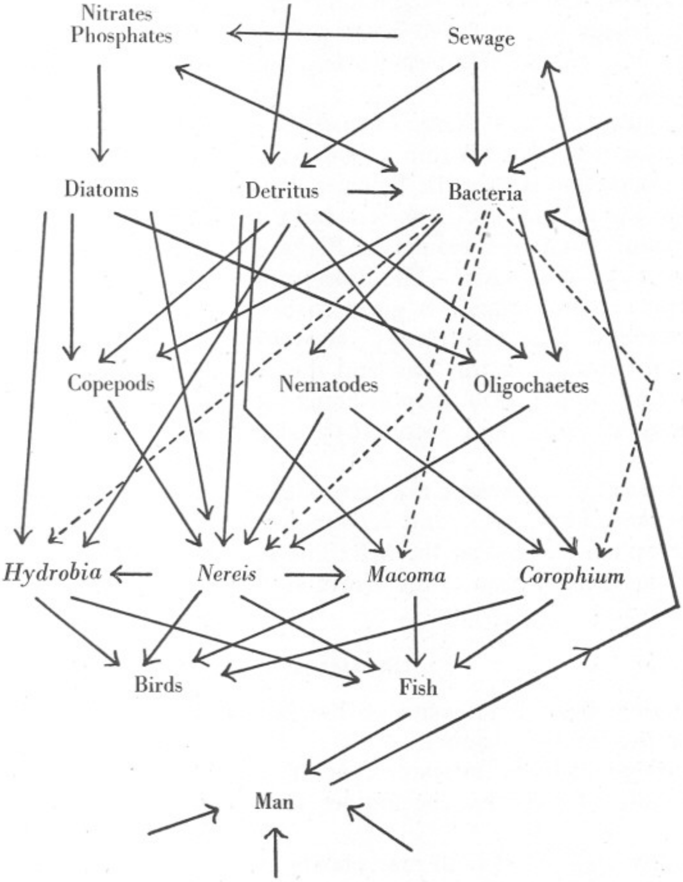

Fig. 4. The simplified food cycle in the mud-flat.

The organic content, derived partly from the decay of the *Salicornia* and partly by sedimentation out of the sea water, must also be greater in the upper levels.

Of considerable importance is the proximity of the sewage outfall from which is derived, directly and indirectly, a constant and rich supply of organic matter, bacteria, phosphates and nitrates.

A striking feature is the inverse relationship between the numbers of *Nereis diversicolor* and some of the microfauna groups (Fig. 3). At Sts. 1 and 2 *Nereis* was comparatively low and the numbers of copepods, nematodes, oligochaetes and ostracods high. At St. 3, where *Nereis* reached its maximum number, these microfauna groups were much decreased. *Nereis* decreased to St. 5 and copepods and nematodes increased (oligochaetes increased to St. 4); then, with an increase in *Nereis* at St. 6, there was a decrease in the two microfauna groups. While it cannot be insisted upon there is a strong suggestion that these microfauna groups are controlled by the predatory effects of *Nereis diversicolor*, which may also control *Macoma balthica* and *Hydrobia ulvae* through their young stages.

It is of course clear that *Nereis diversicolor* has an effect of ecological value simply because it is placed within a food cycle. As the food cycle is the main biological interaction within the fauna, a simplified form for the mud-flat is presented in Fig. 4. This cycle has been built up partly from personal observation but mainly from the results of Blegvad (1914), Rauschenplat (1901), Thamdrup (1935) and others. The linkages for *Corophium* are derived from Hart (1930), and importance is given to bacteria in view of the results of MacGinitie (1935). Thamdrup (1935) states that *Hydrobia ulvae* feeds on green algae. Its distribution in this area and the probable distribution of diatoms introduces some doubt as to diatoms being the sole, or even the main, source of food. Blegvad (1914) and Nicol (1935) place it among the detritus eaters.

I take pleasure in expressing my gratitude to Prof. W. M. Tattersall, under whom I worked, for his help and encouragement, and I am, also, obliged to Dr A. C. Stephen for reading the MS. The field work was done while I held a Postgraduate Studentship of the University of Wales.

SUMMARY

Ten stations, from high water to low water, were investigated along a mud-flat in the Bristol Channel.

The mud was analysed for water content and grade. The values suggested, with other observations, that the stations were distributed over two different areas.

Quantitative analysis of both macrofauna and microfauna revealed a dense mud population.

The operative ecological factors, including the food cycle, are defined.

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OBSERVATIONS ON THE ORIGIN AND FATE OF FLAGELLATED GAMETES IN MULTIPLE TESTS OF *DISCORBIS* (FORAMINIFERA)

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(Plates I–III)

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INTRODUCTION

If one were to select three multiple tests of a *Discorbis* species of Foraminifera from material recently removed from a tide pool, and these groups, consisting of two or more individuals, were crushed in a drop of sea water under a cover-glass, one would probably liberate a small cloud of minute flagellated organisms. Swarmers produced by a group of Foraminifera so associated are the gametes of the species.

A demonstration based on incontrovertible evidence of the occurrence of flagellated gametes in the Foraminifera is important, first, because the small diameter of the amoebula that would result from the union of the gametes in sexual reproduction has been used to explain the small size of the proloculum or initial chamber of microspheric tests, compared with that of the cytologically proven megalospheric generation (Lister, 1895, p. 444) and, secondly, these flagellated gametes might provide a brief pelagic phase that could assure a wide dispersal of reproductive bodies, and account in part for the geographic distribution of species (Vaughan, 1933, pp. 925–9). Perhaps the greatest value to be derived from a satisfactory solution of this problem would be to divert the attention of the biologist interested in the Foraminifera, from taxonomy, and the laborious task of proving or disproving dogmas which are inherent in the study of life-cycles, to problems of ecology, for it is only through knowledge of those factors which contribute to the success of species in recent oceans that we may hope to interpret biotic conditions in oceans of geologic horizons. Significant contributions in which the Foraminifera have been used as guides in this manner have been largely the work of geologists.

HISTORICAL

The possible occurrence of flagellated gametes in the Foraminifera was first discussed by Strethill Wright (1861), after he had observed spermatozoa-like organisms in *Gromia*. J. J. Lister (1895) first explained that where two distinct types of tests occurred within a recognized species, this dimorphism was the result of an alternation of generations, and the gametes were probably flagellated. The so-called gametes of *Polystomella crispa* Linn. (*Elphidium*) were observed in organisms less than half-grown, and Lister recognized that the cytological evidence of their origin was problematical. Later attempts to substantiate these findings have with few exceptions resulted in the description of flagellated organisms, presumably gametes, which might with equal conviction have been described as saprophytes, parasites, or commensals. In *Patellina corrugata* Williamson (Myers, 1935) and *Spirillina vivipara* Ehrenberg (Myers, 1936) the gametes were found to be amoebulae, not flagellated. In these two species it was demonstrated for the first time in the life cycle of a foraminiferan that all nuclei were the result of mitotic division and it seemed likely that the nuclei of all Foraminifera had a similar origin. Føyn (1936*a*), working on *Myxotheca areniliga* Schaudinn, and Calvez (1938) on *Iridia lucida* nov.sp. have since proposed life cycles in which the small nuclei of the gametes were the result of mitotic division. Except for a difference in the number of chromosomes represented there is a remarkable similarity in composition of stages illustrated in these two papers. Both authors have figured flagellated gametes in several species, but the only description of the development of a foraminiferan from flagellated gametes was that by Schaudinn (1903), which immediately followed a paper by Lister

(1903) in which it was stated that although the life cycle of *Polystomella crispa* was generally accepted, the nature and fate of the "zoospore" had not been determined. Reproduction of Foraminifera that had previously associated in groups of two or more was reported by Schaudinn (1895) in *Discorbina globularis* d'Orbigny(?). Since he did not observe the gametes or the union of nuclei he presumed that this was a modified method of asexual reproduction. Had Schaudinn crushed several of these multiple tests, he undoubtedly would have found that about one group in three contained flagellated organisms, the gametes of the species. In a brief account of reproductive activities in groups of Foraminifera similarly associated, Myers (1933) described and gave photographic evidence of the occurrence of triflagellated organisms in *Discorbis patelliformis* Brady. Two-chambered young were also observed in multiple tests of the same species, but no cytological evidence as to the origin or fate of the flagellated gametes was given. The present paper demonstrates a genetic continuity of stages, through nuclear division, in the life cycle of several species of *Discorbis* in which the gametes are flagellated.

Groups of two or more free-living Foraminifera so associated that the several tests are contained within a common cyst, or are held together by animal cement, have been variously explained. Schaudinn (1895) presumed that such an association resulted in a modified method of asexual reproduction, as was stated above, and to which he applied the term "plastogamy". Rhumbler (1913) referred to a similar observation as "cytogamy", and Heron-Allen (1915) suggested that these associated groups of tests were the result of reproduction by "budding". Since "plastogamy", "cytogamy", and "budding" in the sense that these terms were first applied to the Foraminifera do not suggest the sexual processes which occur within these groups of tests, we have applied the protozoological term "syzygy" to this method of sexual reproduction, and "multiple tests" to groups of two or more Foraminifera so associated (Myers, 1933 & 1935).

Material

Multiple tests of several species of *Discorbis*, collected from tide pools during seven successive seasons, have yielded flagellated gametes and developmental stages of sexually produced young. In southern California *Discorbis patelliformis* Brady, and *D. pulvinata* Brady were common. From Monterey Bay north to San Francisco, *D. ornatissima* Cushman, and *D. opercularis* d'Orbigny occurred, the latter being especially abundant, and at Plymouth, England, *D. parisiensis* d'Orbigny was found.

D. patelliformis is a small, free, shallow-water representative of a numerous and widely distributed genus (Pl. I, figs. 1–3; Pl. II, figs. 9–11). The test is smooth and conical, consisting of two or three convolutions of long narrow chambers. On the superior surface the chambers are marked by broad smooth lines, and perforated by depressed pseudopodial pores. The inferior surface is ornamented by radiating riblets provided with low tubercules which become short spines near the umbilicus. The subacute margin of the steeply sloping wall shows a clear line of shell substance which becomes increasingly thickened after the addition of each newly formed chamber. Although *D. patelliformis* is a dimorphic species, the average diameter of the microspheric and megalospheric proloculum or initial chamber does not vary appreciably, the only means of distinguishing the two types of tests being the direction of rotation of the series of chambers. Dimorphism in the Foraminifera is the result of an alternation of generations. In most species the sexually produced microspheric generation has a smaller initial chamber, a greater maximum size, and is multinucleate; while the asexually produced megalospheric generation shows a smaller growth limit, a larger initial chamber, and rarely more than one nucleus. Except for the size of the initial chamber the above characteristics hold for *D. patelliformis*, as evidenced from stained total mounts and several hundred tests removed from cultures immediately following either sexual or asexual reproduction; which left no doubt as to the accuracy of the observation that in this species the direction of rotation in the megalospheric test is sinistral, the microspheric dextral. A reversal in the direction of rotation of megalospheric and microspheric tests of other species studied show numerous exceptions to this rule. In *D. patelliformis* no evidence in support of the theory of trimorphism was observed, either in the tests, or in a deviation from the normal method of sexual reproduction by megalospheric organisms. The ratio of microspheric to megalospheric individuals of this species in the sea during the month of July is about two to one.

D. opercularis is somewhat larger, and more depressed than *D. patelliformis*, the superior surface being more convex than conical. The lines marking the chambers are wider and free from pseudopodial pores, and the surface of the chambers is smooth. The inferior surface is flattened and ornamented by more widely spaced riblets and tubercules. The outer walls of earlier formed chambers are laminated, the clear shell substance along the acute margin of the test showing a graded increase in thickness beginning with the thin-walled terminal or final chamber. In life *D. opercularis* is yellowish pink, while *D. patelliformis* is bright orange red. The empty test of the former is cream white, while the latter retains a part of the original colour, due perhaps to residual cytoplasmic inclusions which remain in the test following reproduction.

D. ornatissima is more robust than the two species described above, the superior surface is subglobular, the peripheral edge subangular, and the inferior surface depressed, the sutures are neither limbate nor depressed, and on the ventral surface finely tuberculate riblets radiate from the umbilicus. Only the final convolution and the first few chambers show on the superior surface and numerous small pseudopodial pores open through the thick translucent walls.

D. pulvinata is a small, fragile, depressed and broadly ovate species, the final chambers being somewhat inflated. The inferior surface is deeply excavated and ornamented with radiating granulose lines.

It is interesting that the inferior surface of the tests of all species of *Discorbis* in which we have observed multiple tests should be ornamented by tuberculose or granulose riblets radiating from the umbilicus.

Active cultures of *D. patelliformis* and *D. opercularis* have been maintained on four occasions of from 3 months to 1 year (see Methods, below). Serial sections of more than 600 groups of organisms showing all phases of sexual reproduction, in addition to those showing asexual reproduction and developmental stages, were prepared from tide-pool and culture material. Since the notes on life activities of *D. patelliformis*, reared in cultures, are more complete, and the stained preparations of organisms from these cultures are free from annoying cytoplasmic inclusions, descriptions will be confined largely to this species. Except for specific characteristics and the number of nuclei in microspheric organisms, which determines the number of asexually produced young, the life cycles of *D. patelliformis*, *D. opercularis*, and *D. ornatissima* do not vary appreciably.

Methods

In collecting species of Foraminifera in which multiple tests occur, handsful of coralline algae should be washed vigorously in a suitable container filled with sea water, provided with a piece of netting that will allow the finer sediments, including the Foraminifera, to settle to the bottom, while retaining the coarser materials. The sediments should be examined for multiple tests under the low power of the microscope, but should not be sorted if the material is to be used to start cultures. Best results were obtained by placing about one teaspoonful of the sediments in each of a number of 4 in. round-bottomed finger bowls filled with sea water recently removed from the sea. Each dish should be covered with a plate of glass to prevent excess evaporation, and the dish placed near a north window where the temperature will not exceed, by more than a few degrees, the average surface temperature in the sea during the summer months; 21° C. was found to be optimum at La Jolla, California. The water should be changed daily, or after several days, every other day, and maintained at a marked level, since many Foraminifera will move up the inclined wall of the dish and collect immediately below the meniscus. If after changing the water these organisms remain exposed they will not move downward into the water, even though the wall of the dish is wet. After a few days a favourable balance will become established. It is not advisable to remove the bits of algae or other debris, for to do so will usually upset this balance, and result in the loss of the culture. Larger organisms, especially annelids, should be removed, for certain of these feed upon small Foraminifera. If the water is not changed frequently the association of Foraminifera in sexual groups will usually result in the production of gametes, but further development should not be expected. Water from salt water systems should be avoided.

No doubt more difficult methods would yield results, but by following this simple procedure we were able at times to remove from a single 4 in. dish from twenty to thirty groups of multiple tests per day, over a period of several weeks; one culture from which material had not been removed for several days contained 128 doubles, three triples, and one group of four. We have maintained genetic cultures of other species of Foraminifera for many generations, but the length of the life span of most species is only one factor that should prevent many investigators from attempting work with pure cultures (Myers, 1937).

In the present investigation technical difficulties which resulted in poorly stained chromosomes and ill-defined achromatic figures were due perhaps to several causes. The small diameter of the pseudopodial pores and the aperture of the test prevented the rapid penetration of fixatives. There was also an unfavourable chemical reaction between most fixatives and the calcium carbonate of the outer walls and the septa of the test. Fixation by very hot as well as cooled solutions proved useful, but strongly acidified fixatives render this material useless for the study of division figures. The further hydrolysis of the chromatin by most fluids used to complete decalcification of the test further diminishes the capacity of the chromatin to react to stain. These factors, together with the problem of obtaining organisms in which the nuclei were in a state of division, may explain in part why various theories as to the origin of nuclei in Foraminifera have been proposed which are not in agreement with modern concepts of protozoan cytology. Isolated examples of mitotic division have been described and figured, but few of these will stand critical examination. In *Patellina corrugata* and *Spirillina vivipara* the rapid dissolution of the test and penetration of the delicate chitinous membrane by hot, strongly acidified fixatives acting only for a brief period may have obviated this difficulty. In the life cycles of *Discorbis* discussed in this paper it was possible to demonstrate an orderly progression of numbers of nuclei during the several periods of nuclear multiplication, and many preparations show evidence of spindles and chromosomes, but without sufficient definition to warrant the publication of drawings of a sequence of stages in nuclear division at this time.

Basophilic cytoplasmic inclusions often made it difficult to interpret cytological preparations of Foraminifera collected from tide pools, and occasionally caused annoyance in organisms reared in cultures. These inclusions consisted chiefly of residual chromatin derived from the nuclei of food organisms. Formerly this basophilic material was regarded as chromidia, which later gave rise to nuclei, or was mistaken for gametic nuclei by investigators whose cytological methods did not result in well-defined nuclei, especially during division stages. The failure of the chromatin of dividing nuclei to stain appreciably has been experienced by investigators in other groups of rhizopods, but where the nuclei are as clearly defined as those of the species under discussion no confusion should result. For the cytological investigation of thickwalled polythalamous species of Foraminifera we do not recommend any of the methods of fixation commonly employed by cytologists, nor do we know of methods that are suitable for the investigation of nuclear division in these species.

ECOLOGY

Multiple tests may be found during the warmer months of the year in almost any rock-bottomed tide pool (Heron-Allen, 1915, p. 247) that supports a close growth of fine, closely branching coralline algae, in which the wash of the surf does not remove the last traces of sediment from around the hold-fasts. When searching for these organisms one should not neglect to examine small rock pools which are soon exposed by the receding tide, especially if the water is renewed occasionally by the splash of waves, for such a pool often supports a relatively dense population of smaller plant and animal organisms, including many species of Foraminifera, and will be accessible when pools at a lower level on the beach cannot be reached.

The distribution of species in which multiple tests occur is somewhat erratic and it may be necessary to explore several pools, or even beaches before material containing appreciable numbers of paired tests is found. An experienced collector will quickly learn to locate not only favourable pools, but areas within a pool in which one or more of these species are numerous. A teaspoonful of sediment washed from coralline algae may yield from a few to more than 100 multiple tests.

In southern California, multiple tests were found from late in April until early November, or during that part of the year when the mean surface temperature in the sea is above 17° C. In northern California these reproductive stages were not numerous until one month later. Where the coast is exposed to the open sea, most Foraminifera are washed from the tide pools into the deeper water during the periods of heavy surf which occur in the late fall. At this same time of year, tests of Foraminifera found in great numbers in ripple marks on sandy beaches are, for the most part, those of species which do not inhabit the intertidal zone. How far these organisms were transported is unknown. From these observations it is evident that the bathymetric range of the species of *Discorbis* studied cannot be based on the reported occurrence of empty tests found in marine sediments. The bathymetric range of these species is limited probably by the distribution of the algae upon which they occur. An investigation of this problem is being attempted at the Plymouth Laboratory by making a comparative study of species actually living on a bottom with those found in the sediments.

Most tide-pool species of Foraminifera are not easily washed from the wall of a culture dish by a stream of water forcefully driven from a pipette, and when we consider the protection afforded by the network of algae, tubes of annelids, cases of amphipods, and similar objects among which they live, we can understand how they persist in tide pools exposed to a pounding surf.

These organisms move and feed by means of finely attenuated filaments of anastomosing ectoplasm, the pseudopodia. While the cytoplasmic inclusions of many Foraminifera reveal the nature of food organisms, the small diameter of the aperture in tests of *D. patelliformis*, *D. ornatissima*, and *D. opercularis* do not admit diatom frustules or similar objects. These species feed upon a substratum composed of plant and animal debris, supplemented by unicellular algae, and an occasional soft-bodied larval stage of a mollusc or other metazoan organism. Proteolitic ferments in the pseudopodia reduce the food to a fluid state so that it can be transported through the small aperture of the test or even through the pseudopodial pores into the endoplasm where liquid vacuoles are formed. Many of these vacuoles contain chromatin, derived from the nuclei of food organisms, which stains heavily with basic stain. The slow rate at which chromatin is metabolized results in the accumulation of this material in the cytoplasm.

The only organisms observed preying upon these smaller tide-pool Foraminifera were certain polychaete annelids. Many Foraminifera become the hosts of nematode worms, but the nature of the test of the species under consideration did not permit the entrance of either worms or eggs. Occasionally individuals were found in which one or more chambers of the test contained vast numbers of bacteria, amoebulae, or flagellates, not gametes; while other tests were partially or completely filled by the plasmodia of a Mycetozoa, and at this time the nucleus was usually abnormal.

Fertilization and the development of the microspheric generation takes place within the common space which forms between the several megalospheric tests comprising a group, as was also demonstrated in *Patellina corrugata* and *Spirillina vivipara*. Since the gametes of the species in which multiple tests occur are at no time free and pelagic, this stage in the life cycle does not constitute a factor in dispersal and distribution. It is evident therefore that dispersal must occur either in the juvenile or adult stages, largely as a result of turbulence and current action. A limited distribution of species may be accounted for by the migration of larger organisms especially arthropods in which the carapace is frequently covered with barnacles, bryozoans, hydroids, algae and other material providing a suitable habitat for many Foraminifera. Encrusted molluscs, especially the abalone, have been an abundant source of more than twenty species of Foraminifera, many of which were difficult to obtain in quantity from any other source. Transportation by sea weed, eel grass, or other floating objects may result in a more extended distribution and account for the dispersal of tests of Foraminifera found in sediments at depths at which these species do not occur, often hundreds of miles from a probable source. We have not observed multiple tests of Foraminifera occurring in deep water, and it is probable that here the gametes of most species are free, and constitute a brief pelagic stage during which, with the aid of such currents as exist, they would surely be a factor in dissemination, and in time distribution.

Discorbis patelliformis found in tide pools of southern California are smaller by one-half, show only two convolutions of chambers, never three, and the superior surface is rough, not smooth, compared with tests described by Brady (1884), otherwise the original description of this species agrees closely with the material studied. Several species of Foraminifera from tide pools of the La Jolla region show a similar reduction in the total diameter of tests of adult organisms, compared with those described from dredgings from other regions. At Plymouth, England, tests of *Elphidium crispum* (*Polystomella*) collected in tide pools seldom show more than one-half the number of chambers observed in organisms of the same species dredged from adjacent channels, at a depth of about 5 m. below mean low tide, during the months of July to December inclusive. It is probable that larger examples of the species taken from tide pools at La Jolla might occur in deeper water in the same region. Foraminifera maintained in cultures at 21° C. reproduced in an earlier growth stage than those recovered from tide pools where the temperature of the water was several degrees colder; the mean temperature in a tide pool is usually several degrees warmer than that of larger bodies of water. From these observations it would seem that the maximum growth attained by certain species of Foraminifera is limited directly, or indirectly, by the mean temperature of the water in which they occur. The distribution of larger geologic and recent species of Foraminifera has been limited to warm shallow seas, hence this statement only applies to organisms of the same species living under different environmental conditions.

LIFE CYCLE

The zygote which results from the union of two gametes in fertilization is considered the natural beginning for the description of the life cycle, but in the present instance the flagellated gamete is the stage of greatest interest; for proof of its existence has been the object of investigation for more than 40 years. It is for this reason that the present account begins with a description of the gamete.

Gametes. Gametes of *D. patelliformis*, removed from multiple tests and observed in life by transmitted light, at a magnification of 1000 × have an average length of 8μ, and a slightly flattened, ellipsoidal shape, but are capable of much distortion owing to the fluidity of the protoplasm and the elastic nature of the delicate bounding membrane (Pl. II, fig. 16). Three long flagella have their origin at one side of the anterior end where a slight notch, suggestive of a cytopharynx, is occasionally observed. This false cytopharynx does not show clearly in stained preparations. At one side and somewhat posterior to this a large hyaline area, with no visible bounding membrane, marks the position of the nucleus. Conspicuous cytoplasmic inclusions, confined largely to the distal half of the gamete, consist of from a few to more than ten vacuoles, the contents of which are often coloured, one or more of the larger usually containing a golden yellow, oil-like substance, while others show irregular yellow-brown bodies having a high index of refraction.

Two of the three flagella are of the same length, and usually beat in unison. The stroke, beginning at one side, carries both flagella forward along the same course in a wide arc, and back to complete a whirling motion that is repeated at more or less regular intervals. The third, a trailing flagellum, originates a short distance posterior to the paired flagella, is somewhat longer, and waves slowly about at random. The amount of forward progress is negligible compared with the energy expended both in body contortions and flagellar activity. Occasionally a gamete becomes attached to the glass slide at the point of contact, or by a protoplasmic process pushed out from one side, and as the organism struggles as if to free itself, the cytoplasm is drawn out into a long hyaline filament: this false pseudopodium frequently includes the trailing flagellum. A gamete attached by the anterior end becomes subspherical in shape, and as it rotates slowly about the point of attachment the paired flagella thrash about more actively than the third, which waves slowly from side to side.

Under favourable conditions the gametes contained in multiple tests persist for about 24 hr. Certain multiple tests placed in isolation cultures still contained active gametes after 22–34 days, but there is no evidence that these gametes were capable of fertilization after the first day. This observation may or may not suggest the persistence of gametes in those species in which the gametes are free and pelagic, and no doubt constitute a factor in dissemination and distribution (Vaughan, 1933).

If conditions in a culture become unfavourable, the gametes develop tumour-like processes containing large pigmented vacuoles, which are finally pinched off together with the surrounding cytoplasm. In the final stage of degeneration of the gametes the paired tests contain only a small amount of brownish granular residual material, largely composed of stercombs.

In a fresh preparation of gametes the three flagella are easily demonstrated by placing a drop of sea water strongly coloured with iodine near the edge of the cover-glass; and as the iodine solution spreads to the gametes, the flagella shorten, thicken, and stain deeply. Gametes exposed to osmic acid vapour, followed by hot Schaudinn's fluid, and stained with iron haemotoxylin resulted in satisfactory preparations, both for nuclei and flagella. Gametic nuclei usually stained intensely. When weakly stained, the nucleoplasm appears finely granular and is bounded by a delicate membrane. Each flagellum originates in a small basal body situated immediately below the periplast, those of the paired flagella being slightly anterior to that of the trailing flagellum. The latter is connected to the nucleus by a rhizoplast, but the relation of this structure, or of the nucleus to the paired flagella, was not determined. Certain vacuoles containing a lipoid substance blacken when treated with osmic acid; while the content of others stained darkly with haematoxylin, especially in organisms recently removed from the sea. These latter no doubt contain residual chromatin derived from organisms utilized as food by the megalospheric gamont. Brown bodies, probably stercombs, have a high index of refraction, and persist apparently unchanged in stained preparations.

The gametes of many plant and animal organisms are provided with either one or two flagella, three is a most unusual number. The flagellated organisms tentatively described as gametes or "zoospores" by Lister (1895, p. 427) were provided with two flagella. Gametes of Foraminifera having two flagella have since been described by several investigators, the one exception being the mono-flagellated gametes of *Peneroplis pertusus* Forskål (Winter, 1907). In the course of the investigation on the biology of the Foraminifera carried on for several years at the Scripps Institution of Oceanography of the University of California at La Jolla, California, flagellated gametes of *Discorbis* and *Tretomphalus* were available for demonstration much of the time, and were observed by many visitors. Brief comments on these observations have been made in earlier papers (Myers, 1933–38), but the unsatisfactory state of the cytological evidence as to the origin and fate of these flagellated organisms, at that time, justified a conservative view as to their significance in the life cycle of the Foraminifera.

The dimorphic nature of the tests, the number of nuclei in microspheric agamonts and megalospheric gamonts, and the morphology of both nuclei and tests in the species of *Discorbis* under discussion are in agreement with the characteristics prevailing in other polythalamous species of Foraminifera in which life cycles have been proposed. It is interesting that the gametes of these small species of Foraminifera should be nearly twice the size of those described by other investigators in relatively enormous species, and that the number of flagella should be three, and never one or two.

Soon after the first progamic nuclear division in gametogenesis, the ventral walls and septa of megalospheric tests of organisms associated in sexual reproduction are slowly dissolved, and the calcium carbonate so derived, assimilated by the protoplasm for redeposition during the secretion of the tests of the new generation (Pl. II, figs. 12, 20). The passage thus formed between the tests permits the fusion of the several somatellae. Following multiple fission of the multinucleate megalospheric somatellae and the development of the gametes, the reproductive bodies are free to mingle within the enclosed space or brood chamber formed by the outer walls of the excavated multiple tests.

Each of the Foraminifera comprising a group of associated *D. patelliformis* produced from 250 to 300 gametes, of these only twenty to thirty were destined to become fertilized and develop into sexually produced young. From material killed and fixed immediately upon being removed from the sea, at least one-third of all multiple tests contained gametes. In cultures, approximately 72 hr. elapsed between the association of the Foraminifera in multiple tests and the final escape of the sexually produced juvenile microspheric agamonts.

From the above it would seem that the gametes normally persist for a period of at least 24 hr. Since only about one gamete in eleven becomes fertilized under conditions that afford the maximum opportunity for syngamy, the probability of actually observing the union of two gametes in fertilization is relatively remote.

SEXUAL REPRODUCTION

Fertilization. From the behaviour of the gametes, and the position of the flagella and nuclei in living and stained preparations, it appears that union begins near the anterior end; the two gametes finally assuming a parallel position so that when fusion is complete, the flagella are near one pole, and the two pronuclei are in line at right angles to the major axis of the somatella. The direct fusion of the two pronuclei completes fertilization.

Growth following fertilization results from the ingestion and assimilation of entire gametes as is evidenced by the content of large vacuoles, and the presence of ten to fourteen picnotic gametic nuclei in the cytoplasm of the primordium of the microspheric agamont (Pl. II, fig. 20). This interesting form of cannibalism is a normal activity, and is not the result of unnatural conditions in cultures, for the number of sexually produced microspheric juveniles both in cultures and in the sea is entirely dependent upon the size of the brood chamber; this was apparent in cytological preparations in which it was observed that the two-chambered juveniles completely fill the common space enclosed by the multiple tests in material obtained from both sources.

The flagella persist during early growth of the post-zygotic amoebula and slowly wave about, but seem to have slight influence upon the movements of the organisms. Vacuoles, nuclei of ingested gametes, and the zygotic nucleus churn about in the vortex set up in the cytoplasm.

Metagamic nuclear divisions. In stained preparations the chromatin of the zygotic nucleus remains optically unchanged while the expanding mass of hyaline nucleoplasm carries the nuclear membrane outward, resulting in a large spherical nucleus with a deeply staining central mass (Pl. II, fig. 17 *a*). The gradual expansion of this central mass brings into view a tangled spireme which soon occupies the entire nucleus. An orderly series of post-zygotic or metagamic nuclear divisions quickly follow, without the intervention of interphase or resting nuclei, the linear aggregates of nuclear substance which marks the position of ill-defined chromosomes apparently retaining their organization from one division to the next (Pl. II, fig. 17 *b*). It is interesting that the zygotic nucleus and the picnotic nuclei should have stained while dividing nuclei usually failed to stain appreciably except in the final metagamic nuclear division (Pl. II, fig. 15). Later, digestive ferments acting upon the nuclei of the ingested gametes caused them to swell and gradually lose their affinity for basic stains.

Cytological preparations showing metagamic nuclear divisions should have been made by first removing the developing microspheric juveniles from the multiple tests, thereby eliminating mechanical and chemical interference to the action of fixatives, although there is little to suggest that this would have resulted in a more favourable staining reaction with the reagents and stains used.

Motility in the gametes and later in the multinucleate post-zygotic stages is more dependent upon a modified type of amoeboid movement than upon flagellar activity, although the flagella persist until the developing agamont has attained a size equal to about two-thirds that of the protoplasmic mass contained within the proloculum, or initial chamber of the microspheric test. About this time the developing agamont becomes surrounded by a layer of hyaline ectoplasm, which gives rise to filose pseudopodia. Within this ectoplasm a thin transparent layer, or wall of calcium carbonate forms in close contact with the bounding membrane. This subspherical primordial test becomes the initial chamber, or proloculum of the test of the microspheric generation, and is perforated by a number of pseudopodial pores and a larger opening, the aperture. The calcium carbonate contained in the juvenile tests was largely derived from the ventral walls and septa of the associated megalospheric tests which were digested and assimilated during gametogenesis (Pl. II, fig. 10).

The diameter of this monolocular juvenile test which becomes the proloculum of the microspheric test is dependent not upon the size of the gametes, as is perhaps the case in species in which the gametes are free and pelagic, but upon the amount of growth taking place before the primordial test is formed. After the secretion of the primordial test, all nuclei may show from three to eight basophilic masses or endosomes pressed against, or in close contact with the nuclear membrane and resemble the vegetative nuclei of other Foraminifera (Pl. II, fig. 17 *c*). The remaining nucleoplasm at this time is often lacking in visible structure and staining capacity, and the nuclear membrane is indistinct, so that when the cytoplasm contains small masses of residual chromatin or other inclusions, the organization of the vegetative foraminiferal nucleus with its multiple endosomes must be known before these nuclei can be recognized; once observed, they show clearly in all organisms within a multiple test. Later, a mass of ectoplasm escapes through the aperture and assumes a subspherical shape in contact with one side of the primordial test. After the secretion of a delicate chitinous membrane, protected externally by a thin wall of calcium carbonate, the more granular endoplasm streams through the aperture, which is now a foramen, into the newly formed chamber. In cytological preparations the gametic nuclei, and the zygotic nucleus resulting from the union of two gametic nuclei in fertilization, stain so that their organization is clearly defined. Later, an orderly progression in numbers of nuclei can be observed which, as a rule, do not stain appreciably, but which do show linear aggregates of nuclear substance indicative of chromosomes. The first vegetative nuclei in the multinucleate microspheric juvenile before it escapes from the multiple tests stain clearly, and are characteristic of the species (Pl. I, fig. 5; Pl. II, fig. 17 *c*). Thus the fate of the triflagellate gametes has been demonstrated on cytological evidence, and further it was observed that the post-zygotic nuclei divide by mitosis.

When multiple tests containing gametes are viewed with the aid of a microscope and oblique illumination it is possible to see the twisting, gliding movements of the gametes through the translucent walls as they mingle in the common space formed by the dissolution of the ventral walls and septa of the several tests. Later, the larger slow-moving post-zygotic amoebulae can be noted, but after the secretion of the primordial tests movement is too slow to be distinguishable. The gametes, together with the earlier developmental stages of the zygotes, persist for about 24 hr. 24 hr. later the animal cement and calcium carbonate, which securely bound the megalospheric tests, is dissolved by the pseudopodia of the juveniles, and the two- and three-chambered microspheric young glide slowly from between the tests to the substratum where they are soon dispersed; by the next morning only a few of the juveniles are to be found in the vicinity of the now empty and separated tests from which they escaped. The usual number of sexually produced microspheric juveniles derived from a pair of associated megalospheric gamonts varies from eighteen to thirty-two, although larger and smaller numbers of young have been observed.

Development of microspheric test. At the time of escape, each microspheric juvenile contains eight to sixteen nuclei. After each period of active foraging a new chamber is added to the juvenile test. These chambers, which are formed one at a time, result in a graduated series in which each additional chamber is larger than the one preceding. In an occasional test, the regularity of the series is interrupted by the addition of an unusually narrow chamber. In cultures an abrupt change in temperature or food organisms in the substratum has been known to result in a similar reduction in the size of chambers in numbers of individuals. In the microspheric generation, the direction of rotation of the series of chambers is to the right, or clockwise. In *Discorbis patelliformis* an exception to this rule is most unusual. In megalospheric tests no exceptions were found in which the direction of rotation was not the reverse of that observed in microspheric tests (Pl. I, figs. 1, 2). This statement is based on observations of permanent preparations of tests of three hundred organisms associated in sexual reproduction which were separated and cleared in balsam before measurements and chamber counts were made. A similar study of microspheric tests was also made from preparations of organisms removed from cultures during asexual reproduction, or while the juvenile Foraminifera were still in close association with the parent test. A reversal in the direction of rotation of microspheric and megalospheric tests was reported in *Spirillina vivipara* (Myers, 1936). Føyn (1936*b*), in the same year, described a similar condition in *Discorbis vilardeboana* d'Orbigny where exceptions to the rule were not uncommon. In megalospheric tests of *Tretomphalus bulliodes* d'Orbigny, exceptions were even more numerous (Myers, in manuscript).

Table I shows the relative size of the proloculum or initial chamber of microspheric to megalospheric tests in four species of Foraminifera. In the first two species listed, the gametes are confined within a brood chamber; in the remaining species, the gametes are free and pelagic.

TABLE I

	Microspheric			Megalospheric		
	Proloculum			Proloculum		
Species	Extremes	Means	No. of tests	Extremes	Means	No. of tests
D. patelliformis	15·3–21·3 μ	17·0 μ	100	15·3–28·9 μ	17·8 μ	300
D. opercularis	15·0–24·2 μ	20·3 μ	100	18·2–29·3 μ	22·3 μ	100
*D. concinnus**	6·4– 9·1 μ	9·4 μ	41	13·6–22·1 μ	15·2 μ	300
P. crispa	6·3–13·4 μ	9·2 μ	31	51·0–87·4 μ	64·7 μ	300

* Microspheric stage of *Tretomphalus bulloides* has been identified as *Discorbis concinnus* Brady by Arthur Earland.

Table II shows the growth stage at the time of reproduction, both in the sexual and asexual phases of the life cycle, based on the number of chambers in a test.

TABLE II

	Chambers at time of reproduction					
	Microspheric			Megalospheric		
Species	Extremes	Means	No. of tests	Extremes	Means	No. of tests
D. patelliformis	12–24	17·2	300	6–16	10·2	100
D. opercularis	10–19	14·4	100	4–12	8·8	100

The addition of a new chamber to a foraminiferan is the result of a discontinuous method of growth only, and the nucleus, or nuclei, do not divide when a new chamber is added to the test. Therefore the addition of a chamber should not be considered an abortive attempt on the part of a foraminiferan to reproduce by budding, any more than the addition of a new chamber to the shell of a *Nautilus* suggests binary fission in this cephalopod mollusc.

The outer wall of the test of *Discorbis patelliformis* consists of laminated layers of calcium carbonate, separated by a mere trace of animal matter deposited on a basic chitinous membrane of insufficient strength to show the characteristics of the species after decalcification, unless the chitinous structures are supported by the protoplasmic body or somatella. In many species of *Discorbis* the chitinous portion of the test is brown in colour, has considerable substance, and shows characteristics similar to those of the entire test. Growth in *D. patelliformis* is accomplished by the addition of chambers and, during the interval when a new chamber is being added, protection is necessary because any slight injury to the developing chamber at this time would result in a malformed chamber, and with the addition of subsequent chambers, an irregular test.

Addition of a new chamber to a test. When a foraminiferan of this species is about to add a new chamber it comes to rest on a flattened surface from which it removes any bits of debris that may be present. Long filose pseudopodia collect residual plant and animal matter, including many diatom frustules as well as small mineral crystals, from the substratum and these are heaped about the base of the test. This mass of debris is held together with animal cement and is lined by a smooth membrane secreted by the ectoplasm, which also covers the organism and is sealed at the margin of the test to the substratum. After the development of the growth cyst, the foraminiferan moves to one side, or is forced back from the wall of the cyst by a mass of clear colourless cytoplasm which escapes through the ventral aperture and gradually assumes the shape and size of the developing chamber. Bright points on the surface of the protoplasmic mass show where crystals of calcium carbonate are forming and these fuse to become a continuous layer of shell substance covering not only the new chamber but several of the adjacent chambers as well. The former aperture is now a canal or foramen between the new and preceding chamber, and a new aperture develops in the new or terminal chamber. In *D. patelliformis* we could not determine how the pseudopodial pores were formed; but in *Tretomphalus bulloides*, especially in the final chamber of the megalospheric test, the pores were observed to result from the deposition of shell material around the base of short pseudopodia extending through the chitinous covering of the developing chamber to the wall of the cyst, and were not formed after the shell substance had once been deposited. About 12 hr. are required for the completion of one of the larger chambers of the test, from the time when the growth cyst can first be detected; while in the two- and three-chambered juveniles, two chambers may be added within the first 24 hr., allowing a period of 12 hr. or more for active foraging between the deposition of the two chambers. After the escape of the foraminiferan from the growth cyst, the amount of cyst material remaining on the wall of the culture dish may be negligible, but if considerable loose material is available, a small hollow mound of debris may persist for several days.

Nuclei of microspheric agamonts. During early growth the nuclei of a microspheric agamont remain in the initial chamber or proloculum. Later, as new chambers are added, the nuclei become distributed farther along the series and increase in size according to the size of the chamber in which they occur, although nearly one-half the total number usually remain within the proloculum until the organism approaches maturity. Nuclei rarely occur in chambers less than two removed from the terminal chamber in organisms that are more than one-third grown. The total number of nuclei varies from eighteen to twenty-five, and in size from 3 to 10 μ (Pl. I, fig. 6). During the vegetative life of the microspheric agamont, large nuclei show numerous masses of basophilic material, or multiple endosomes, in close contact with the nuclear membrane. These endosomes develop from small granules and several may coalesce to form larger endosomes; but they do not seem to divide at this stage, nor do the nuclei divide so long as these endosomes retain their affinity for basic stain, nuclear division being limited at this time to the smaller nuclei within the proloculum or adjacent chambers. There is no evidence that the division of these small nuclei coincides with the addition of a new chamber, while in the megalospheric gamont the nucleus does not divide until gametogenesis (Pl. II, fig. 11). In *Discorbis patelliformis* microspheric agamonts observed in asexual reproduction usually show from sixteen to eighteen chambers, the extremes being twelve and twenty-four chambers: the age of these agamonts averaged about 42 days. When conditions were less favourable the microspheric agamonts continued to grow, or remained relatively inactive for more than twice that period before undergoing asexual reproduction.

ASEXUAL REPRODUCTION

Division of nuclei. Asexual reproduction in a microspheric agamont is initiated by the development of a multiple fission cyst, which is formed of diatom frustules and other debris in much the same manner as that described as the growth cyst, except that it is more rigidly constructed. No appreciable part of the debris in this structure consists of defecatory material eliminated by the foraminifer in the reorganization of the cytoplasm as was observed by Føyn (1937, p. 5) in *D. vilardeboana*. This statement is based on the observation that in *D. patelliformis* and related species rigid cytoplasmic inclusions show fragments of diatoms, but entire frustules or other large objects were not observed. After encystment all nuclei move farther along the series of chambers, the smaller nuclei increasing in size and developing numerous small dense bodies which are evenly distributed below, and in contact with the nuclear membrane, and which stain weakly. In larger nuclei, the intensely staining multiple endosomes become reduced in size, and stain less intensely with basic stains. Only the larger nuclei divide, and from the size and total number of nuclei after the final division it is evident that only the largest nuclei divide a second time.

In *D. opercularis* all nuclei in the somatella of a microspheric agamont may divide at least once. In this species the number of megalospheric juveniles asexually produced is from ninety to one-hundred and twenty, or about three times that observed in *D. patelliformis*; however, the final number of nuclei in microspheric organisms of both species prior to asexual reproduction is rarely in excess of twice that occurring in free microspheric agamonts having a similar diameter.

Multiple fission. In *D. patelliformis* multiple fission is preceded by a reorganization of the cytoplasm in the vicinity of each nucleus, where it becomes more homogeneous in appearance than the surrounding cytoplasm; which in stained preparations appears coarsely vacuolated. The nuclei at this time do not differ appreciably, either in size or staining capacity; and the inner side of the nuclear membrane bears numerous small masses of nuclear substance or endosomes which are uniform in size and distribution, but stain poorly (Pl. I, fig. 7). The cytoplasm and contained nuclei recede from the earlier formed chambers, while the septa and much of the test substance, especially in the ventral wall, is digested and assimilated in the same manner, and for a similar purpose as that described in multiple tests in the sexual phase of the life cycle. Multiple fission results in the separation of the cytoplasm bounding each nucleus from the surrounding cytoplasm, each mononucleate mass approximating in size to the protoplasmic mass contained in the proloculum of the megalospheric test. These mononucleate somatellae become surrounded by a plasma membrane and later by hyaline ectoplasm which gives rise to filose pseudopodia. When multiple fission is complete, small angular anucleate masses of cytoplasm remain which are later utilized as food by the developing mononucleate megalospheric gamonts.

Development of the gamont. The mononucleate amoebulae move about within the excavated microspheric test and continue to digest the calcium carbonate in the walls and septa as well as the residual cytoplasm that remained after multiple fission. Following the development of the monolocular test, or megalosphere, the multiple endosomes in the nucleus stain intensely. A second chamber is added in much the same manner as that described in the development of the tests of the microspheric generation (Pl. I, fig. 8). It is difficult to explain why in certain stained preparations the more granular endoplasm lines this first chamber, while a more hyaline cytoplasm forms a distinct central mass, unless it represents a stage prior to the secretion of the third chamber (Pl. I, fig. 4). It is evident that the shell substance is deposited by the ectoplasm in all cases. About 70 hr. after the first bits of substrate debris becomes noticeable in the developing multiple fission cyst, the ventral wall of the test of the microspheric agamont breaks down, and from thirty to forty, two- and three-chambered megalospheric gamonts glide slowly from the parent test and collect in a closely associated group, not unlike a brood of chicks about a mother hen.

The nucleus of the megalospheric gamont may remain in the proloculum or initial chamber as long as the organism is free, or it may move along the series of chambers, but rarely beyond the chamber that is numerically near the middle of the series (Pl. II, fig. 11). The nucleus increases in size with the growth of the organism and may exceed in magnitude the largest nucleus observed in microspheric agamonts (Pl. II, fig. 13). Nuclei of megalospheric organisms have an average diameter of 10μ; while the largest nuclei in microspheric agamonts seldom exceed 8μ. These large nuclei are similar in appearance in both generations. In order to determine the rate at which these Foraminifera develop in cultures, culture dishes which had been previously inoculated with material from the substrate of a culture was allowed to develop a similar substrate. These dishes were then planted with as many day old Foraminifera as were available. By observing the average rate at which new chambers were added to the primordial test, it was possible to determine the rate of growth and the age at which these organisms reproduce. As might be expected, in organisms in which the initial stage of both the sexual and asexual generation is about equal in size, a greater difference was observed in the rate of development of individual organisms of the same age than between organisms of the two generations, although a slightly accelerated rate of growth was noted in the multinucleate microspheric agamonts: this apparent variation in the rate of growth being influenced perhaps by the number of nuclei occurring in organisms in the respective generations. The metabolic rate of a Foraminifera is influenced perhaps by the surface area of contained nuclei.

The total number of chambers in tests of megalospheric gamonts associated in sexual groups varies from six to sixteen, the largest test showing fewer chambers than was observed in the majority of tests of microspheric agamonts after asexual reproduction. Multiple tests in *D. patelliformis* usually include one or more organisms showing ten, eleven, or twelve chambers, which in cultures require about 16 days to develop. These Foraminifera had not attained the maximum size for the sexual phase of the life cycle and might have continued to grow as free organisms for weeks or even months under other conditions.

The final chamber in a mature microspheric agamont is usually smaller than the several which preceded it and occupies the angular space formed by the preceding chamber and the final whorl of chambers so that the inferior surface of the test is nearly level. In megalospheric tests the distal face of the final chamber terminates more abruptly, so that an angular space remains between the inferior surface of the test and the substrate.

Syzygy. Foraminifera of different species, or of the same species, usually avoid one another in cultures. When two megalospheric organisms, each provided with a test consisting of ten or more chambers, were observed in close contact on the wall of a culture dish, the position was marked on the outside of the dish by a numbered wedge-shaped piece of gummed paper. Many groups so marked could be observed at frequent intervals. The slow rate at which these organisms move made it necessary to trace these movements in series of drawings.

From the behaviour of two Foraminifera immediately prior to their association in syzygy in the sexual phase of the life cycle, it would seem that a conditioning process is necessary in one or both individuals, for two megalospheric gamonts rarely approach and fuse directly. While one megalospheric gamont remains quiescent, the other, which is frequently the smaller, shows unusual activity, and makes many attempts to move under the test of the larger at the point where it fails to make contact with the substratum. The inferior surface of the two tests thus brought into juxtaposition may separate and the smaller organism resume its random movements over and around the larger, the two organisms at times being separated by a distance equal to as much as ten times the diameter of the larger test. After effecting one or more temporary unions, the two gamonts finally come together, the one rotating on the other, so that the distal or apertural face of the final chamber of each test is opposed and the ventral surfaces are in close contact at all points (Pl. II, fig. 9). Both organisms are provided with long filose pseudopodia, which extend in all directions. The lower organism of a pair rests on one side of the conical superior surface, and while in this position the paired tests glide over the surface of the dish a distance equal to ten or more times the diameter of the multiple tests. The multiple tests soon become firmly attached to the substratum by a deposit of animal cement. Animal cement and calcium carbonate also seal the two tests together so that no opening larger than a pseudopodial pore communicates with the outside. So firmly are the tests fused that if an attempt is made to separate them, the inferior surface of one is frequently broken away. The described activities require from 1 to more than 5 hr. One multiple test transferred to a depression slide moved about for 4 hr. before becoming attached. Union is not always effected in a symmetrical manner and it is not essential that the apertures of the several tests be opposed. When a multiple test consists of three or four gamonts, they may assume almost any position that will allow the ventral surface of each to make contact with at least one other test; thus permitting the development of a wide passage between the several tests by the dissolution of the walls at the point of contact. Since one of a pair of Foraminifera associated in sexual reproduction may consist of five chambers or less, Heron-Allen (1915) had reason to presume that multiple tests were the result of budding. It was observed that the gamonts associated in syzygy may or may not have been asexually derived from the same microspheric agamont. The variation in the size of gamonts in multiple tests further supports this observation.

Gametogenesis. The association of megalospheric gamonts is probably a response to a chemical activator. These gamonts are further activated so that subsequent events in the several organisms are nearly synchronous. After the union of the gamonts in syzygy there is a gradual dissolution of the septa and ventral walls of the respective tests so that the cytoplasm in the later formed chambers becomes confluent in the umbilical region and the somatellae fuse in the passage formed between the several tests. As is characteristic of the nuclei of all polythalamous Foraminifera studied, the large basophilic masses of nuclear substance, or multiple endosomes, lose their affinity for basic stains and become greatly reduced in size or disappear entirely prior to nuclear division (Pl. II, fig. 15). The first progamic nuclear division in which the large single nucleus of each gamont divides takes place about 24 hr. after the association of the gamonts. There immediately follows an orderly series of progamic nuclear divisions without the intervention of interphase or resting nuclei. These divisions result in a gradual reduction in the size of the nuclei, although this reduction in size is not in proportion to the number of nuclei produced (Pl. II, figs. 12, 14 and 18).

The nuclei of one gamont are usually larger, and fewer in number, than those of the other gamont as a result of one less nuclear division. During this series of progamic nuclear divisions the nuclei become equally spaced in the cytoplasm. A slight difference in the appearance of the nuclei of the respective gamonts makes it possible to determine that no exchange of nuclei occurs during gametogenesis. Indistinct linear aggregates of nuclear substance in nuclei which are spherical, elliptical, or constricted in the middle are indicative of mitotic division, as is the orderly increase in numbers of clearly defined nuclei. In a later paper on the Cytology of the Foraminifera we hope to be able to demonstrate conclusively the nature of the chromatic and achromatic elements of the division figures in larger nuclei of this and other polythalamous Foraminifera.

Multiple fission in the multinucleate somatella, as evidenced in cytological preparations, show open spaces between oblong masses of cytoplasm which are provided with a centrally situated nucleus. Nuclear division and plasmotomy take place in rapid succession, the spindle-shaped nuclei showing chromosomes which stain (Pl. II, fig. 19). Since the basic plan of this life cycle closely parallels that of *Patellina* and *Spirillina* it would seem that these mononucleate oblong bodies are diploid gametocytes and that the spindle-shaped nuclei are indicative of the anaphase of the meiotic or reduction division. This final nuclear division and the binary fission of the gametocytes results in numerous small spherical bodies each having an eccentrically situated nucleus; these develop into the triflagellate gametes.

Comparative Study of Life Cycles of Foraminifera

In the life cycle of *D. patelliformis* multiple tests result from the union of two mononucleate megalospheric gamonts associated in syzygy. About 24 hr. are required for the reorganization of the cytoplasm and the contained nuclei. Gametogenesis and fertilization occupy another 24 hr. period; while a third period of 24 hr. is necessary for the development of the two-chambered multinucleate microspheric agamonts, making a total of about 3 days that are required for sexual reproduction. The test of the microspheric agamont at the time of asexual reproduction shows an average of about seventeen chambers, indicating an age of at least 45 days. The asexually produced mononucleate megalospheric gamonts in multiple tests average about eleven chambers, and were not less than 14 days old at the time. 60 hr. or more elapse from the time the multiple fission cyst can first be detected until the juvenile megalospheric gamonts make their escape: therefore the minimum period required to complete the life cycle in cultures is in excess of 64 days.

The life cycle of many species of Foraminifera includes an orderly succession of sexual and asexual generations. This alternation of generations results in test dimorphism. The multinucleate microspheric agamont asexually produces mononucleate megalospheric gamonts, which in turn give rise to gametes. The union of two gametes in fertilization results in the formation of a zygote which develops into a microspheric agamont, thus completing the life cycle. This brief statement of the succession of stages applies equally to the life cycle of *Polystomella crispa* Lister (1895), *Patellina corrugata* (Myers, 1935), *Spirillina vivipara* (Myers, 1936), and the present account of the life cycle of *Discorbis patelliformis*. These four life cycles constitute an interesting series in which modifications of morphology and behaviour have no effect upon the basic plan of the life cycle.

In *Spirillina vivipara* the tests of both mononucleate gamonts, and multinucleate agamonts, consist of a proloculum that is continuous with a spiral chamber, the only obvious difference in the tests of the two generations being the larger diameter of that of the agamont. In asexual reproduction, the cytoplasm and contained nuclei escapes from the test of the agamont, and multiple fission and the development of the juvenile mononucleate gamonts follows. In sexual reproduction the gamonts associate in groups of two or more while in a horizontal position, and are enclosed within a protective cyst. Gametogenesis results in amoeboid gametes, not flagellated, which unite in pairs in fertilization, the zygotes so produced developing into juvenile agamonts. All nuclei in this life cycle are the result of mitotic division, the final division in gametogenesis being the reduction division.

The sequence of events in the life cycle of *Patellina corrugata* parallels closely that of *Spirillina vivipara*. The tests of the mononucleate gamonts like those of *Spirillina* seldom consist of more than a proloculum and a spiral chamber, while that of the multinucleate agamont shows, in addition to the proloculum and spiral chamber, five or six semi-lunar chambers, and is considerably larger.

In *Discorbis patelliformis* the tests of both generations consist of many chambers, that of the agamont being the larger as was true in both of the preceding species. Again the prolocula of the tests of both generations are about equal in size. In this species the mononucleate gamonts associate in such a manner that the inferior surfaces of the tests are opposed, and never assume a horizontal position during sexual reproduction. In this life cycle, as in those of the preceding genera, there are three periods of nuclear division, but in *Discorbis* post-zygotic divisions continue during the vegetative life of the agamont.

In *Polystomella crispa* agamonts do not associate prior to gametogenesis, the flagellated gametes being free and pelagic so that the zygote which results from the union of two gametes in fertilization do not have an opportunity to feed and grow at the expense of unsuccessful gametes. For this reason the proloculum of the test of the sexually produced agamont is small compared with that of the test of the asexually produced gamont, and the probability of survival is greatly reduced. Tests of both generations are provided with many chambers and are about equal in size. The sequence of events in the life cycle of this species, including the periods of nuclear division, closely parallels that of *Discorbis patelliformis*.

The stratigraphic distribution and morphology of the tests of *Spirillina* attest to the antiquity of this genus, compared with *Patellina*, *Discorbis* and *Polystomella*. It has been presumed that flagellated gametes recapitulate the progenitor of all animal organisms. If it were not for this popular concept, one might propose that the increasing complexity of the tests of these genera and the modifications of events and stages in the life cycles are suggestive of an evolutionary series.

CONCLUSIONS

In the account of the life cycle of *Spirillina vivipara* it was stated "if flagellated gametes, or zoospores, do exist in the Foraminifera their origin and fate can and will be demonstrated cytologically" (Myers, 1936, p. 139). The present paper meets both of the requirements specified above. Much of the evidence herein presented, including many cytological preparations of critical stages and recorded observations, had been made during the four seasons preceding the publication of this statement (Myers, 1933). Calvez, 1938, p. 173) has criticized Dr C. A. Kofoid and myself for assuming the attitude that organisms, flagellated or otherwise, observed in tests of Foraminifera were in all probability saprophytes, parasites, or symbionts until their genetic relation had been proven cytologically. Calvez has described flagellates, presumably gametes, in twelve species of Foraminifera. According to his descriptions the gametes of these twelve species are small and bear two flagella, one longer than the other. These characteristics are common to many flagellates, especially saprophytic species which enter the tests of dead, or dying Foraminifera, particularly in cultures, and also resemble certain flagellates observed by Lister (1895, p. 427) which he recognized as "products of some other organism which had entered the shell of *Polystomella*".

We have studied the origin and fate of flagellated gametes in several genera of Foraminifera in cultures and from permanent cytological preparations. It is significant that the flagellated gametes observed by us bear slight resemblance to those described by Calvez, even in the same species. This evidence will be described and figured in papers now in preparation.

The investigation of the biology of the Foraminifera gives promise of becoming an active field, due largely to the use of the tests of these marine rhizopods as guides in stratigraphic geology. The geographical distribution of many genera and species extends throughout the more populous sea-coast regions of the world, therefore we may expect that observations may be repeated. In so ancient and diverse a group, variations and modifications in stages and cytological behaviour are to be expected, and much caution is necessary in the interpretation of cytological preparations owing to the difficult nature of the material and the many types of organisms which inhabit the tests of both living and dead Foraminifera.

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The classic contributions of J. J. Lister on the life history of the Foraminifera were largely the result of observations made at the laboratory of the Marine Biological Association at Plymouth. It has been the privilege of myself and my wife Ethel, who assists me, to extend these observations in this and other species while working at the Plymouth laboratory. We wish to express our appreciation and gratitude to the Director, Dr Stanley Kemp, and the members of the staff who have co-operated to make our stay in Plymouth both instructive and pleasant. We are especially grateful to Dr E. J. Allen for his interest in the cytological preparations and other phases of the work and for his helpful suggestions. Multiple tests in *Discorbis ornatissima* were first called to my attention in 1934 by Helen Jean Plummer. Later we obtained multiple tests of this species in considerable numbers near Moss Beach, California. The photograph of multiple tests and contained young in Pl. III are of a preparation made by Dorothy Palmer which Miss Plummer kindly forwarded to me.

SUMMARY

It has long been presumed that the gametes of certain Foraminifera are flagellated; however, the lack of conclusive evidence as to the origin and fate of these flagellated gametes has made their existence problematical.

In syzygous species of *Discorbis* the gametes are flagellated and the genetic relationship of these gametes is easily demonstrated, since gametogenesis, fertilization, and the development of two- and three-chambered multinucleate microspheric agamonts takes place within the excavated tests of two or more mononucleate megalospheric gamonts associated in syzygy.

The life cycle of *Discorbis* herein described is in general agreement with the life cycle of *Polystomella crispa* proposed by J. J. Lister, and completes an interesting series of life cycles in which a progressive modification in behaviour and test morphology can be traced.

Behaviour, ecology, and distribution of four syzygous species of *Discorbis* are discussed.

Multiple tests of these syzygous species of Foraminifera can be found in most rock-bottomed tide pools that supports a growth of coralline algae. These sexual groups provide a sure source of material for the demonstration of flagellated gametes in the Foraminifera.

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EXPLANATION OF PLATES I–III

Figures of *Discorbis patelliformis* in Pls. I and II are based on camera lucida drawings. The technique used was to select the foraminiferan from the culture with the aid of a dissecting binocular, the reproductive stages being recognized either from a protective cyst or as syzygous groups. The fixative used was hot Schaudinn's fluid. Total mounts were stained in Ehrlich's acid haematoxylin, and the paraffin sections in Heidenhein's iron haematoxylin.

PLATE I

Fig. 1. *Discorbis patelliformis*; superior surface of the test of a microspheric agamont.

Fig. 2. Superior surface of a megalospheric gamont. The direction of rotation of microspheric tests is dextral, megalospheric sinistral.

Fig. 3. Inferior surface of the test of a microspheric agamont.

Fig. 4. Cross-section of a two-chambered mononucleate megalospheric gamont.

Fig. 5. Cross-section of a two-chambered multinucleate microspheric agamont.

Fig. 6. Decalcified total mount of a seventeen-chambered microspheric agamont showing twenty-five nuclei.

Fig. 7. Transverse section of a microspheric agamont showing the distribution and appearance of the nuclei prior to multiple fission.

Fig. 8. Transverse section of microspheric agamont test and cyst containing two-chambered mononucleate megalospheric gamonts.

PLATE II

Fig. 9. Multiple test consisting of two megalospheric gamonts associated in syzygy.

Fig. 10. One of a pair of excavated megalospheric tests following the escape of the sexually produced microspheric agamonts.

Fig. 11. Decalcified total mount of thirteen-chambered mononucleate megalospheric gamont.

Fig. 12. Cross-section of two megalospheric gamonts associated in syzygy, the gamonts showing one and two nuclei respectively.

Fig. 13. *a*, Nucleus of vegetative megalospheric gamont with multiple endosomes; *b*, early prophase nucleus showing the characteristic reduction in size and staining capacity of the multiple endosomes compared with those of the vegetative nucleus shown in Fig. 13 *a*.

Fig. 14. Cross-section of associated megalospheric gamont. One gamont contained four nuclei, the other eight, which suggests that two and three nuclear divisions had occurred in the respective organisms.

Fig. 15. Division figures of the final post-zygotic series prior to the development of typical vegetative nuclei.

Fig. 16. Triflagellated gametes of *Discorbis patelliformis* after fixation with osmic acid vapour followed with hot Schaudinn's fluid, and stained with iron haematoxylin. The gamete on the right bears a false pseudopodia in addition to three flagella.

Fig. 17. *a*, Zygotic nucleus during early growth; *b*, prophase of the first metagamic nuclear division; *c*, one of the vegetative nuclei of a juvenile microspheric agamont; the large multiple endosomes may or may not develop until after the escape of the megalospheric agamonts from the multiple tests.

Fig. 18. Partially excavated multiple tests showing the two multinucleate somatellae fused at the point where the inferior walls of the two tests have been dissolved.

Fig. 19. Two gametocytes showing anaphase nuclei of what is probably the reduction division. Three nuclei in the somatella of the second gamont. Multiple fission to form mono-nucleate gametocytes is usually delayed in the larger of a pair of gamonts associated in syzygy.

Fig. 20. Post-zygotic amoebulae within the brood chamber formed by the outer walls of the excavated multiple tests. Each amoebula contains, in addition to the zygotic nucleus, many picnotic nuclei of ingested gametes.

PLATE III

Discorbis opercularis; Photomicrographs of cytological preparations. The Foraminifera were killed and fixed in hot Schaudinn's fluid, sectioned in paraffin, and stained in iron haematoxylin.

Fig. 21. Multinucleate microspheric agamont. Section passes through the lower portion of the proloculum and the upper whorl of chambers.

Fig. 22. Multiple fission in a microspheric agamont. Section shows a portion of the content of three chambers.

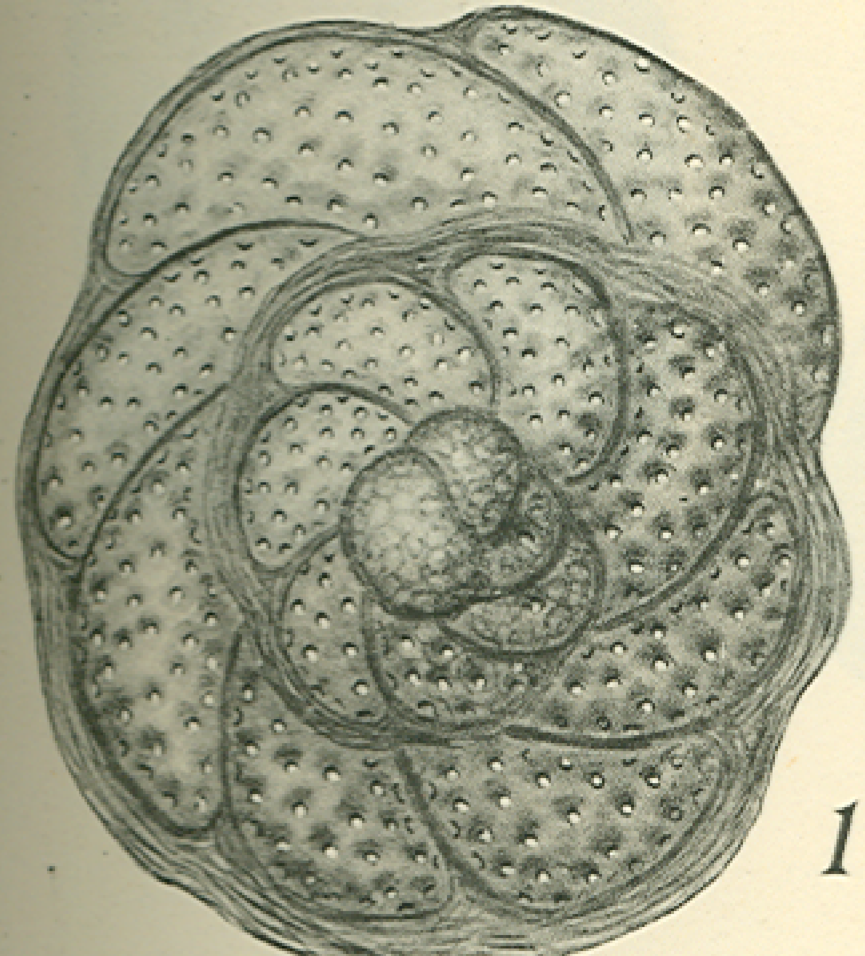
Fig. 23. Earliest free stage of mononucleate megalospheric gamonts.

Fig. 24. Section through the major axis of a mature mononucleate megalospheric gamont.

Fig. 25. Median section through two gamonts associated in syzygy showing gametes within the brood chamber formed by the excavated megalospheric tests. *Inset.* Free gamete showing a trailing flagellum and the two tractile flagella as they would appear at mid-stroke (untouched).

Fig. 26. Monolocular, multinucleate microspheric agamonts within a multiple test. A second or occasionally a third chamber is added before the two tests forming the brood chamber separate and the juvenile agamonts are free to escape.

Fig. 27. *Discorbis ornatissima. a* and *b*, multiple tests consisting of pairs of megalospheric gamonts associated in syzygy; *c*, pair of tests previously associated in syzygy which were separated before the first progamic nuclear division. The ventral walls of the two tests begin to dissolve during early gametogenesis; *d*, multiple tests containing juvenile megalospheric agamonts; *e*, more advanced stage than that shown in *d*, the opening between the two tests having been further enlarged and the juveniles ready to escape; *f*, one of a pair of excavated tests following the escape of the megalospheric agamonts.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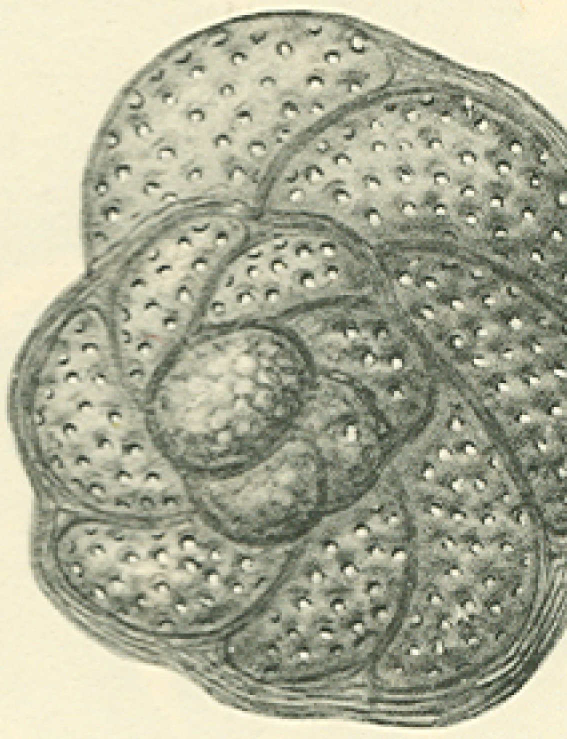
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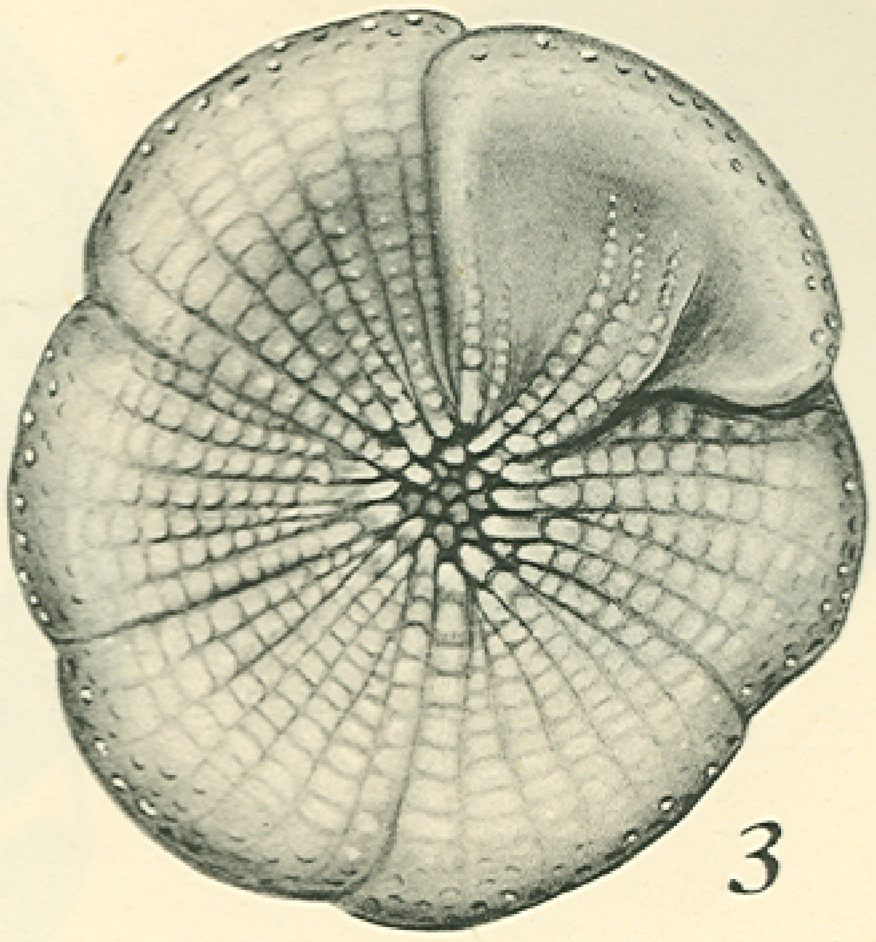
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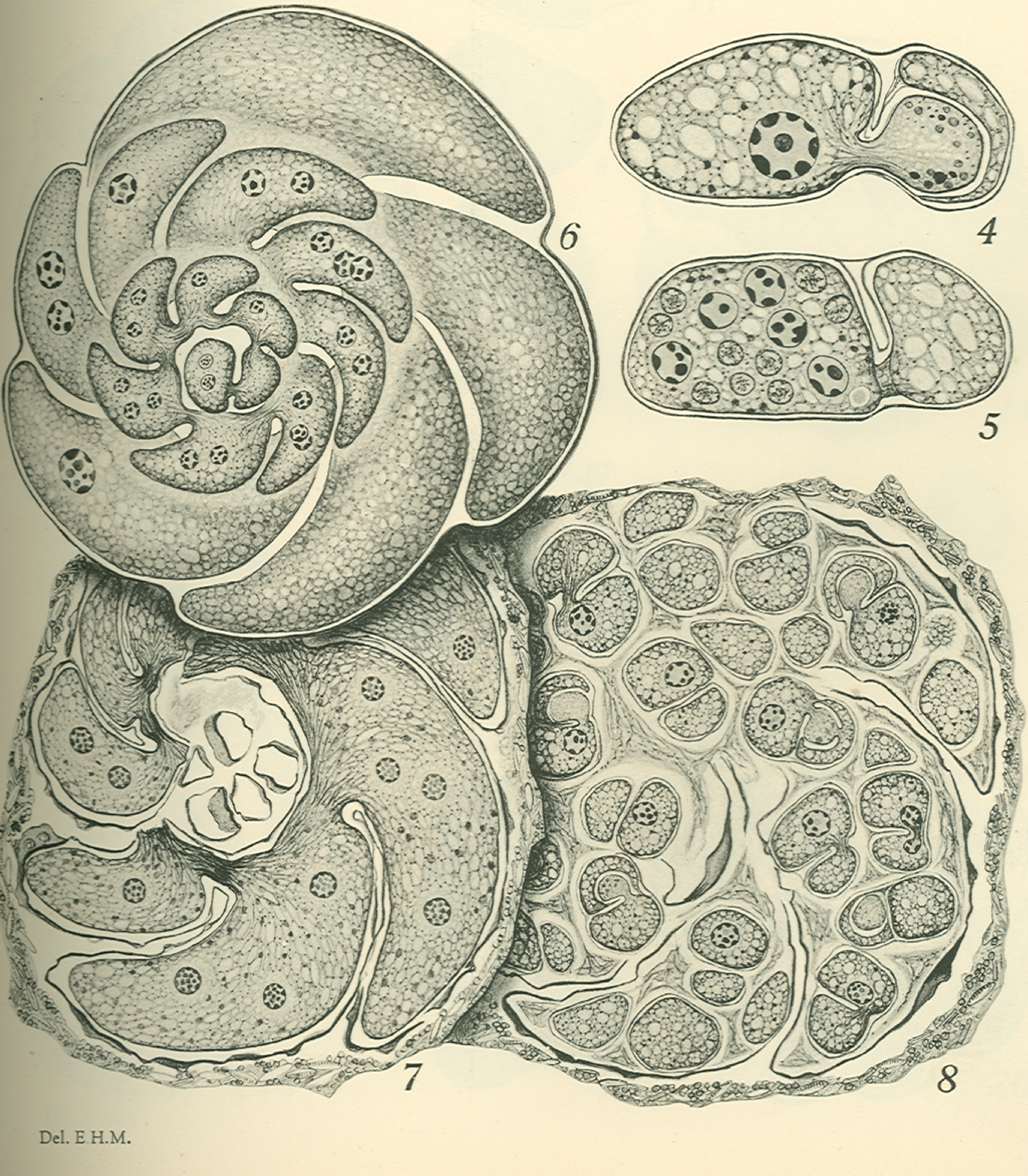

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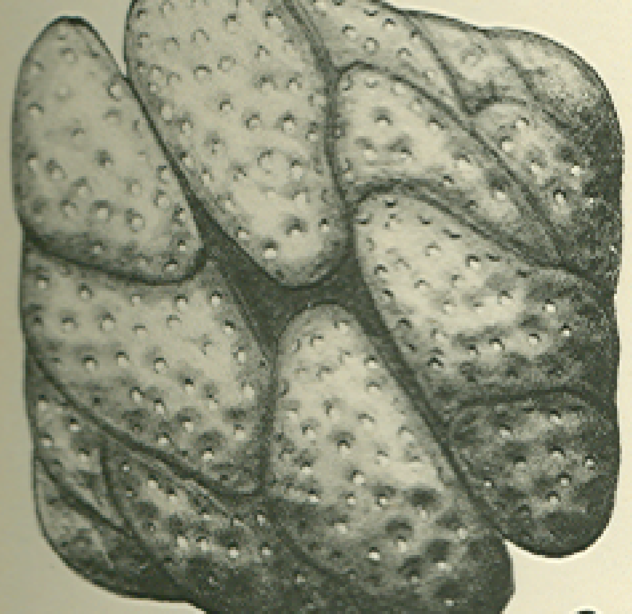

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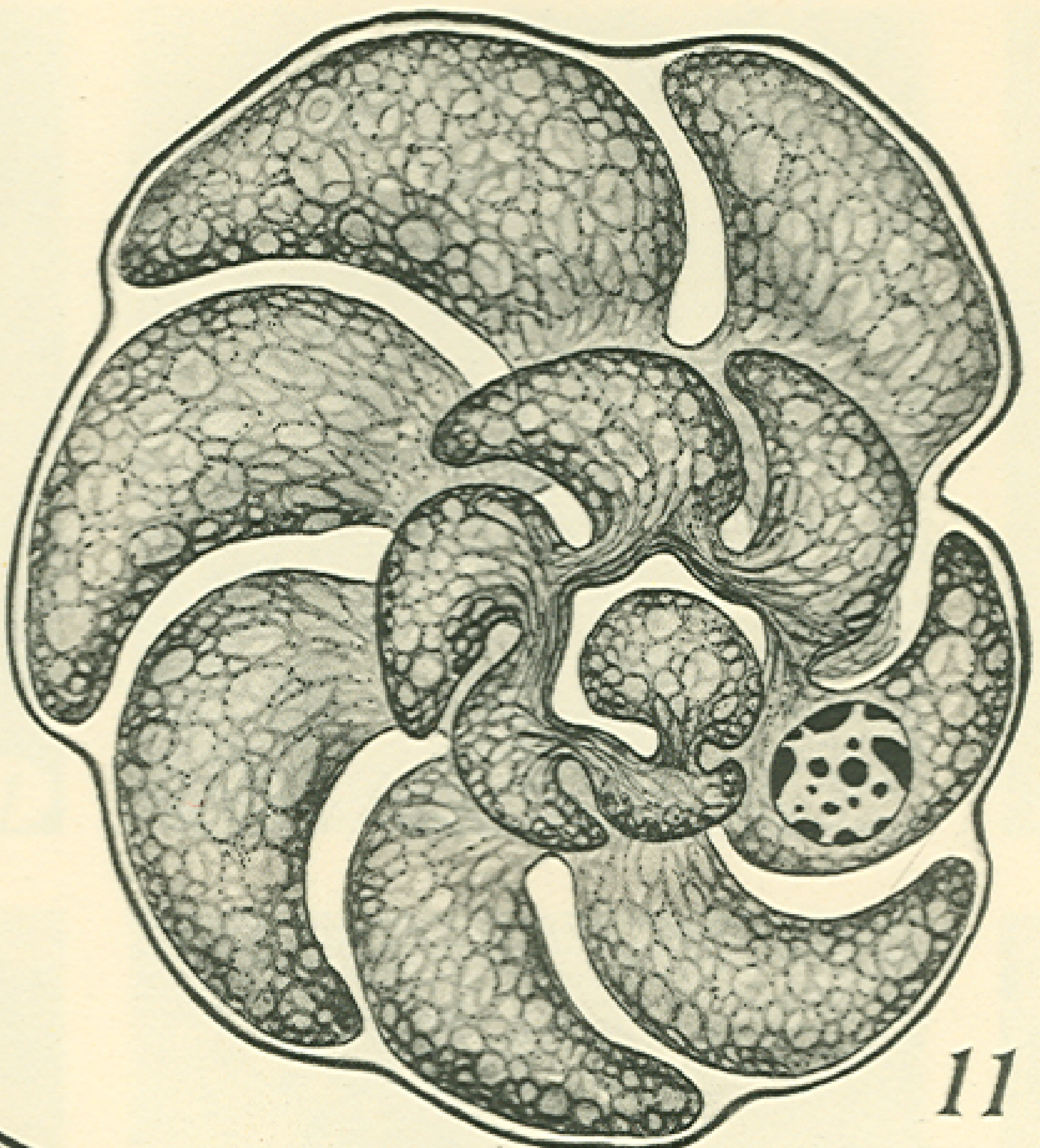

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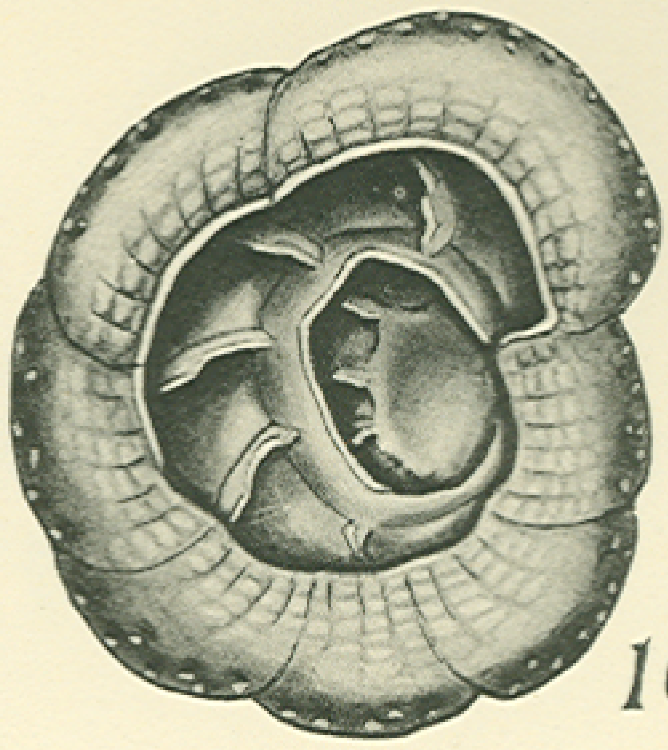

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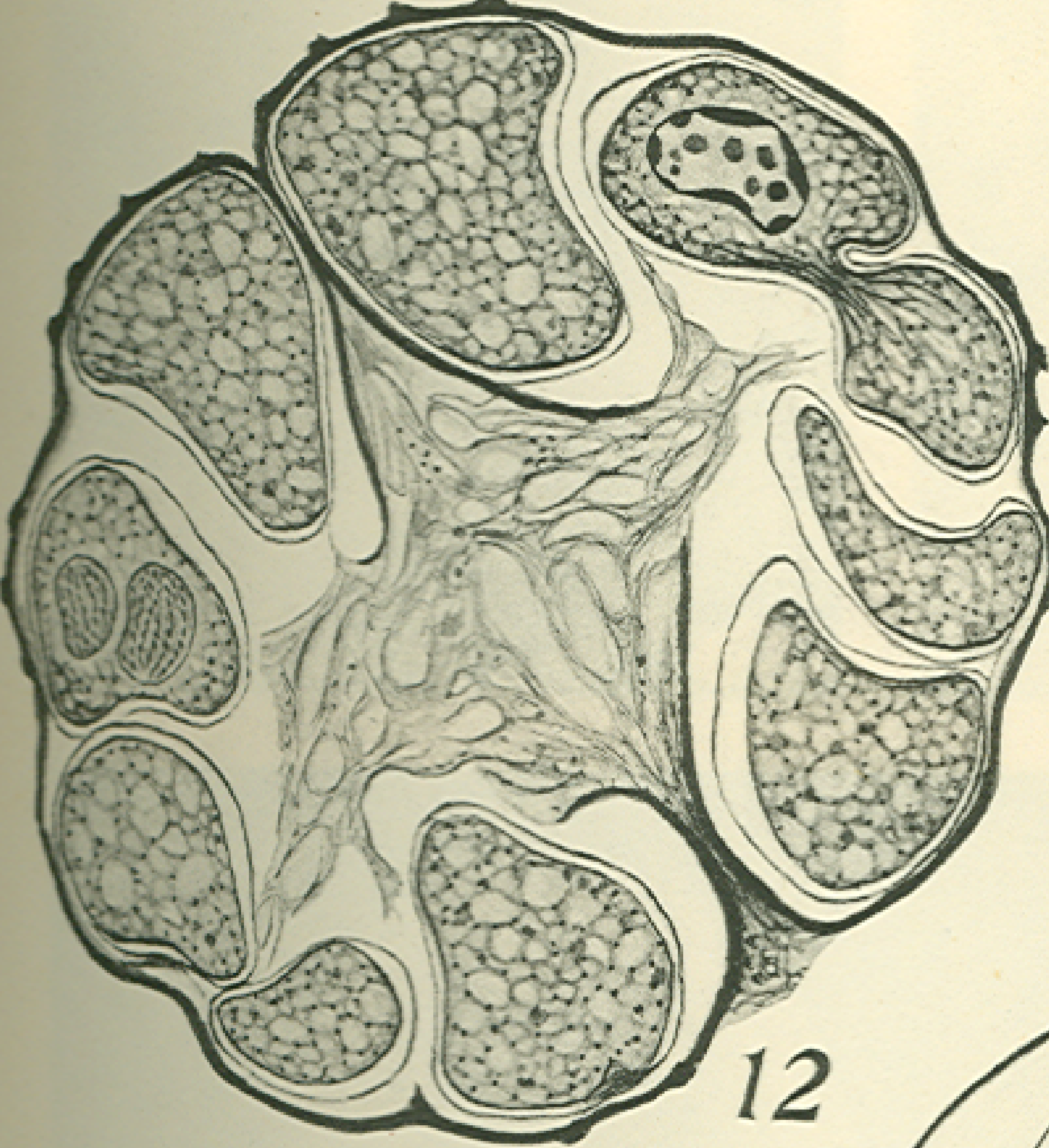

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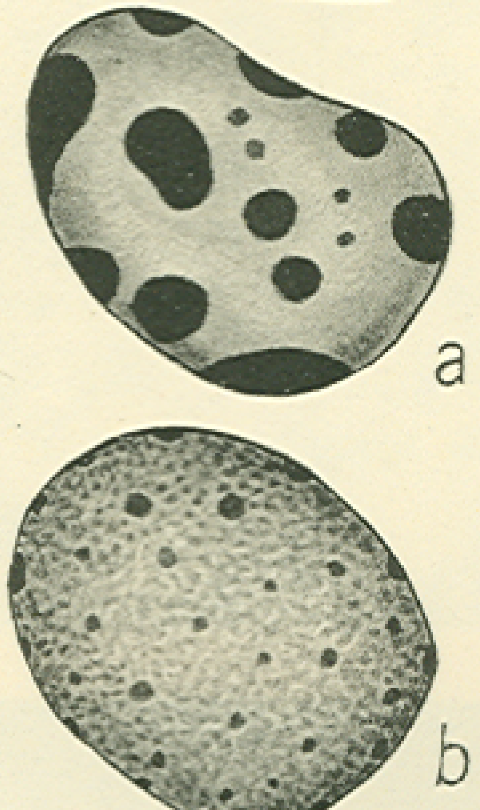

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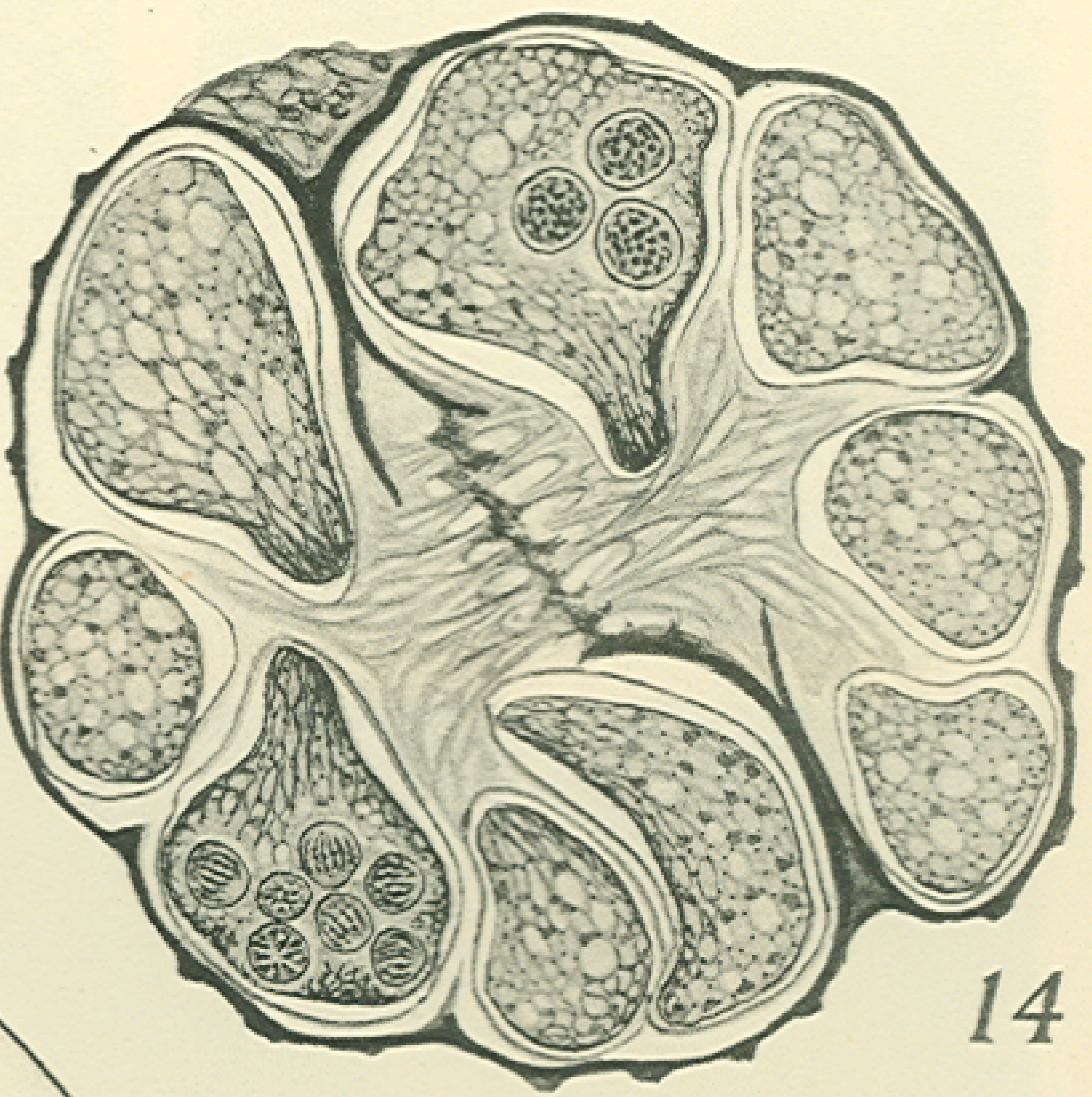

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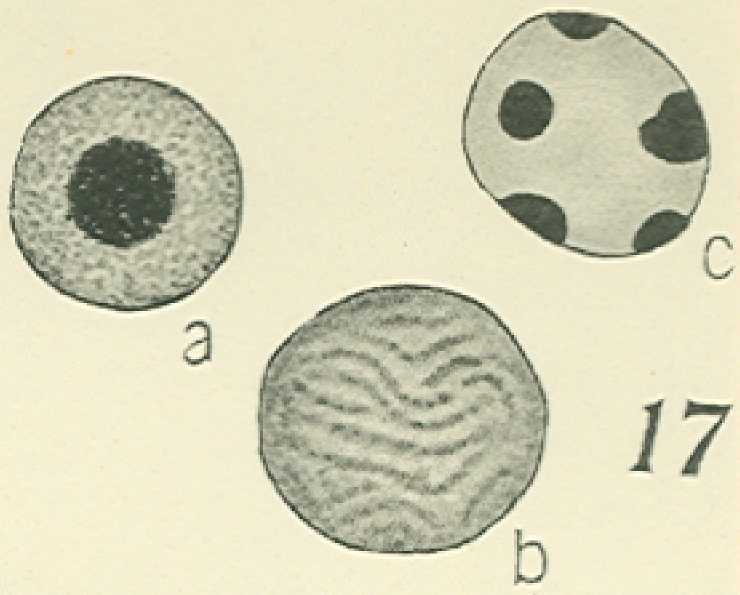

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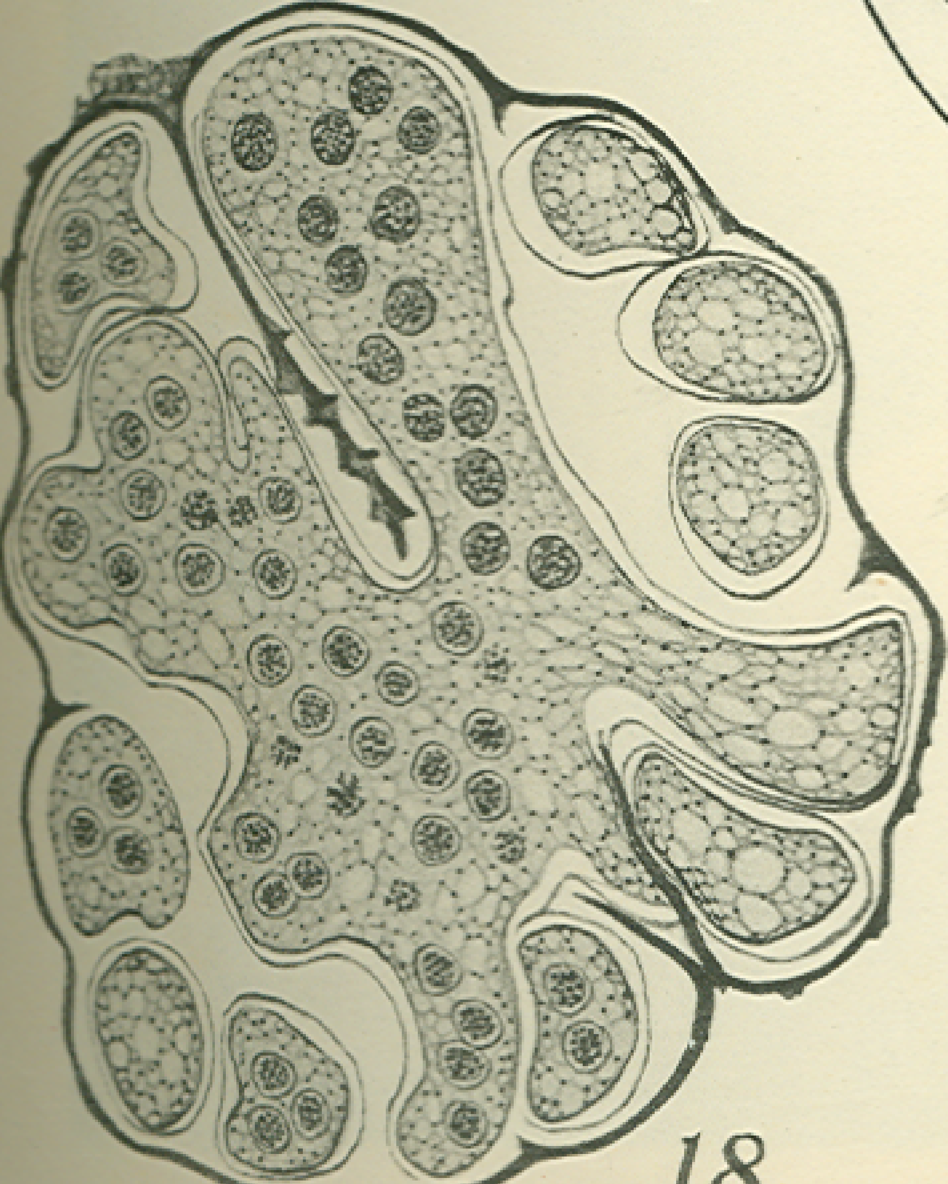

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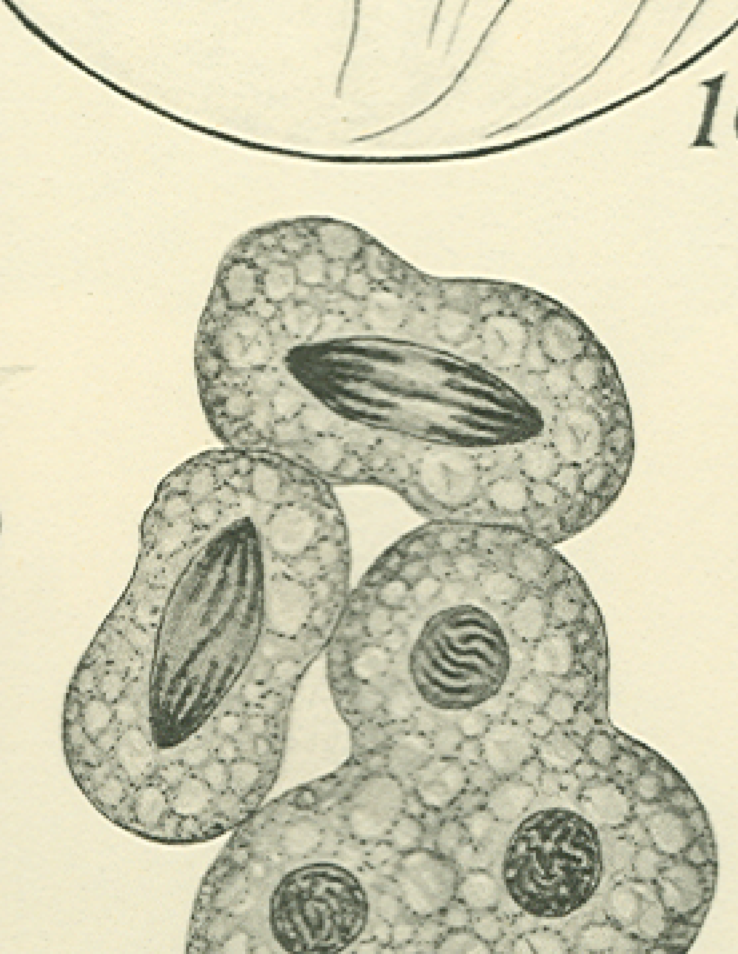

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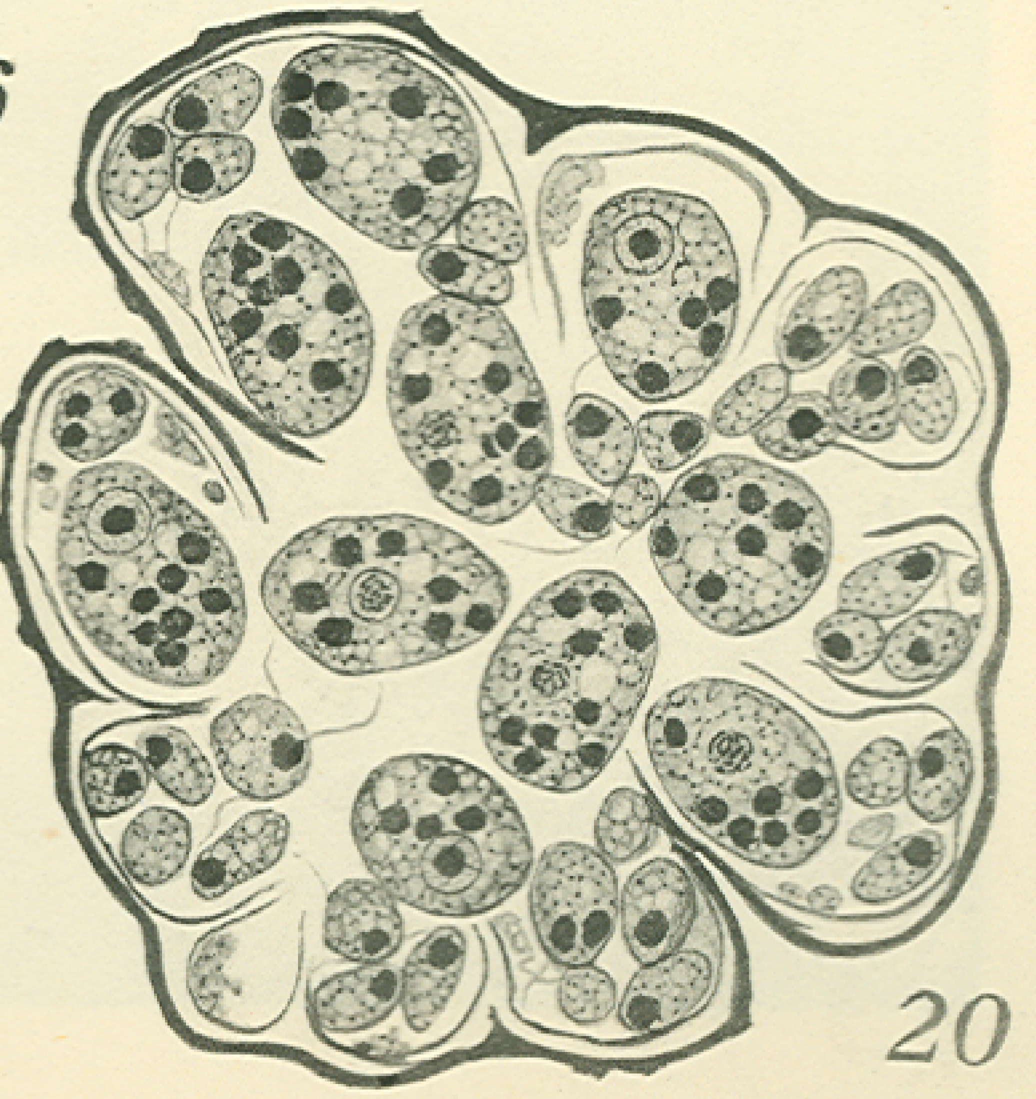

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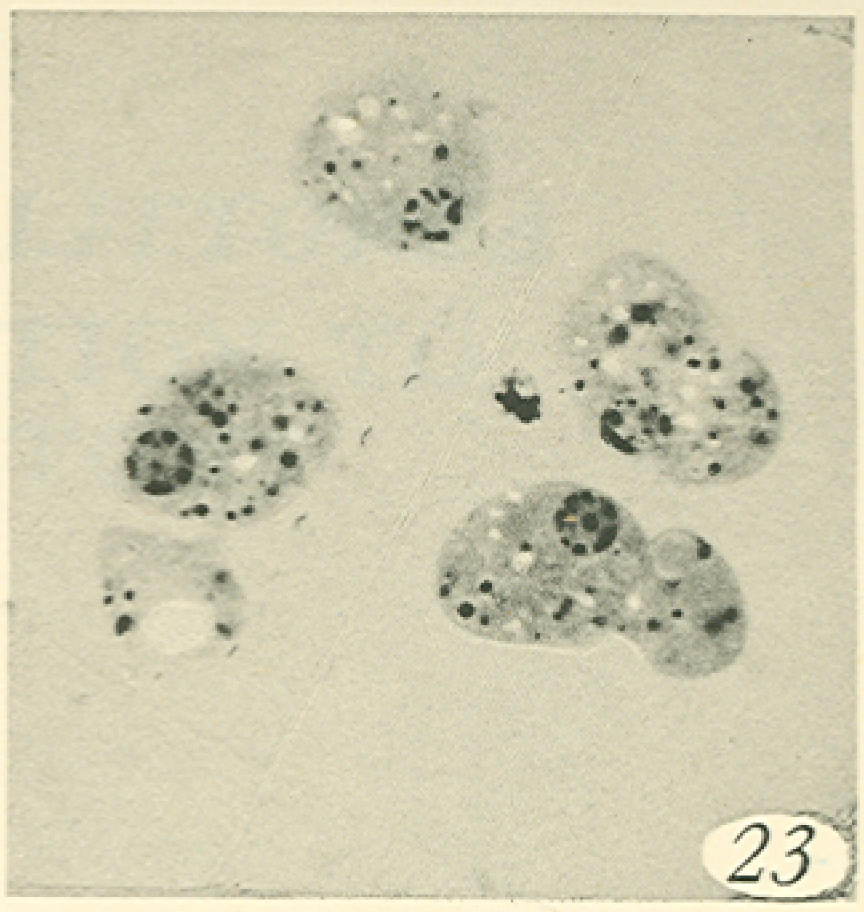
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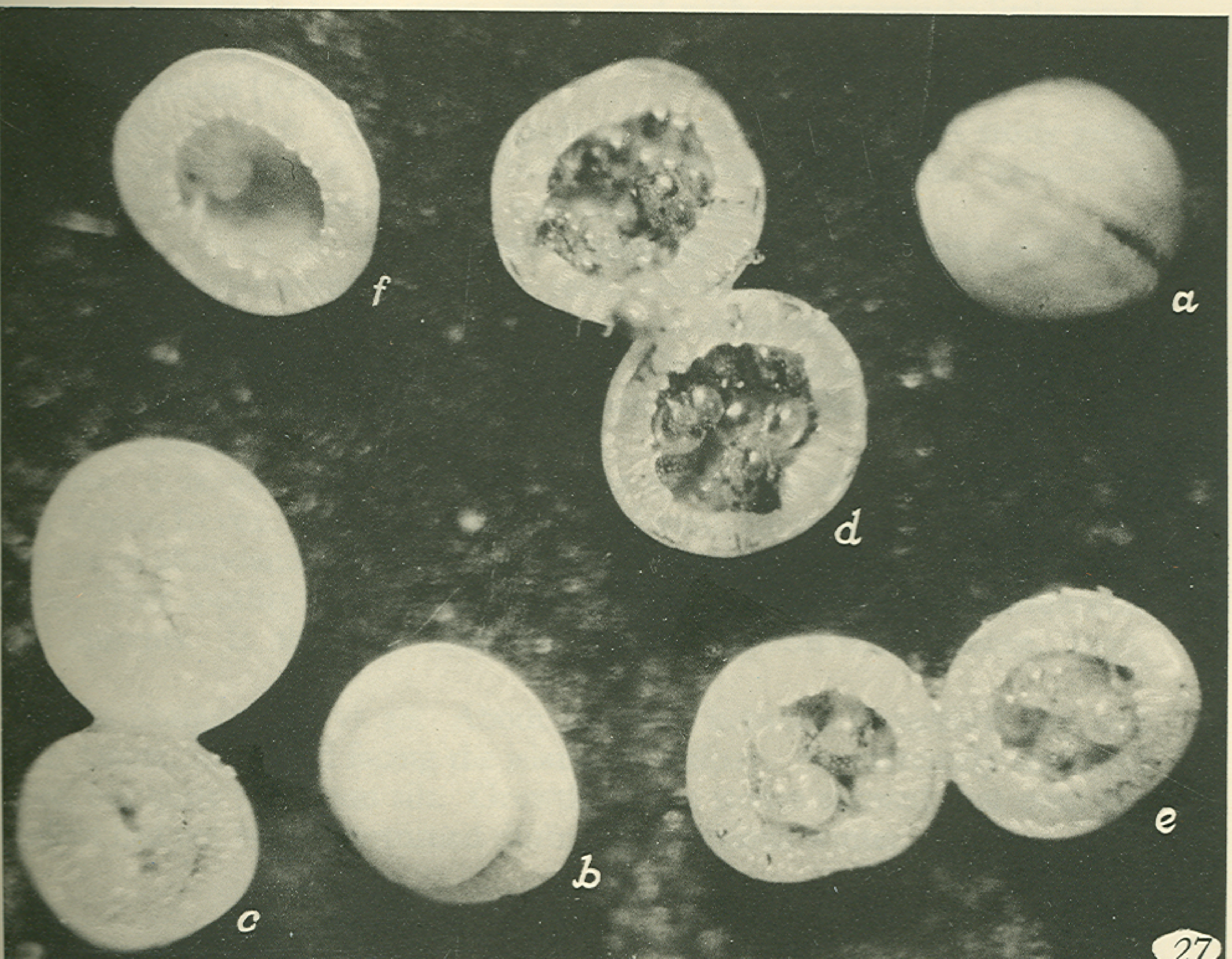

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Photo. E.H.M.

THE BIOLOGY OF *LITTORINA LITTOREA* PART II. ZONATION IN RELATION TO OTHER GASTROPODS ON STONY AND MUDDY SHORES

By Hilary B. Moore, Ph.D.

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(Text-figs. 1–8)

The survey, the results of which are described in this paper, was primarily intended to investigate the zonation of *Littorina littorea*, but notes have also been included of the zonation of such other gastropod species as occurred with it. The material was collected from the following localities:

Torpoint. 2. x. 36. Just west of the ballast dock at Torpoint, Cornwall. The shore consists of stones, many of them bedded in mud, and thickly overgrown with fucoids. There is little wave-action, but at times a considerable drop in salinity (Hartley & Spooner, 1938; Milne, 1938).

Drake's Island. 5. viii. 36. On the north side of Drake's Island, in Plymouth Sound. The shore is fairly steep, rocky, and with comparatively little mud. The locality is the same as that used for growth experiments on *L. littorea* and other species (Moore, 1937, 1938).

Rum Bay. 2. x. 16. On the east side of Plymouth Sound. A stony gully considerably overgrown with fucoids. The lower part of the traverse is probably considerably polluted by a neighbouring sewer.

Wembury. 16. ix. 36. A gulley traversing the reefs near Wembury Point, Devon. The substratum is sand or rock, covered with stones of all sizes. Although the situation is exposed, the rocks on either side of the gulley afford considerable protection from wave-action. This, and to a lesser extent Rum Bay, are the only localities where the zonation levels are likely to be appreciably raised by splash.

Yealm. 2. ix. 36. Misery Point, on the south side of the estuary of the river Yealm, Devon. The substratum is hard mud, covered with stones, which increase in abundance towards the top of the shore, which is dry and very barren. This locality is sheltered from the sea, but subject to considerable tidal currents. It also was used for growth experiments (Moore, 1937, 1938).

Caolas Scalpay. 13. vi. 36. About half-way between Broadford Bay and Loch Ainort, Skye, and facing the island of Scalpay. An extremely sheltered shore, but quite free from silt. Growth on the stones showed that even the smallest had not been overturned during the previous winter.

The method of collecting was to mark out a number of quarter square metre areas at each of a series of levels down the beach. All stones and all free molluscs were then collected from each area, the stones being taken back to the laboratory for examination except at Caolas Scalpay where the examination had to be made in the field. With the same exception all levels were fixed with a dumpy-level and staff, and referred, by means of simultaneous observations of water level at low water on a calm day, to a known level below the Biological Laboratory. At Caolas Scalpay levels were referred to predicted and observed high-water level on a series of days. No great accuracy is therefore claimed for the absolute values of the levels given, especially for the Skye ones.

For the identification of rissoids I am indebted to Dr M. V. Lebour, and for *Hydrobia* to the Hon. M. Rothschild and Mr R. Winckworth.

Littorina littorea (L.) (Fig. 1).

The lower limit for this species was more uniform than the upper. At all localities it was abundant at mean low water of neap tides, and less so, where sampled, at mean low water of springs. This is in agreement with the levels given by Orton (1929)—present at mean low water, less at mean low-water springs; by Gowanloch & Hayes (1926)—lowest low-tide level; and by Colman (1933)—mean to equinoctial low-water springs; but Huntsman (1918) says that, while only intertidal at St Andrews, they extend down to 20 fathoms at Chitticamp.

The upper limit seems to depend considerably on local conditions. At the Yealm, where the upper beach was stony, with little algal growth, they hardly passed mean low-water neaps. At the other localities they attained equinoctial high-water neaps in some abundance, and a few stragglers occurred even higher. Orton gives the upper limit as between mid-tide and mean high-water neaps; Gowanloch & Hayes as mean high water; and Colman as lowest mean high-water neaps. *L. littorea* thus seems to require wetting by the sea every tide, and in the localities where it occurs above high-water neaps the effective levels are raised by splash. The question of the effect of age on zonation in this species is discussed later in the paper.

Littorina rudis (Maton) (Fig. 2).

In contrast with *L. littorea*, this species has a well-defined upper, and a much more variable lower limit. At three localities the upper limit was about mean high-water springs and at the other two about equinoctial high-water

Fig. 1. Vertical distribution of *Littorina littorea* (numbers per square metre). Vertical heights are shown in metres above and below mean sea level. I = high water of equinoctial spring tides. II = mean high water of spring tides. III = mean high water of neap tides. IV = high water of equinoctial neap tides. V = mean sea-level. VI = low water of equinoctial neap tides. VII = mean low water of neap tides. VIII = mean low water of spring tides. IX = low water of equinoctial spring tides. Localities: *a*, Torpoint; *b*, Drake's Island; *c*, Rum Bay; *d*, Wembury; *e*, Yealm; *f*, Caolas Scalpay.

Fig. 2. Vertical distribution of *Littorina rudis*. Symbols as in Fig. 1.

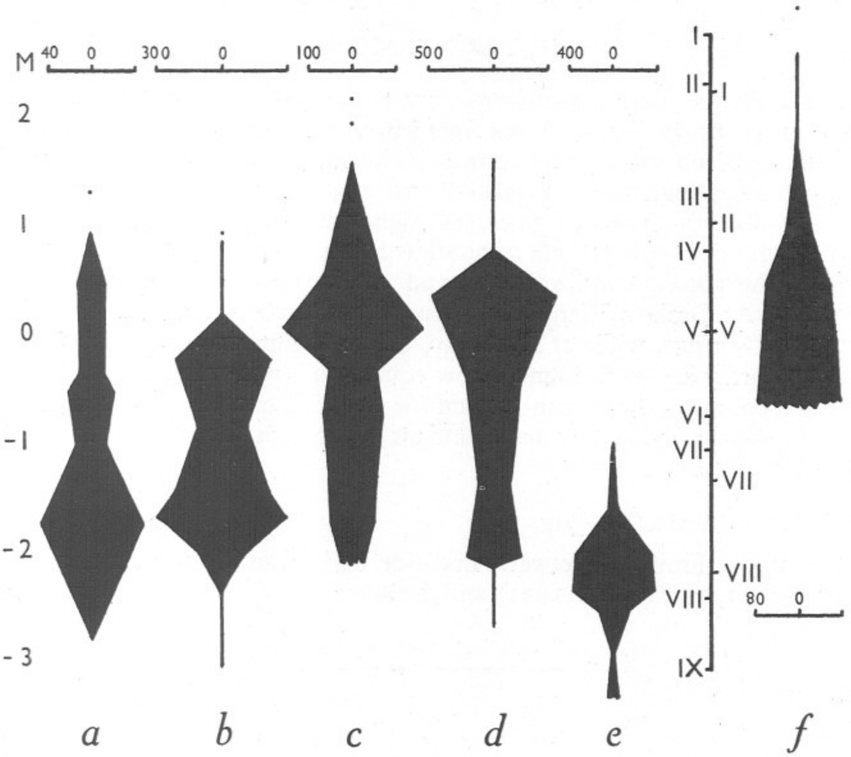
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Fig. 1.

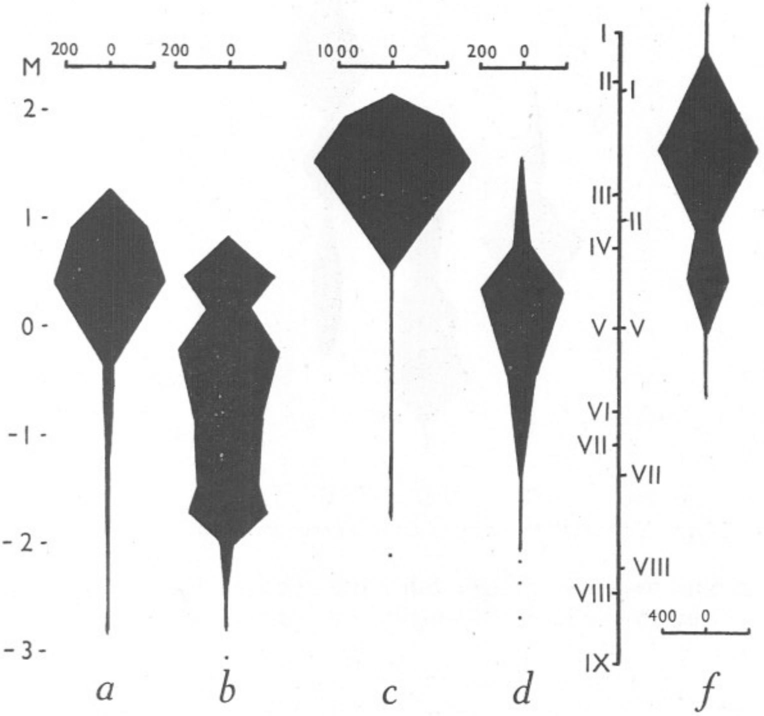
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Fig. 2.

springs. At the Yealm, again probably because of the dryness and lack of algae in the upper levels, it was found in very small numbers only. Other authors agree on these levels: Orton, mean high-water springs; Gowanloch & Hayes mean high water; Fischer-Piette (1936) just above mean high-water springs. Colman however gives the high value of 3 ft. above equinoctial high-water springs, his locality doubtless being more affected by splash.

Both the absolute lower limits, and the limits of abundance, are very variable. At Drake's Island they were abundant between mean low-water neaps and springs, while at Rum Bay, where conditions are apparently very similar, hardly any were found below equinoctial high-water neaps. Neither lack of food nor of shelter can account for this difference, nor can competition with *L. littorea*, since they are abundant along with the latter at low levels at Drake's Island.

Littorina obtusata (L.) (Fig. 3).

The upper limit lies between mid-tide and mean high-water neaps (see also Orton, 1929; Colman, 1933), and the lower limit, at any rate of abundance, about mean low-water springs. Since this species is far more abundant on fucoids than on the stones themselves, it is not surprising that it was not

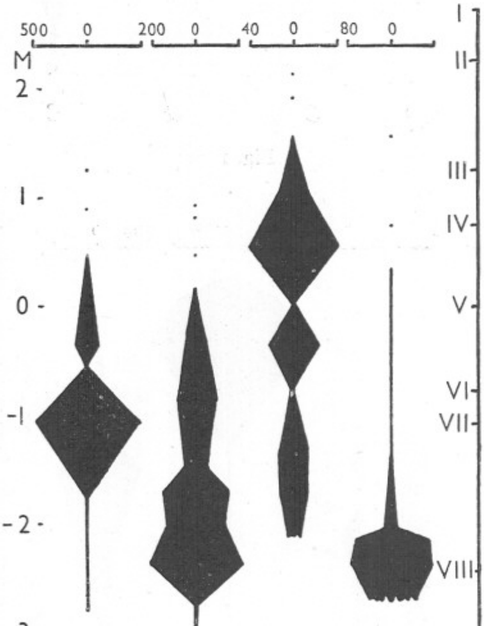

Fig. 3. Vertical distribution of *Littorina obtusata*. Symbols as in Fig. 1.

found at the Yealm where fucoids were so scarce. At Caolas Scalpay also it was present only in very small numbers round low water.

Hydrobia ulvae (Penn.) (Fig. 4).

This is not typically a rocky shore gastropod, occurring in far greater numbers on estuarine saltings and mud flats. The level of the former is usually above high-water neaps, and *H. ulvae* may be extraordinarily abundant on them. Its frequent absence at low water on estuarine mud flats is probably due in many instances to strong tidal action. It is interesting therefore to note its occurrence in small numbers below mean low-water springs at Torpoint where the shore combines muddiness with protection by fucoids and stones. It is also interesting that at Caolas Scalpay, where the shore was strikingly free from silt, the *Hydrobia* were confined to a very limited zone round mid-tide.

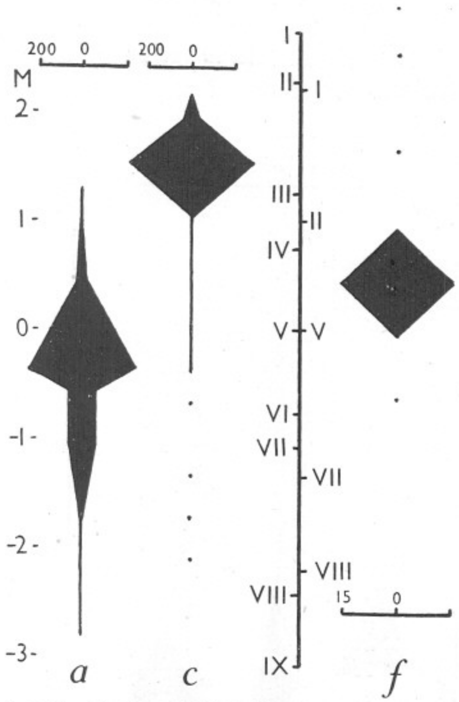

Fig. 4. Vertical distribution of *Hydrobia ulvae*. Symbols as in Fig. 1.

Alvania crassa (Kanmacher), **Rissoa parva** (da Costa), **Cingula semicostata** (Mont.), **Barleeia unifasciata** (Mont.).

All recorded from mean low-water spring tide at Wembury and not elsewhere.

Cingula cingillus (Mont.).

A few at Rum Bay from mean high-water neaps to mean low-water neaps, and at Wembury from mean low-water neaps to mean low-water springs.

Osilinus lineatus (da Costa).

Found only at Wembury, from mean high-water neaps to mean low-water neaps. Colman records it from mean high-water neaps to mid-tide, but it is known to extend lower under the influence of fresh water.

Gibbula cineraria (L.) (Fig. 5).

Except at Caolas Scalpay, this did not occur in any numbers above mean low-water neaps, and was never found above mid-tide. At most localities the level of maximum abundance seemed to be below the lowest level sampled. For the Isle of Man it is recorded from low water to 15 fathoms, and more rarely deeper (Moore, 1937*a*), and in the Plymouth Fauna (Marine Biological Association, 1931) down to 10 fathoms.

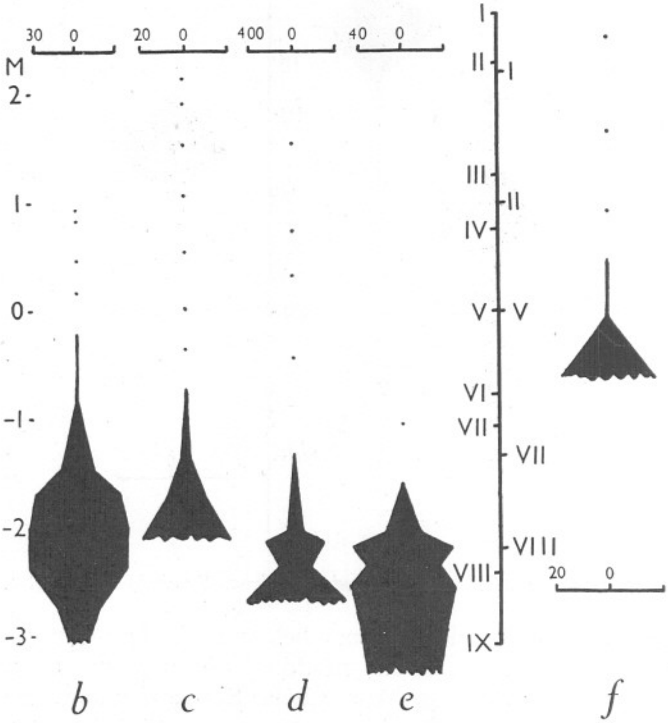

Fig. 5. Vertical distribution of *Gibbula cineraria*. Symbols as in Fig. 1.

Gibbula umbilicalis (da Costa) (Fig. 6).

A few above mid-tide, but maximum numbers between mean low-water neaps and mean low-water springs, and few or none below low water. This species does not usually extend so far below low water as the preceding: Plymouth Fauna, down to 3 fathoms; Moore, never below low water: and most authors record it as extending to a higher level on the shore than *G. cineraria*. The Plymouth Fauna gives its upper limit as high water; Moore, for the Isle of Man, as mid-tide, and Dolfus (1914) even gives its lower limit as the upper limit of *G. cineraria*. Our localities, however, suggest that, while stragglers were certainly found a lot higher than any *G. cineraria*, the zones of maximum abundance showed less difference.

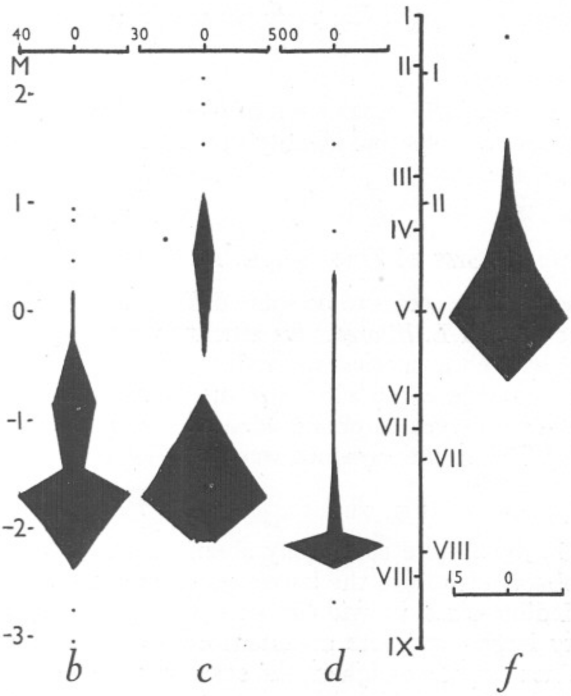

Fig. 6. Vertical distribution of *Gibbula umbilicalis*. Symbols as in Fig. 1.

Buccinum undatum L.

A few young individuals were found about mean low-water springs at the Yealm. Gowanloch (1927) has discussed in detail the unfitness of this species for intertidal life.

Purpura lapillus L.

The zonation of this species has been discussed already in another paper (Moore, 1938).

Nassarius reticulatus (L.).

At Rum Bay and the Yealm, from between mid-tide and mean low-water neaps down to below low water.

Calyptraea chinensis (L.).

At the Yealm from just above mean low-water springs to just below equinoctial low-water springs. Up to 40 per square metre.

Patella spp.

As these are not typically inhabitants of loose stones, and as there is still considerable doubt as to specific identity in the British *Patella* spp., the few found were not counted.

RELATION OF SIZE TO ZONATION IN *LITTORINA LITTOREA*

On many shores there seems to be some difference in vertical distribution in the different sizes of *L. littorea*. An attempt was therefore made at four of the localities where the species was sufficiently abundant, to collect large enough samples at all levels to allow size distribution analyses to be made. It proved difficult however to obtain adequate samples towards the upper and lower limits. The results obtained were as follows:

Drake's Island, 5. viii. 36 (Fig. 7).

Young (1936 brood) were completely absent from the upper part of the range, and probably also from the lowest part (sample too small to include in Fig. 7). Medium-sized individuals were present throughout the entire range, but very large ones were abundant only at the middle and lowest levels, and did not extend so high on the beach as the medium ones.

Wembury, 16. ix. 36 (Fig. 7).

Young (1936 brood) were present at all levels, though more abundant (relative to adults) round the centre of their range. Very large individuals, as at Drake's Island, were confined to the middle and bottom of their range.

Yealm, 2. ix. 36 (Fig. 8).

Young (1936 brood) were rare in the lowest levels, and large individuals absent from the highest. If the numbers are to be considered adequate, which seems rather doubtful, there is a suggestion of greater growth rate in the first year towards high water. This is interesting when compared with

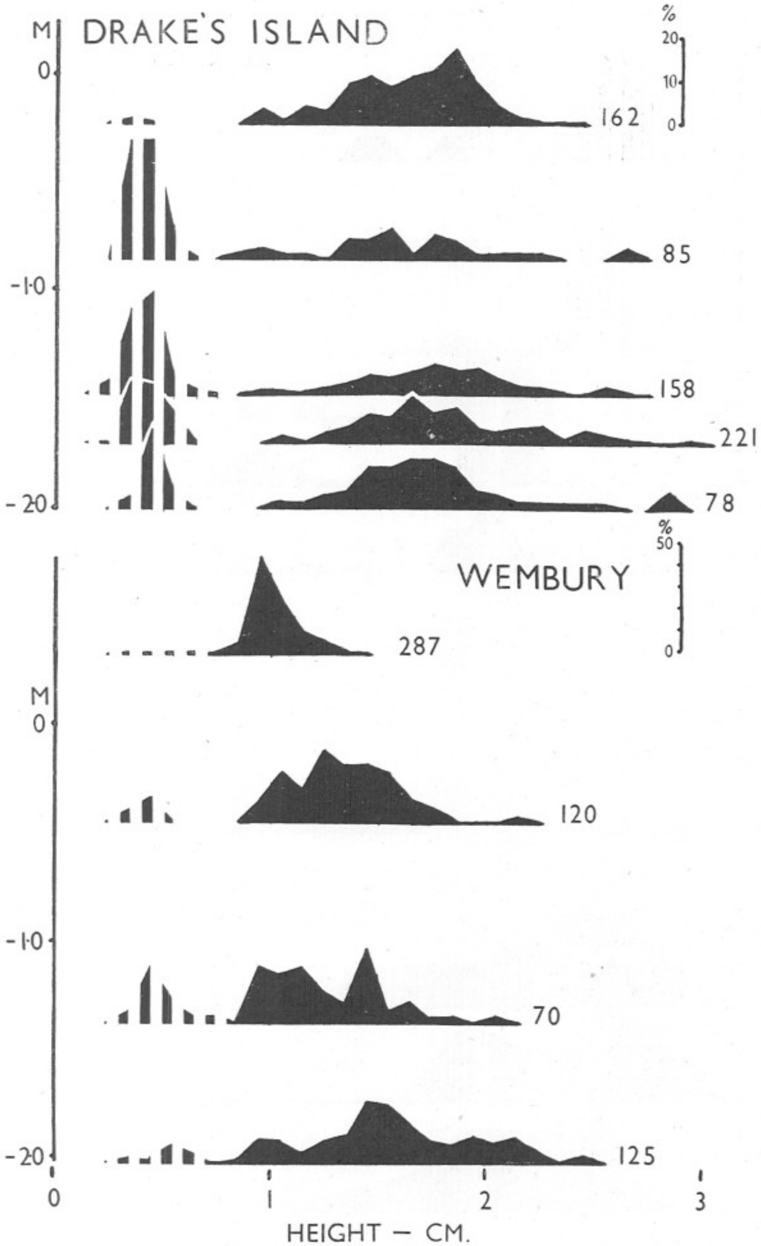

Fig. 7. Size distribution of *Littorina littorea* in relation to tidal level at Drake's Island and Wembury. Heights of shells are measured in centimetres and the numbers of shells measured in each sample are shown by the figures at the right of each graph. For each locality, all samples are drawn to the percentage scale shown, except in the case of the top sample from Wembury, which is drawn to half-scale. The extent of the 1936 group is indicated by vertical hatching.

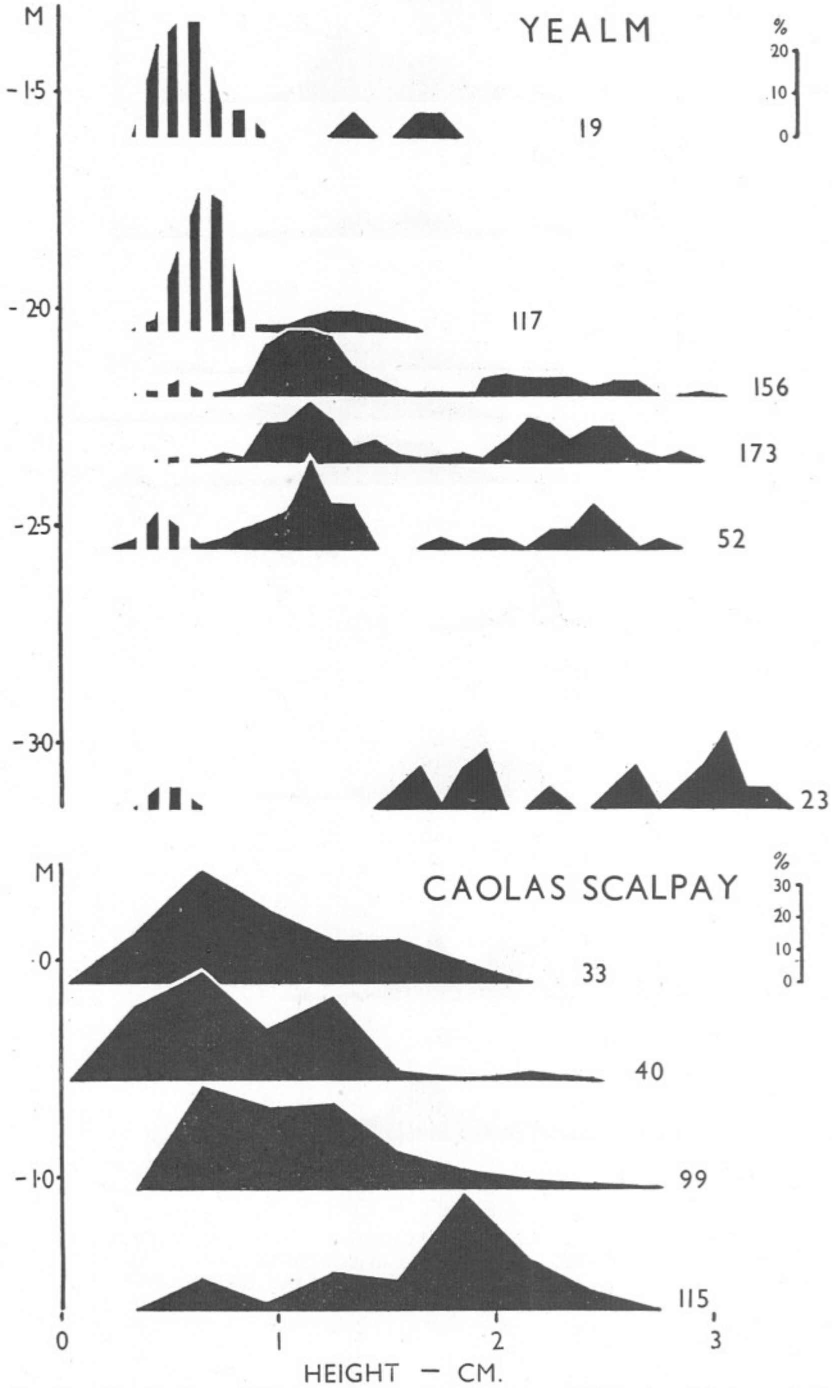

Fig. 8. Size distribution of *Littorina littorea* in relation to tidal level at Yealm and Caolas Scalpay. Symbols as in Fig. 7. The 1936 group is not indicated at Caolas Scalpay as the material was collected there too early in the year for the new brood to have settled.

Hayes's (1929) statement that at St Andrews the growth rate of young *L. littorea* is greatest towards low water. It may be noted that the rate of growth at the Yealm was considerably less at all sizes than at Drake's Island (Moore, 1937).

Caolas Scalpay, 11–18. vi. 36.

Young (probably 1935, as 1936 brood were unlikely to have settled yet), scarce, but not absent, towards the bottom of their range, and large ones similarly scarce towards the top.

The general result, then, from this admittedly small number of localities, is that medium-sized individuals occur throughout the local vertical range of the species; the largest individuals tend to be rare or absent at the top levels, and may be most abundant at the lowest levels. Very young individuals, on the other hand, tend to be scarce or absent in the lowest levels, and more rarely in the highest levels also.

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THE LARVAE OF THE PANDALIDAE

By Marie V. Lebour, D.Sc.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–12)

Little is known of the larvae of the Pandalidae as is shown by Gurney (1939) in his Bibliography of the Larvae of Decapod Crustacea. Berkeley (1930, 1938) describes the life histories of several species of *Pandalus* and of *Pandalopsis dispar* from British Columbia, and Gurney (1937) the larvae and post-larvae of *Chlorotocella*, but beyond these the information is fragmentary. Sars' (1900) work on *Pandalus borealis* and *P. bonnieri* was formerly regarded as typical of pandalid larvae but these were proved to be *Caridion* (Lebour, 1930). Sars (1900), however, described in part in an excellent manner the larvae of *Pandalus montagui* and *Pandalina brevirostris* and Stephensen (1935) the early larvae of *Pandalus propinquus*. Whilst in Bermuda it has been possible to follow the whole larval and post-larval history of *Parapandalus richardi* and the first five larval stages of *Pandalus bonnieri* have been obtained by rearing from the egg by Dr A. G. Nicholls at Millport. These latter he has kindly given to me to describe. We have thus eight species of *Pandalus* whose larvae are known, one *Pandalina*, one *Pandalopsis*, one *Chlorotocella* and one *Parapandalus*. Besides these Gurney (1924) has described three pandalid larvae, one of which he has shown to be *Chlorotocella* (Species 2, fig. 44), one is probably some genus related to *Pandalus* (Species 1, fig. 43) and the third as will be shown below is probably a *Plesionika*.

It is interesting to compare these and to try to find the general characters of this family and those of its genera. We may with some justification place them in the following order, beginning with the most primitive:

? *Plesionika* sp. (larvae described by Gurney, 1924).
Parapandalus richardi (larva and post-larva described in the present work).
Pandalina brevirostris (larva described by Sars, 1900).
Pandalus montagui (larva described by Sars, 1900).
P. bonnieri (larvae described in the present work).
P. propinquus (larva described by Stephensen, 1935).
P. borealis (larvae described by Berkeley, 1930).
P. stenolepis (larvae described by Berkeley-Needler (=Berkeley), 1938).
P. hypsinotus (larvae described by Berkeley, 1930).
P. danae (larvae described by Berkeley, 1930).
P. platyceros (larvae described by Berkeley, 1930).
Pandalopsis dispar (larvae described by Berkeley, 1930).
Chlorotocella sp. (larvae described by Gurney, 1937).

The larvae of the family Pandalidae may be thus defined:

Caridea with rostrum in all stages; antennular peduncle concave on the outer margin (except sometimes in the first stage); antennal flagellum a simple rod ending in a seta with or without an accessory seta; mouth parts well developed; 5th leg never prematurely developed; none of the legs oar-shaped. No exopod on leg 5. Rostrum toothed in late stages. Legs 3–5 ending in simple dactyls. Leg 1 simple or with rudimentary chela. Leg 2 chelate in late stages.

Genus *Plesionika* (?). Early stages probably very like *Parapandalus*. Exopods on legs 1–4. Long series of larval stages (?); epipods in late stages.

Genus *Parapandalus*. No legs on hatching; antennal scale jointed at tip in first larva; flagellum unjointed: exopods on legs 1–4. Long series of larval stages. Telson with 7 + 7 spines in the first stage, 8 + 8 in the second, indented in hind margin. No epipods in late stages.

Genus *Pandalina*. No legs on hatching; antennal scale jointed at tip in first larva; flagellum unjointed; exopods on legs 1–3. Usual number of larval stages (8 or 9). Telson as in *Parapandalus*.

Genus *Pandalus*. All legs present on hatching, either rudimentary or functional; antennal scale jointed or not jointed at tip, flagellum unjointed or jointed; exopods on legs 1–2 or 1–3, never on 4 or 5. Usually 6 larval stages, probably more in *P. montagui*.

Telson as in *Parapandalus*.

The genus *Pandalus* may be divided into 2 groups:

Group I. Legs rudimentary on hatching; antennal scale jointed. *P. montagui*, *P. bonnieri*, *P. propinquus*.

Group II. Legs functional on hatching, antennal scale unjointed. *P. stenolepis*, *P. hypsinotus*, *P. danae*, *P. platyceros* (*P. borealis* has the legs rudimentary but the scale unjointed and thus comes between the two groups).

Genus *Pandalopsis*. Legs functional on hatching; exopods on legs 1–3; antennal scale unjointed; telson with 24 spines on hatching; 5 larval stages.

Genus *Chlorotocella*. No legs on hatching; exopods on leg 1 only; antennal scale jointed on hatching; telson rounded with 7 + 7 and 8 + 8 setae in first and second stages. 6 larval stages.

Pandalid, species I (Gurney, 1924), has a very long rostrum on hatching, armed with fine setae at the tip, and has no legs. It is probably not a true *Pandalus* but belongs to some closely related genus.

THE BRITISH SPECIES OF PANDALIDS

Four species of *Pandalus* are recorded as British: *P. montagui*, *P. bonnieri*, *P. propinquus* and *P. borealis*; three of these belong to Group I, *P. borealis* coming between the two groups; none belong to Group II. Of these *P. montagui* is the commonest and most widely distributed, occurring at times close to the shore, whilst all the others occur in more open water. *Pandalina brevirostris* is also a common form in fairly shallow water. *Pandalus* *montagui* and *Pandalina brevirostris* are both common at Plymouth their larvae occurring abundantly in the plankton. The larvae of *P. bonnieri* have been found in plankton off the Seven Stones Light Ship.

Pandalus montagui Leach (Fig. 2)

Sars (1900) describes the third (as about the fifth) stage and the last larva (as the first post-larva). Miss Webb (1921) describes briefly and figures the first larva. Her drawing, however, is not quite accurate as she shows no jointing on the antennal scale, nor any flagellum. The concave margin of the antennular peduncle is also not indicated.

The larvae are very pale and transparent with a little yellowish and red on the front margin of the eye, faint pink on the last segment and yellow on the telson. The newly hatched larva measures 3–4 mm. in length. There is a short but quite conspicuous rostrum. The antennal flagellum is a strong unjointed rod terminating in a spiny seta with an accessory seta on the outer side about half-way up. There is an outer seta on the scale which bears 9 setae round the inner margin and tip and one minute one on the outside of the tip. There are no lateral spines on the fifth abdominal segment. The exopods of the maxillipedes bear 3 terminal setae and 2, 6, 6 laterals, that is to say 5, 9, 9 in all. The third stage is well figured by Sars, who however shows a pair of lateral spines on the 5th abdominal segment not present in the Millport and Plymouth specimens. Here the two last pairs of legs are still non-functional and point forwards, the supraorbital spines are well developed and there are many setae on the exopods. The telson is like that of a typical third stage carid with non-setose inner branches of the uropods. It is to be noted that this stage is much less developed than the third stage in any of the *Pandalus* larvae described by Miss Berkeley from British Columbia. *P. montagui* follows the usual carid course whilst the British Columbian forms all have their development accelerated and the third stage has all the legs functional as well as the uropods cut off from the base and the inner branch setose. The first post-larval stage described by Sars is really the last larval stage, measuring 12 mm. in length. Having regard to the backwardness of the third larva it is probable that there are the usual 8 or 9 larval stages in this species. In the last larva the rostrum projects well beyond the eyes and bears several teeth on its dorsal margin. The first leg ends in an incipient chela; the second is chelate and the carpus is not yet divided. The pleopods are well developed and bear a few setae. The telson is long with almost straight sides and bears 3 pairs of lateral teeth, the third at the outer angle, and the straight hind margin bears 10 setae.

Pandalus (Dichelopandalus) bonnieri Caullery (Fig. 1)

The larvae here described were hatched by Dr A. G. Nicholls at Millport and reared by him to Stage V. Stages III and IV were also obtained from plankton near the Seven Stones Light Ship. This species is an open water form and not nearly so common as *P. montagui*. The adult retains the exopod on the third maxillipede and is in this respect more primitive than *P. montagui* and others. On hatching it is very like *P. montagui*, having a well pronounced rostrum, concave outer margin to the antennule, antennal scale jointed with 2 outer setae, and the flagellum unjointed with an accessory seta. The legs are all present but rudimentary, the first, second and third being bilobed.

First larva. Length 3·7–4·5 mm. The margin of the carapace is denticulate ventro-laterally. The mandible has a well developed cutting and grinding portion. The maxillule has a non-jointed setose endopod and well defined inner lobes. The maxilla has a non-jointed setose endopod and four well defined inner lobes, the exopod armed with 5 setae. The exopods of the maxillipedes bear 3 terminal and 1, 2, 2 setae, 4, 5, 5 in all. There is a conspicuous pair of lateral spines on abdominal segment 5; the telson is fairly deeply indented behind.

Second larva. Length 6 mm. The eyes are free and there are small supra-orbital spines. The antennal flagellum is very short, the scale segmented only at the extreme tip, which is narrowed. The proximal outer seta has disappeared. Legs 1 and 2 are functional with exopods; the carapace is still denticulated. The telson has 8+8 setae. There are 6–10 setae on the exopods.

Third larva. Length 8 mm. (including rostrum 1 mm.). The rostrum is slightly curved and projects well beyond the eyes and bears 3 teeth in front of the dorsal organ. The antennal scale is unjointed and bears no outer seta. There are exopods on legs 1–3, legs 4 and 5 are uniramous. There are very minute pleopods. The exopods bear 8–12 setae; the telson has the same form as in *P. montagui* with uropods not cut off at the base, the inner ramus being short and non-setose.

Fourth larva. Length 9 mm. (including rostrum 1·7 mm.). The rostrum has 5 teeth dorsally. All the legs are functional. There are no exopods on legs 4 and 5 which end in long simple dactyls. The carapace is still denticulate. There are antennal and pterygostomial spines. The telson is elongated with 7+7 terminal spines and 2 pairs of lateral spines. The uropods are cut off at the base and the inner uropods are setose.

Fifth larva. Length *ca*. 11 mm. There are 7 dorsal and 5 ventral spines on the rostrum. The pleopods are long and bilobed. The telson is long and nearly straight with 2 pairs of lateral spines and one at the angle and 10 terminal setae. The carapace is still denticulate. There are many setae on the exopods. Epipods are beginning to appear on legs 1–4. The second leg has a simple dactyl. From the well developed state of this larva, which corresponds in many ways with some of Miss Berkeley's penultimate stages, this seems to be the last but one. The last stage has not been seen. It is thus probable that here there are 6 larval stages, for this species is much further advanced than *P. montagui* in corresponding stages.

Pandalus propinquus G. O. Sars

This species is rare in Britain. Stephensen (1935, Figs. 21, 22) has described its early larvae, apparently stages I and II, as he figures two different telsons, one with 7+7 setae and the other with 8+8. Stage I has a jointed antennal scale with 2 outer setae, the flagellum having a large accessory seta; the rostrum is conspicuous and the antero-ventral edge of the carapace and posterior edge of the third and fourth abdominal segment fringed; there are conspicuous lateral spines on abdominal segment 5 as in *P. bonnieri*. The telson is similar to *P. montagui* and *P. bonnieri*. There are indications of exopods on legs 1–3 and the first leg is functional. It is not, however, quite clear if this belongs to stage I or II. The exopods bear 6, 8, 12, 8 setae and there are apparently 4 terminal setae.

Pandalus borealis Kröyer

Miss Berkeley (1930) has described fully the larvae of this cosmopolitan species from British Columbia, which are apparently the same as those described by Stephensen (1912) as *Pandalus propinquus*. It is much further advanced on hatching than the other British larvae, having a non-segmented antennal scale without outer setae and very short but unjointed flagellum with small seta; the legs are rudimentary, but the exopods of the maxillipedes bear many setae. In the second stage all the legs except the last are functional with exopods on 1–3 and the pleopods are beginning to appear; in the third stage all the legs are functional and the telson corresponds more to the usual fourth stage than to the third, the uropods being cut off at the base and the inner ramus setose. The fourth stage has an almost straight elongated telson, the fifth has epipods. The sixth stage is apparently the last larva with a few setae on the pleopods and the second leg chelate.

Thus the British species of *Pandalus* run in a series from *P. montagui* hatched in a very early state to *P. borealis* which is much further on at hatching. The latter is the only one common to the Atlantic and Pacific coasts and comes between the usually backward Atlantic forms and the usually forward Pacific forms.

Pandalina brevirostris (Rathke)

The only other British pandalid is *Pandalina brevirostris* whose larva closely resembles that of *Pandalus montagui*. It differs however in its much smaller size, very short rostrum and absence of legs in the first stage. Like *P. montagui* it has no lateral spines on the fifth abdominal segment.

First larval stage (Fig. 3). Length 1·84 mm. Very like *Pandalus montagui* but without leg rudiments. The antennule is not yet concave on its outer margin. The antennal flagellum bears a long accessory seta and the scale is segmented at the tip and bears 2 outer setae. The telson bears 7+7 spines and is deeply indented at its hind margin. The exopods of the maxillipedes bear 3 terminal setae and one lateral.

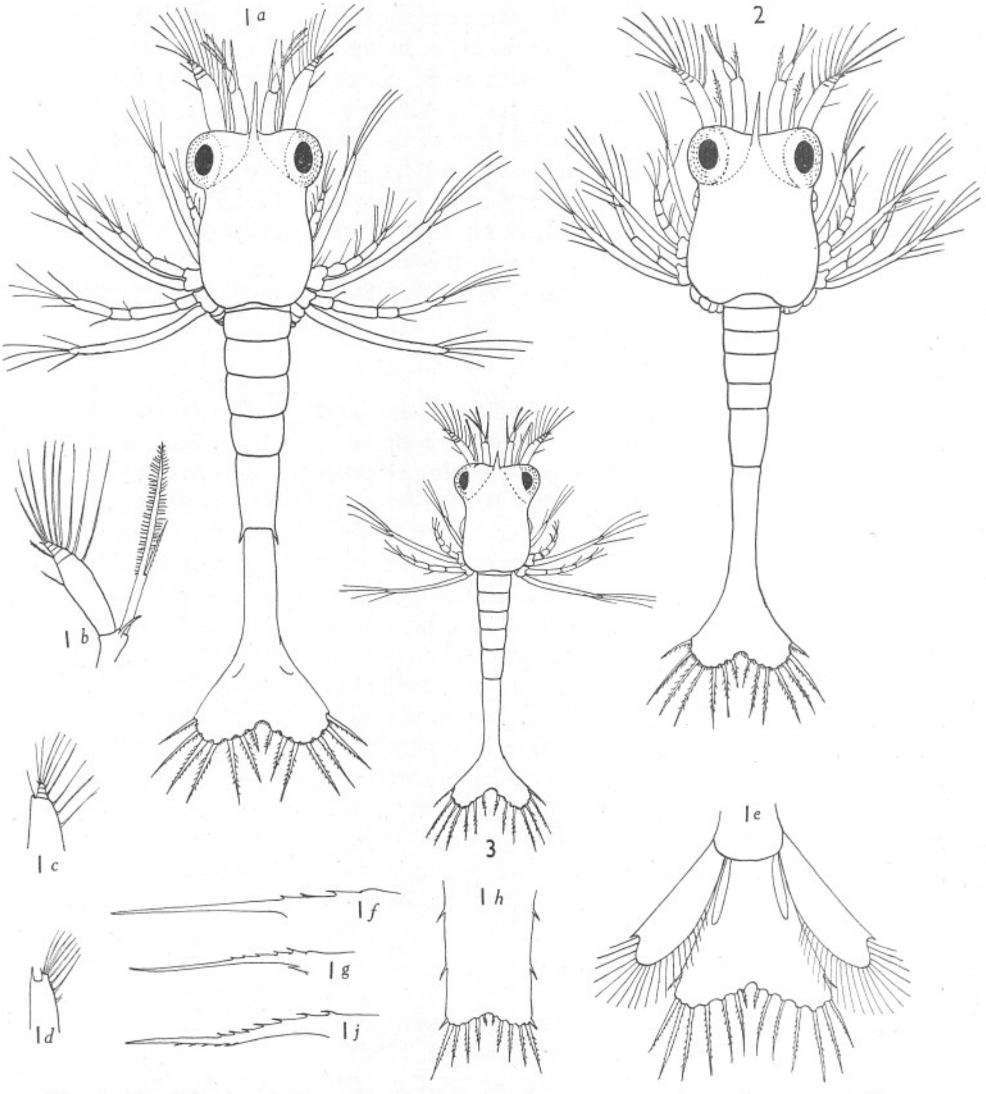

Fig. 1. *Pandalus bonnieri*. *a*, dorsal view, first larva, 3·7 mm. long; *b*, antenna of same; *c*, tip of antenna of second larva; *d*, tip of antenna of third larva; *e*, telson of third larva; *f*, rostrum of third larva; *g* rostrum of fourth larva; *h*, telson of fifth larva; *j*, rostrum of fifth larva.

Fig. 2. *Pandalus montagui*, 3 mm. long.

Fig. 3. *Pandalina brevirostris*, 1·8 mm. long.

This species is very common at Plymouth, its larva occurring with that of *Pandalus montagui* in fairly shallow water. The antenna of the first stage is figured by Gurney (1926) and the fifth stage by Sars (1900). It almost certainly has 8 or 9 larval stages.

Parapandalus (Stylopandalus) richardi (Coutière)
Pandalus (*Stylopandalus*) *richardi* Coutière (1905)
Parapandalus richardi (Cout.) de Man (1920)

(Figs. 4–12)

This species has so far not been recorded from Bermuda but it was obtained there in the adult stage in 1939 and the larvae are very common in the outside tow-nets. A male, 45 mm. long, was obtained by the "Culver" about 5 miles off Bermuda at a depth of about 750 metres and a female in berry 55 mm. long at about 800 metres (June 13 1939). The larvae occur almost anywhere outside from near the surface to about 350 metres or more.

The first and second stages were, rarely, also taken in shallow water from tow-nets let down from the Swing Bridge over the Reach, near the Biological Station. The later stages were always from outside. The first and second stages occurred from August to October; this species must therefore breed at least from June to October, later larvae occurring at any time of year. This is the first time that any larva of *Parapandalus* has been described.

In general form the early larvae are rather like those of *Chlorotocella* sp. described by Gurney (1937) from the Red Sea, but they differ in detail, notably in the third abdominal segment, which is not humped at all in *Parapandalus*, and in the telson. In the later stages, however, they differ considerably and the series of larval stages are not comparable as there are far more in *Parapandalus* which must have a very much prolonged larval life.

The eggs measured 0·64 × 0·48 mm. and were nearly ready to hatch, but unfortunately both parent and eggs died. The last larva changed to a post-larva in a bowl in the Laboratory and several moults were obtained in the later stages.

It is interesting that in the post-larva there are two large red organs on each side of the thorax, probably luminous, in the same position as those in *Chlorotocoides* (see Kemp, 1925, p. 277). These organs closely resemble, in colour, size and position, the organs of Pesta in some of the Sergestids. Dr Kemp kindly allows me to quote from his manuscript notes on this species: "the patches of red pigment on the pleopods may be luminous organs and it appears very probable that two pairs of large organs on the carapace have this function. Of the latter, one pair is situated at the base of the mandible, beneath the carapace, and one pair postero-dorsally underlying both the posterior edge of the carapace and the ligament of the first abdominal somite."

There appear to be more than the usual nine larval stages in this species, for after the first six stages, which progress normally, there may be about four ranging from 7 to 10 mm. in length which are all much alike and only differ in the length of rostrum, pleopods and slight changes in the limbs. The rostrum in these is rather short and the telson usually bears 10 terminal spines (rarely 12). Following these is an anti-penultimate stage with fairly long and very slender pleopods, measuring about 12·5 mm., a penultimate stage of about 15 mm. and a last larval stage of about 17·5 mm. or more. It is probable, however, that some of these are alternative. A still later stage, which seemed to be between the ordinary last stage and the post-larva, moulted from a larva similar to the form which changed to a post-larva. In this specimen the exopods were twisted and still setose, the pleopods were very setose and well developed like those of the post-larva and the terminal setae of the telson were reduced to 2 pairs and 2 long inner setae but with no central tooth.

It seems that after the pleopods have appeared and all the legs are developed the number of larval stages may vary.

The larvae are extremely transparent and glass-like with rose-red chromatophores scattered on the body and appendages. In the early larvae there is a little yellow mixed with a large red patch in the thorax, and red chromatophores on both endopod and exopod of the third maxillipede. The post-larva has very little colour, but has scattered rose-red chromatophores on the antennule, antenna and legs and the above-mentioned round red organs on the thorax.

First larval stage (Fig. 4 *a–d*). Length 1·7 mm. The rostrum is sharp, reaching slightly beyond the eyes. The carapace is denticulated anteroventrally. There is a dorsal organ and a papilliform organ dorsally at the posterior end of the carapace. There are no abdominal spines. The telson (*c*) is fairly deeply indented in the centre of the hind margin and bears the usual 14 setae. The antennule is unjointed, with an internal thin seta, the internal flagellum being represented by a very thick seta, the outer thick with 3 aesthetes (*d*). The antenna has a flagellum nearly as long as the scale, the latter being jointed at the tip and bearing an outer seta and 10 setae round the tip and margin. The maxillipedes are well developed with 4 setae on the exopods. There is a red chromatophore on each branch of the second maxillipede and 3 on the endopod and one on the exopod of the third maxillipede (*b*). There are no legs. A first stage changed to the second in a small glass dish.

Second larval stage (Fig. 5 *a–c*), reared from first. Length 2 mm. The colouring is like the first stage and the structure closely similar, except for the eyes, which are on long stalks, and the extra pair of spines on the telson (*c*). There is a very small pair of supra-orbital spines. There are now 6 setae on the exopods of the maxillipedes, the antennal scale is no longer segmented and the flagellum is longer than the scale. There are no traces of legs.

Third larval stage (Fig. 6 *a–e*). Length 3 mm. The antennule has 2 segments and the peduncle is concave on its outer margin. The antennal flagellum is much shorter and thicker at the base. The exopods of the maxillipedes have 6 setae. There are rudiments of the first and second legs. The carapace is still denticulate antero-ventrally and the spine on the angle distinct. The telson is triangular, the greatest width equal to the length, the hind margin conspicuously indented, the inner ramus of the uropods short with 2 setae. The mandible (*c*) has a cutting and grinding portion, the maxillule (*d*) has an unsegmented endopod with 3 terminal and 2 lateral setae, the inner lobes well developed. The maxilla (*e*) has an unsegmented endopod with one terminal and 3 lateral setae and 4 inner lobes.

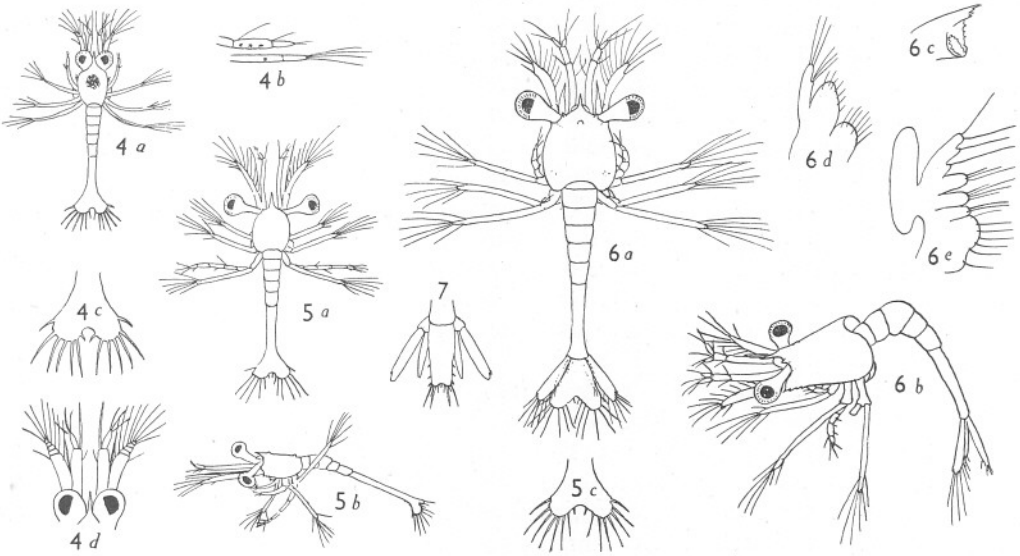

Fig. 4. *Parapandalus richardi*. *a*, first larval stage, 1·7 mm. long; *b*, tip of endopod and exopod of third maxillipede; *c*, telson; *d*, head region.

Fig. 5. *Parapandalus richardi*. *a*, second larval stage, 2 mm. long, dorsal; *b*, side view; *c*, telson.

Fig. 6. *Parapandalus richardi*. *a*, third larval stage, 3 mm. long, dorsal; *b*, side view; *c*, mandible; *d*, maxillule; *e*, maxilla.

Fig. 7. *Parapandalus richardi*. Fourth larval stage 3·5 mm. long, telson.

Fourth larval stage (Fig. 7). Very like stage III. Length *ca*. 3·5 mm. Legs 1 and 2 longer, 3–5 small rudiments. The telson is elongated with 3 pairs of lateral spines and 10 terminal setae, the hind margin slightly indented.

Fifth larval stage (Fig. 8 *a–c*). Length 4·5 mm. No pleopods. The rostrum is very short. The eyes are long, the antennular flagella are thick and nearly equal. The antennal scale has no outer seta and is long and narrow with a terminal tooth. The endopod of the second maxillipede has 6 setae, of the third 6, of the first leg 8, of the second leg 10, of the third leg 8 and of the fourth leg 4. The last leg is uniramous and is still rudimentary and bent forward under the abdomen. The telson (*c*) has a pair of dorso-lateral spines in front of the first half, two pairs of lateral spines, a spine at each angle and 10 terminal setae, the first of which is much the largest, the inner pair very small. The hind margin is still indented.

Sixth larval stage. Length *ca.* 5·5–6 mm. All the legs are long and functional. There is no exopod on the last leg. The rostrum is beginning to lengthen and reaches nearly half way along the eyes. Pleopods are beginning as minute buds. There is still a spine at each angle of the telson and 10 terminal setae, but the hind margin is hardly indented.

From this stage up to a length of 10 mm. (including rostrum), the stages are difficult to distinguish and are probably alternative. The rostrum rapidly elongates and acquires two posterior teeth immediately in front of the dorsal organ. One of these is on the carapace. There is an antennal spine more or less developed and a distinct pterygostomial spine. One specimen of 8 mm. still had 10 terminal teeth plus the spines at the angles of the telson, but most of them had 8 setae and the hind margin is no longer indented but slightly convex. There is a pair of dorso-lateral spines proximally and two pairs of lateral spines on the distal half. The pleopods are small.

Antipenultimate larva (Fig. 9 *a–c*). Length *ca.* 12·5 mm. including rostrum, 3 mm. long projecting far beyond the eyes (*a*). The pleopods are small and slender. The rostrum is armed with 2 large teeth just in front of the dorsal organ and one very small one near the tip. The supra-orbital spines have become very small. The telson (*b*) bears 8 terminal setae, the tooth on the angle having disappeared. The hind margin is rounded. The second leg ends in a pointed dactyl. This changed to the penultimate stage.

Penultimate larval stage (Fig. 10 *a*, *b*). Length *ca.* 15 mm. The pleopods are long but not setose. The telson is like the previous stage (*b*). The rostrum is much longer, 4 mm. in length, and besides the 2 large basal teeth it has indications of teeth along its length dorsally, 1 or 2 being distinct near the tip, and there are also indications of teeth ventrally and one distinct near the tip. This changed to a last larva.

Last larval stage (Fig. 11 *a–f*). 17·5 mm. long including rostrum which was broken (*c*). The rostrum of another specimen measures 4·5 mm. in length. The pleopods are long and have a few setae. The rostrum besides the 2 large basal teeth had 10 teeth dorsally and 14 ventrally. It was slightly curved twice (*f*) and is very like the adult. The antennal flagellum is rather longer than the body. The supra-orbital spines have almost disappeared. The antennal spine is more or less distinct. The telson (*b*) is like the penultimate stage. The exopods of the second and third maxillipedes and legs have many setae and are very long. The second leg is chelate (*d*) but the carpus is not divided. There is an anal spine. The mandible has a minute rudiment of a palp. The maxillule has a simple endopod with a bilobed tip and distinct inner lobes. The maxilla has an unsegmented endopod and the third inner lobe has almost disappeared. The first maxillipede has a large epipod, the second a large gill (podobranch) and the third a plate-like epipod and two arthro-

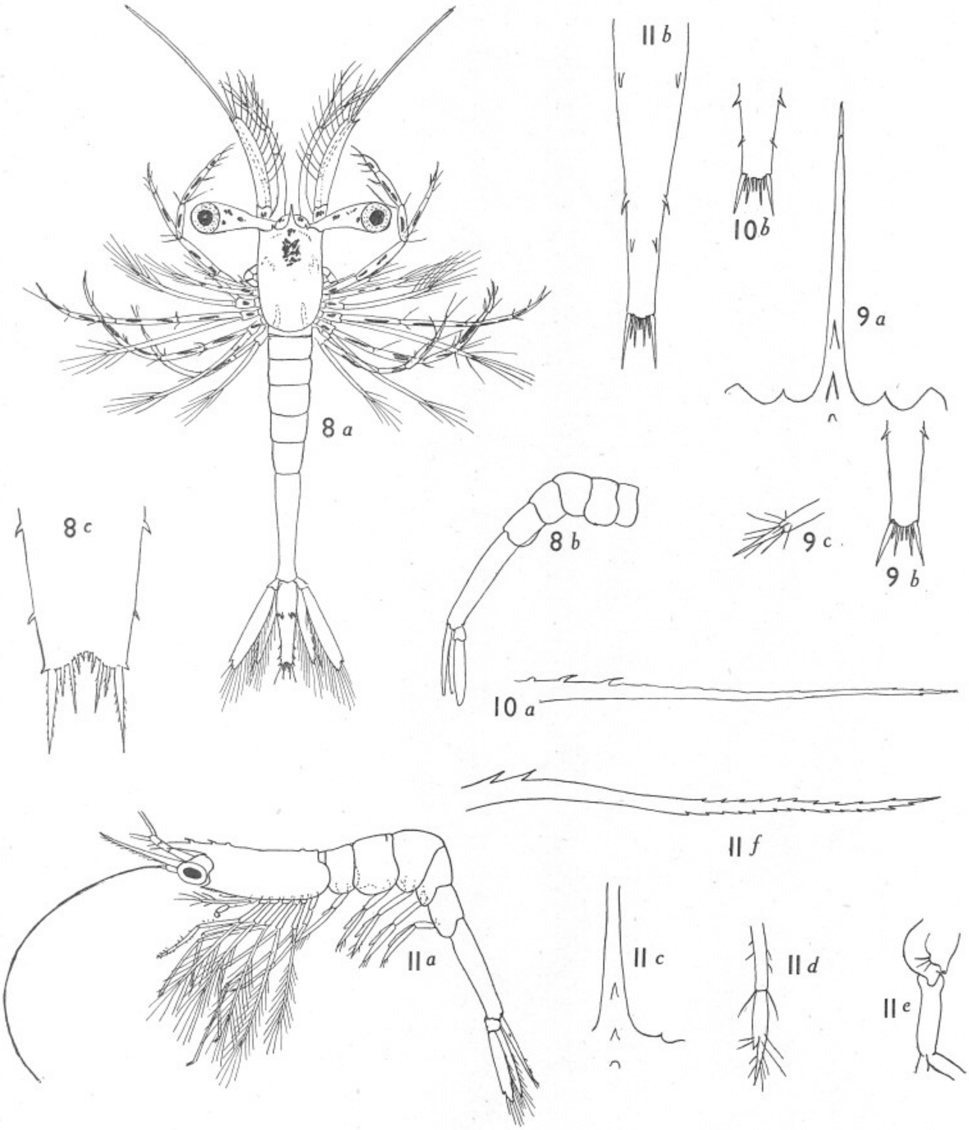

Fig. 8. *Parapandalus richardi*. *a*, fifth larval stage, 4·5 mm. long; *b*, abdomen; *c*, telson.

Fig. 9. *Parapandalus richardi*. *a*, anti-penultimate stage, 12·5 mm. long, rostrum and front of carapace; *b*, telson; *c*, end of second leg.

Fig. 10. *Parapandalus richardi*. *a*, penultimate stage, 15 mm. long, rostrum; *b*, telson.

Fig. 11. *Parapandalus richardi*. *a*, last larva, 17·5 mm. long (rostrum broken); *b*, telson of cast skin (into post-larva); *c*, rostrum; *d*, end of second leg; *e*, proximal end of third leg; *f*, rostrum of another specimen.

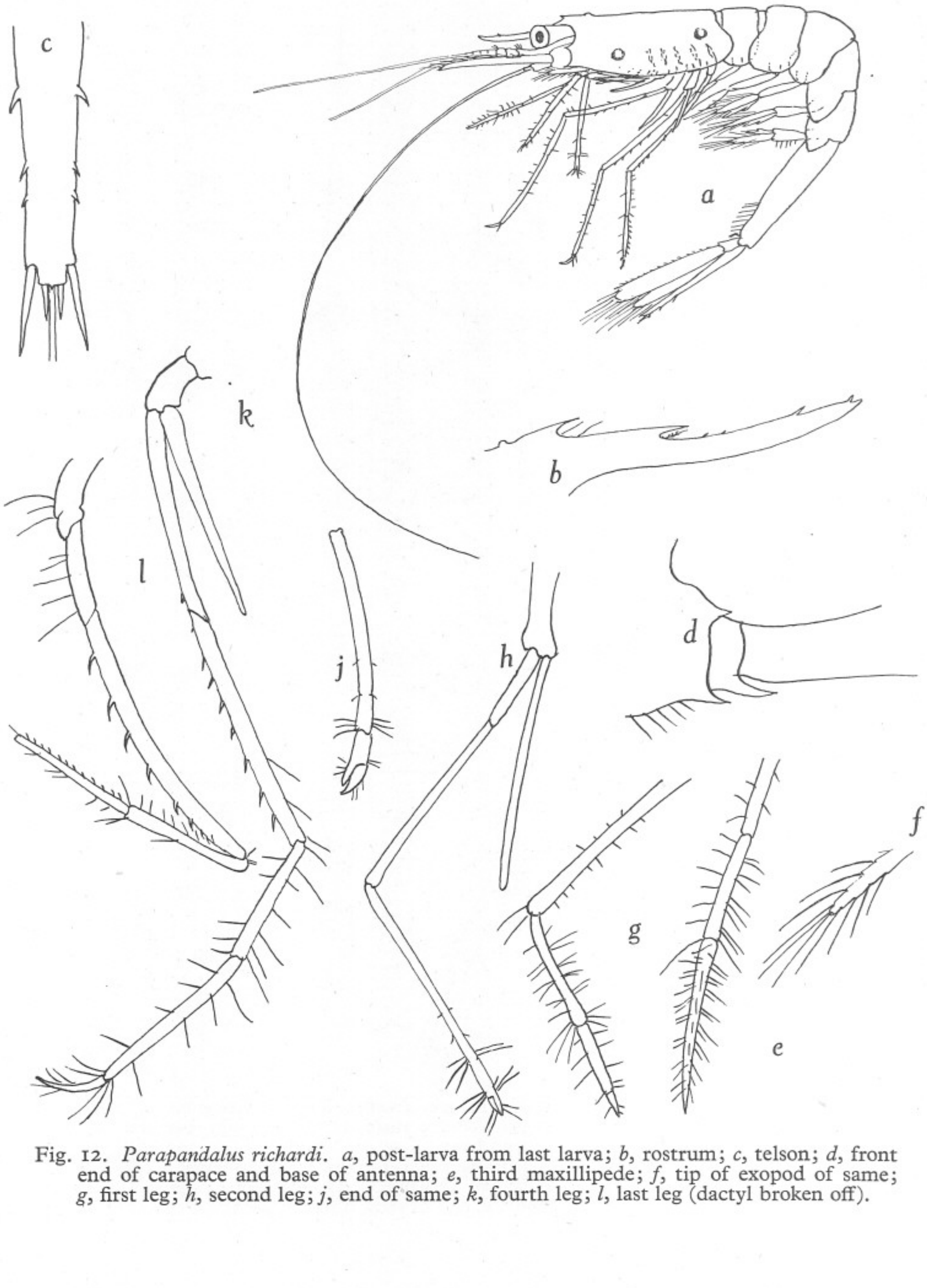

Fig. 12. *Parapandalus richardi*. *a*, post-larva from last larva; *b*, rostrum; *c*, telson; *d*, front end of carapace and base of antenna; *e*, third maxillipede; *f*, tip of exopod of same; *g*, first leg; *h*, second leg; *j*, end of same; *k*, fourth leg; *l*, last leg (dactyl broken off).

branchs. There is an arthrobranch and a pleurobranch on legs 1–4 and a pleurobranch on leg 5. The gill formula is thus complete as in the adult. On the third maxillipede and legs 1–4 in the cast skin there were seen small processes with 3 setae on the base. These appear to be rudiments of the epipods which disappear. The second maxillipede closely resembles the adult.

One of the penultimate stages changed to a form which was intermediate between the true last larva and the post-larva, having exopods on the legs which were still setose although much curled up and the pleopods being quite as much developed as they are in the post-larva. In this specimen the telson has 6 thick setae on the hind margin and an inner pair of long very thin feathered setae.

Post-larval stage (Fig. 12 *a–l*). The post-larva from the first larva is 16 mm. long, but the rostrum is abnormal owing to its being broken in the last larva and is much shorter than it should be (*b*). This approaches the adult in form. The antennal and pterygostomial spines are distinct but the supra-orbitals have disappeared. The antennal flagellum is slightly longer than the body. The second leg has the carpus divided once (with indications of a second division) distally, therefore its segmentation is not nearly complete (*h*, *j*). The first leg ends in a simple pointed dactyl (*g*). The remains of the exopods are unusually long. The telson has 3 pairs of lateral spines and ends in a straight narrow portion with a minute central tooth. There are 4 stout setae terminally and a long hair-like seta on each side of the central spine. There are no epipods on the legs. The red round organs, in a similar position to the organs of Pesta in Sergestids, are conspicuous.

The pandalid larva III described by Gurney (1924, Figs. 45 and 46) is very like that of *Parapandalus* but the last larva has epipods, which fact shows that it cannot belong to that genus. It therefore almost certainly belongs to the closely related *Plesionika*. It is thus very probable that all the larvae known as *Icotopus* described by Bate (1888) and Coutière (1907) belong to *Plesionika*.

All these pandalid larvae appear to be closely related to *Processa* and the Hippolytidae, especially *Caridion* and *Spirontocaris*, in sharp contrast to the Alphaeidae and Palaemonidae. *Parapandalus* larvae agree fairly closely with some of the Hoplophoridae (*Acanthephyra* and relatives), but never have an exopod on the last leg and in other ways are less primitive.

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NOTES ON THE LIFE HISTORY OF *SACCULINA CARCINI* THOMPSON

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INTRODUCTION

The present paper is the outcome of the suggestion made to me some years ago by Prof. Edward Hindle that the life history of *Sacculina* would repay further study. Observations on living specimens of *S. carcini* parasitic on *Carcinus maenas* were commenced at the Zoological Laboratory in the University of Glasgow and at the Marine Station, Millport. Later it became apparent that, in order to make certain points clear, a collection of parasitized crabs representative of a whole year would be necessary. Thus such a collection was formed, and it is this collection which forms the basis of this paper, the previous observations being introduced only when they serve to amplify or to confirm the deductions drawn from the study of the collection. This study has been carried out in the Department of Zoology, University College, Cardiff.

I desire to express my thanks to Prof. E. Hindle for the suggestion referred to above, to Prof. W. M. Tattersall for the facilities for my work at Cardiff, to Mr R. Elmhirst for ensuring a regular supply of material from Millport, and to the University of Wales for a grant towards the expenses of forming the collection.

The life history of *Sacculina*, first worked out by Delage (1884), has recently been the subject of further investigation by Day (1935), and Orton (1936) has elucidated additional details.

Whilst Delage's classical observations were made at Roscoff on *S. carcini* parasitic on *Carcinus maenas*, Day, in the Mersey area, worked on the same species of parasite but parasitizing *Portunus holsatus*. It seemed, therefore, that some of the differences between Day's account and that of Delage might be due to the fact that observations were made on a different species of host, and that others might be associated with the more northerly latitude from which Day's material was obtained. It thus appeared that, if observations were made on *Sacculina carcini* parasitic on *Carcinus maenas* in the Clyde Sea area, it might be possible to detect the effect of latitude on the life history of the parasite, and it might, at the same time, give some indication as to whether the parasite showed any modification correlated with its occurrence on a different host species.

It was decided to pay particular attention to the following points: (*a*) the breeding season of the *Sacculina*, (*b*) the date of the appearance of the young *Sacculina* externa, (*c*) the fate of the *Sacculina* externa.

Before turning to the details of the collection it is necessary to draw attention to two important points which will not be discussed further. First, Day has clearly shown that the *Sacculina* externa does not become external at a moult of the host, as was previously thought, but when the exoskeleton of the crab is hard. Secondly, the time that elapses between the infection of a crab by the *Sacculina* cypris larva and the emergence of the externa is approximately 9 months, as shown by Day for *Portunus holsatus* and Orton (1936) for *Carcinus maenas*, and not 21 months as postulated by Delage.

THE COLLECTION

The collection of parasitized crabs was made by the Marine Station, Millport; the majority of specimens were collected at a point near the pier at Fairlie, Ayrshire, but some were obtained near Millport itself. These localities are, however, only some 2 miles apart, so that there seems to be no objection to dealing with crabs from the two sources together.

It should be made clear that the collection is one of parasitized crabs; that is, of crabs which, on collection, showed some visible sign of parasitization by *Sacculina*. It may be pointed out that this method does not follow that of Day who worked on a collection of crabs and began by finding the percentage infection of the crab population.

The exact dates on which the collection was made varied from month to month according to weather conditions; these were particularly unfavourable in October 1938, when the number of specimens obtained was very small.

The collection extends over the 12 months commencing in June 1938, the total number of crabs bearing *Sacculina* externa was 181, and, owing to multiple infections, the number of externa was 188. The distribution of the specimens over the months of the year is shown in Table I.

TABLE I. SUMMARY OF THE COLLECTION

Month	No. of crabs	No. of *Sacculina* externa	No. of double infections	No. of triple infections
1938				
June	15	15	..	..
July	11	11	..	..
Aug.	18	18	..	..
Sept.	25	25	..	..
Oct.	7	9	..	1
Nov.	24	25	1	..
Dec.	18	19	1	..
1939				
Jan.	12	12	..	..
Feb.	9	10	1	..
Mar.	12	13	1	..
Apr.	13	14	1	..
May	17	17	..	..
Total	181	188	5	1

It will be noted that double infection occurred in 2·8 % of parasitized crabs, and that the one case of triple infection, if expressed as a percentage, works out at 0·6.

THE BREEDING SEASON OF *SACCULINA CARCINI*

One of the chief objects of the investigation was to fix, if possible, the time and duration of the breeding season of the parasite. Day had found that, in the Mersey area, *Sacculina carcini*, parasitic on *Portunus holsatus*, bred in March, April and May; whereas Delage had found at Roscoff that *Sacculina carcini*, parasitic on *Carcinus maenas*, produced the greatest numbers of ripe externa and nauplii in June, July and August. Orton (1936) gives March or April to September or November as the breeding season of *Sacculina carcini* at Plymouth. Day postulated that the difference observed by him was caused by a different species of crab being the host, and made some suggestions, which will be touched on later, as to why this should be so.

In any attempt to fix a breeding season for *Sacculina* a point which would appear to be of great importance is the presence of eggs or nauplii in the mantle cavity of the externa. Delage pointed out that the eggs, when laid, are passed into the mantle cavity which is used as an incubatory pouch, and the ovary then becomes engaged in producing the next batch of eggs. After each batch of larvae is cast out the lining of the mantle cavity is also shed—thus the finding of a partially cast mantle lining protruding from the opening of the *Sacculina* externa is also of great importance. Indeed it may be of greater significance than the finding of nauplii in the mantle cavity for we have no accurate knowledge of the possibility, or otherwise, of the nauplii being retained in the mantle cavity pending the onset of favourable conditions. In this connexion Day remarks "...the examination of the samples from the Mersey area indicated that the externa is able to retain the larvae for some considerable time should conditions not be suitable for the survival of the larvae".

It seems convenient to call the presence of nauplii in the mantle cavity and the incompletely shed mantle lining "signs of ripeness", and the occurrence of these signs throughout the year is shown in Table II. In this table only *Sacculina* externa of over 12 mm.* in breadth have been included as it was concluded from the study of the collection that this is the smallest size at which breeding normally takes place. It may also be noted that, as in some cases it is difficult to determine whether a given specimen should be included as "eggs" or "nauplii", it was decided to include as nauplii all those embryos in which the eye pigment had appeared.

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* This table omits one specimen of 11 mm. breadth which from its colour and internal organization resembled larger specimens. As it contained neither eggs nor nauplii its omission does not affect the results. Altogether this specimen was small for its colour and degree of development; it is one of a pair in a case of double infection (February 1939) and, as its partner was 23 mm. in breadth, suggests that, when two parasites are in competition on one host, one may be dwarfed, particularly if infection was not simultaneous. For it may be supposed that the first parasite to infect a host would succeed in establishing a more extensive root system than a later arrival.

An inspection of Table II shows that if the presence of the partially shed mantle lining be taken as the chief indication that breeding is taking place then we have an indication that the breeding season extends from July to December. It must be noted, however, that during some of these months nauplii were not found. On the other hand, nauplii were found in several months when the cast mantle linings were not obtained; thus if we take the two "signs of ripeness" together the breeding season would extend to the whole year excluding January and March. When keeping parasitized crabs in captivity in earlier years it was found that it was relatively common for the nauplii to be shed in the warmer months, notes about this were made in August 1936 and 1937, but no records were made in the cooler months although the crabs survived well. The earliest date of which I have record of *Sacculina* larvae being liberated in the laboratory at Glasgow was on May 17, but, on this occasion, the host had just arrived from Millport and many unripe eggs were also extruded, so that it appears likely that the emission of the larvae was slightly premature and was probably due to the increase in temperature to which the specimen was submitted on being brought into the laboratory.

TABLE II. DETAILS OF THE *SACCULINA* EXTERNA SHOWING "SIGNS OF RIPENESS"

	Sacculina externa				
Month	Total	No. over 12 mm. broad	No. eggs in mantle cavity	No. nauplii in mantle cavity	No. with mantle lining partly extruded
1938					
June	15	15	10	2	0
July	11	11	5	1	1
Aug.	18	16	8	0	2
Sept.	25	13	7	0	1
Oct.	9	7	2	0	1
Nov.	25	21	11	5	2
Dec.	19	18	5	3	1
1939					
Jan.	12	11	6	0	0
Feb.	10	8	5	3	0
Mar.	13	12	6	0	0
Apr.	14	14	5	1	0
May	17	17	13	1	0

Additional evidence as to the duration of the breeding season can be obtained from the time of emergence of the young externa now that it is known that this takes place approximately 9 months after the infection of the host. The young externa, when they appear, are a few (up to four) millimetres in breadth and quite white; they grow quickly, keeping their white colour, and are believed to be in a breeding condition some 6 weeks or 2 months after their appearance. Table III shows the number of the small white externa and their distribution through the year. Those of 12 mm. maximum breadth and under are included in this table.

A study of Table III shows a preponderance of small white externa in September and a smaller number in August and during the months October to February. Counting back 9 months, the appearance in September indicates breeding in the previous December, August, in the previous November, and October to February in the previous January to May. This extends the breeding season to nearly the whole year; but there are certain points which must be mentioned.

TABLE III. DETAILS OF THE DISTRIBUTION THROUGH THE YEAR OF SMALL WHITE EXTERNA

	Sacculina externa			
Month	Total	12 mm. and under not white	12 mm. and under white	Total 12 mm. and under
1938				
June	15	..	..	0
July	11	..	..	0
Aug.	18	..	2	2
Sept.	25	..	12	12
Oct.	9	..	2	2
Nov.	25*	2	1	3
Dec.	19	..	..	0
1939				
Jan.	12	..	1	1
Feb.	10	1†	1	2
Mar.	13	..	..	0
Apr.	14	..	..	0
May	17	..	..	0

* In addition to the specimens tabulated for this month another with small white externa may be included. It was forwarded to me from Millport and consisted of an isolated crab abdomen with a note to the effect that it had been taken from the tanks during this month.

† This is the smaller of two externa in a double infection and is referred to in the footnote on p. 255.

Although small white externa are to be found during several months of the year, as is shown in Table III, they are seen to be most common in September. The appearance of a large number of small white externa had been noted in August in 1936 and 1937 and there can be no doubt that it is a common feature in August and September. Attention may be drawn here to Table IV which deals with the colour of the externa and this shows that white predominates in the months August to November and also that breeding size (over 12 mm. in breadth) is reached by white specimens in late summer.

From all the foregoing considerations it is obviously not possible to name any two or three months of the year as a "breeding season". Rather the conclusion must be drawn that breeding takes place under favourable conditions during most months of the year and that a maximum is reached in the late summer and autumn (August to December) and that there is probably a minimum in the winter (January to March).

A further point to which consideration should be given is that the time taken by the parasite over its internal development has been assumed in the paragraph above to be 9 months, but there seems a possibility that it might be affected by temperature, and might be slightly slower when infection takes place during the colder months; however, no evidence in support of this view can be offered.

If we compare these deductions with the findings of Day it seems conclusive that the difference in the breeding season of *Sacculina carcini* when parasitizing *Carcinus maenas* and when parasitizing *Portunus holsatus* is caused by the different host, and is not due to any cause of geographical origin. Day suspected this and put forward an hypothesis to account for it. He suggests that the difference is due to variation in the breeding season of the host. Day says "Thus Delage's seasonal table which is true for *Carcinus maenas* from Roscoff does not hold for *Portunus holsatus* from the Mersey, but in both cases the nauplii appear a little earlier than the zoea; and the young internae become evident when the ovaries of the uninfected crabs are beginning to ripen. The growing parasite in the female is thus able to absorb nourishment that would normally be stored as yolk."

The breeding season of *Carcinus maenas* in the Clyde has been summarized by Elmhirst (1922) as follows: "full" females are found in October and November, spawning November to May, hatching of zoeas late March to late August. Here, then, if we accept the late summer and autumn as the chief breeding period of *Sacculina*, the nauplii will be appearing later than the crab zoeas, not earlier as found by Day. This may indicate that Day's explanation is not complete, for the breeding seasons of host and parasite do not bear the constant relationship which Day's explanation seems to demand.

There is no doubt, however, that the breeding period of the parasite is greatly influenced by its host, and, in particular, the breeding periods of host and parasite bear a marked resemblance in duration, as has been noted by Orton (1936, p. 624).

While it is clear that the difference in host species accounts for the chief differences between the time and duration of the breeding period of *Sacculina carcini* when parasitizing *Carcinus maenas* on the one hand and *Portunus holsatus* on the other hand, if the results of the observations made on the material from the Clyde are compared with Delage's from Roscoff it is possible to detect a distinct effect of latitude. Delage found the young externa common in April and May, in the Clyde they are most frequent in August and September; again, while at Roscoff most ripe externa are found in July (primiparous August–October), in the Clyde they are to be found from August to December. Thus in the Clyde the seasonal sequence of events appears to take place some two to three months later than at Roscoff.

Plymouth occupies a somewhat intermediate position between Roscoff and the Clyde and it is perhaps worth noting that Orton (1936) gives the breeding season of *Sacculina* at Plymouth as from March to November, thus it probably begins somewhat earlier here than at Millport. It may also be noted that the host (*Carcinus maenas*) appears to have a more restricted breeding season in the Clyde than at Plymouth where it is stated to continue all the year round with a maximum number of larvae in the spring (*Plymouth Marine Fauna*, 1931).

THE FATE OF THE *SACCULINA* EXTERNA

Day found, after the breeding season, a large number of crabs present in the collections which bore the blackened stump of former *Sacculina* externa. He concluded that it was a general phenomenon for the externa to shrivel and fall off after the comparatively short breeding season. This is, of course, in marked contrast to the older beliefs that the normal life of the *Sacculina* externa was approximately equal to that of the host, see for instance Tattersall (1920). Delage noted that in November "on trouve un certain nombre de Crabes portant les traces d'une Sacculine détruite". As the collection at my disposal was of parasitized crabs no numerical evidence of a general falling off of the externa can be available; but from the fact that abundant material was available all the year round it did not appear that when *Carcinus maenas* is the host there is any general falling off of the externa. In fact the presence of some very dark brown externa on crabs bearing heavy incrustations of epizootic organisms directly suggested that in some *Carcinus*, and perhaps the majority, the externa persist for a considerable time producing larvae when conditions are favourable. For this reason the colours of the various externa were noted and also the degree of the incrustation of the host by epizootic organisms.

As regards colour it is interesting to note that Day does not remark on any darkening of the externa, whereas Delage noted that the ripe externa were violet, this coloration being caused by the pigmentation of the nauplii within.

TABLE IV. SHOWING THE COLOURS OF THE *SACCULINA* EXTERNA OF 12 MM. IN BREADTH AND OVER

Month	White	Grey	Yellow	Brown	Total
1938					
June	6	1	2	6	15
July	1	0	3	7	11
Aug.	14	0	0	3	17
Sept.	12	0	0	2	14
Oct.	8	0	0	0	8
Nov.	12	1	4	6	23
Dec.	2	0	5	12	19
1939					
Jan.	2	0	2	7	11
Feb.	1	0	2	5	8
Mar.	5	0	3	4	12
Apr.	5	0	4	5	14
May	4	0	5	8	17

The colours of externa with a breadth of 12 mm. and over have been recorded in Table IV. The numbers are not sufficiently large for statistical treatment but justify the conclusion, which has been reached in working through the collection and in previous years' work, that the small white externa appearing in August rapidly enlarge and produce larvae. The externa then gradually darken either through varying shades of yellow, or of grey, to brown, and finally to dark brown. Thus the age of the externa can be judged to some extent by their colour, those which are brown having probably been in position for at least some 6 months.

Additional evidence as to the age of the externa can be obtained from a study of the epizootic organisms which the host may bear. Before proceeding to discuss this point it may be noted that Day remarks "...crabs bearing barnacles and serpulid tubes have not much vitality..."; but I do not think that this is always a justifiable statement. Rather the presence of incrusting organisms indicates an absence of moulting; in support of this it may be noted that I have had a berried female, living in the laboratory, which carried several barnacles on the carapace; also Table V shows that there were always crabs with epizootic organisms found in each month's collection.

In Table V the total number of crabs for each month is given and then the number with no epizootic organisms. Those bearing incrustations other than balanids and serpulids are not further mentioned. The balanids and serpulids have each been divided into three groups, small, unspecified and large, according to any notes made about them when working through the collection.

TABLE V. SUMMARY OF THE INCRUSTING ORGANISMS FOUND ON THE CRABS IN THE COLLECTION

(For full explanation see text)

Month	No. of crabs	No. without epizootics	No. with balanids			No. with serpulids		
			Small	Unspec.	Large	Small	Unspec.	Large
1938								
June	15	7	4	..	..	4	2	1
July	11	3	1	3	2	2	5	..
Aug.	18	9	1	..	..	5	1	..
Sept.	25	16	1	..	3	6	..	..
Oct.	7	4	..	..	..	3	..	..
Nov.	24	8	..	8	..	3	10	2
Dec.	18	6	4	1	1	9	1	..
1939								
Jan.	12	4	..	..	1	2	4	..
Feb.	9	2	1	..	1	4	2	..
Mar.	12	8	1	..	..	2	..	1
Apr.	13	4	6	..	..	2	1	..
May	17	8	8	..	2	..	3	1

Before proceeding to the deductions to be drawn from Table V one point must be made clear. It was not ascertained that the epizootic organisms were living at the time of collection and the grouping has been made from the hard parts only. There is thus room for considerable error, as if a young serpulid settled in the autumn and then died after only a short existence its tube would remain and the young serpulid worm would be recorded in the month in which the crab that bore it was collected. However, allowing for this large error, small freshly spatted barnacles were prominent in April, May and June, and the young serpulids from June onwards in increasing numbers towards the autumn. This, of course, is what would be expected from our knowledge of the breeding seasons of these animals.

This aspect of the study becomes of greater interest when it is correlated with the probable history of the moults of the host. It has been shown that the greatest number of new externa appear in the late summer and autumn, and it has also been established by Day that the emergence of the externa takes place when the exoskeleton of the host is hard and not at a moult. It is well known that in *Carcinus* moulting of the host ceases when the externa of the parasite has appeared. Thus the last moult previous to the appearance of the externa would probably take place in May or June, and the crab with the new externa would be more likely to carry a serpulid than a barnacle as the young balanids would have been cast at the moult; this point is clear in the table. Thus it seems likely that a crab carrying externa which appeared in the summer would not acquire barnacles until the following spring. If this were quite certain we could then say that every crab carrying a barnacle had had the externa for some 6 months before it acquired the barnacle. However we cannot be quite sure, particularly in large crabs (which may only moult once a year), that the host would moult in the spring of the year in which the externa appeared, and, in some therefore, the barnacle might be some 3 months older than the externa. Thus although it is probable that the externa are some 6 months older than the barnacle it cannot be said that they are always so.

There is, however, the additional point that sometimes a crab will bear two generations of barnacles. Two such crabs were obtained in August 1937; Mr H. G. Stubbings has kindly identified these for me and finds them to be the smooth variety of *Balanus crenatus* Brug. Mr Stubbings pointed out that there were two generations of barnacles present, and, that, according to the views of H. B. Moore, *Balanus* spp. breed only once per annum, and the two generations would therefore belong to the spattings of 1936 and 1937. Here it seems certain that the crab had not moulted since early in 1936, and there is a possibility that the last moult was in 1935; it therefore appears that the externa on this crab had been in place at least a year and perhaps longer. Another case is that of a specimen picked up at Dawlish, Devon, in September 1938; the externa was dark brown, the carapace of the host bore a barnacle which from its size must have been spatted in 1937; the barnacle was smothered by a young frond of *Laminaria* the holdfast of which grasped the barnacle. The crab thus gave every indication of not having moulted since the spring of 1937 and it was again concluded that the externa had been in position for at least a year. In the collection of 1938–9 there were several crabs bearing two generations of barnacles.

Taking the evidence of colour and the incrusting organisms together it is impossible to avoid the conclusion that there is no evidence of any definite allotted span of life for the externa when the parasite occurs on *Carcinus maenas*. It is true that "scarred" crabs are met with and that sometimes a crab with externa bears the scar of former externa. This, of course, may be due either to the regeneration of the parasite or to a second infection. When keeping crabs in captivity it was found that damage to externa usually resulted in their disintegration and also in the death of the host. No evidence has been obtained to suggest that the shrivelling and dropping of the externa is a normal part of the life history when *Sacculina* is affecting this host. The "scarred" crabs which are found may easily have lost the externa by suffering accidental damage.

Note on the Modification of Male Hosts

There has been much controversy as to whether there is any correlation between the size of the male host and the degree of modification of its secondary sexual characters caused by the presence of the parasite. Potts (1909), working on *Carcinus maenas*, failed to find any such correlation, whereas Day, working on *Portunus holsatus*, found a degree of correlation which he summed up thus: "This shows quite clearly that among externally parasitized crabs...the smaller the crab the greater the liability to be modified to a maximum extent. This is not the same as saying that the smaller the crab the greater the degree of modification...."

In the present work the degree of modification of the male hosts has been noted by a method rather similar to that used by Day but which differs in certain details. The males have been divided into three groups. In group 1 were placed those males which had undergone little or no modification of the abdomen and redivision of the fourth and fifth abdominal segments was not complete; in group 2 were placed all those which showed moderate modification; and, in group 3, were placed the few that showed closest approximation of the abdomen to the female condition. The results are tabulated in Table VI. The carapace breadth was measured to the nearest millimetre and is the distance between the postero-lateral spines.

Table VI. Modification of Abdomen in Male Crabs

	Group 1	Group 2	Group 3
No. of males occurring in group	22	63	6
Width in mm. of carapace of smallest and largest crabs in group	48–77	39–68	38–52
Average width of carapace in group in mm.	63·5	51	48

These results are closely comparable with those of Day and show that while the degree of modification of a crab does not depend on its size, the larger the host the less liable it is to modification, and the smaller it is the greater the amount of modification which may take place. Thus *Carcinus maenas* behaves here in the same way as *Portunus holsatus*.

DISCUSSION

The life history of *Sacculina carcini* as it occurs in the Clyde sea area, where *Carcinus maenas* is the host species of crab, shows two important differences from the life history which has been recorded for it when *Portunus holsatus* is the host. These differences are: (1) The breeding season on *Carcinus maenas* is long and in the Clyde probably extends from late spring until late autumn (June or July to December), whereas, on *Portunus holsatus* in the Mersey area, the breeding season is comparatively short and is at a maximum in the early spring, at a time when the breeding in the Clyde is almost minimal. Correlated with this difference in the breeding season the young *Sacculina* externa appear at different times in the two localities. (2) When *Carcinus maenas* is the host the evidence suggests that there is no definite limit to the longevity of the externa; on *Portunus holsatus* the persistence of externa after a short breeding period was considered by Day to be abnormal.

When the breeding period of *Sacculina carcini* on *Carcinus maenas* in the Clyde is compared with what has been found at Roscoff and Plymouth a geographical effect can be noted, and, as would be expected, the phases of the life cycle occur somewhat later in the year in the more northerly locality. Thus it is clear that the differences found when *Sacculina carcini* is parasitizing *Portunus holsatus* are not geographical in origin but can be ascribed to a difference in the host-parasite relationship.

It has been shown that the length of the breeding period of the parasite bears a close relationship to the length of that of the host, and it has also been noted that while it is considered abnormal for the externa to be retained on *Portunus holsatus* after the breeding season, there is evidence that, on *Carcinus maenas*, the externa may persist for the remainder of the life of the host. Thus it might be said that *Sacculina carcini*, with its longer breeding period and longer external life, is more perfectly adapted to parasitizing *Carcinus maenas* than *Portunus holsatus*.

These points might be more acceptable if the parasites of the two species of crab were to be regarded as different species, but, according to Boschma (1937), there are no constant differences of sufficient magnitude between the parasites to warrant their separation into two species on morphological grounds. However, it may not be without significance that, in the Clyde area, although *Portunus holsatus* is not an uncommon species, there are as yet no records of it being parasitized by *Sacculina* in this locality. If we accept the view that variation in host species is the sole cause of the variations met with in the life history of the parasite we might reasonably expect some proportion of the *Portunus holsatus* in the Clyde area to be parasitized.

In the present state of our knowledge it seems best to regard the parasites of the two species of crab as identical, but it may be suggested that we are seeing a division into biological races. It may well be that *Sacculina carcini* is primarily a parasite of *Carcinus maenas*, but that, under certain circumstances, it can adapt itself to parasitize *Portunus holsatus* and that in so doing its life history undergoes some modification.

SUMMARY

The life history of *Sacculina carcini* parasitic on *Carcinus maenas* in the Clyde sea area is discussed and the breeding period and the time of the emergence of the young externa are indicated. The time and duration of the breeding season are compared both with what has been found at Plymouth and Roscoff for the same species of parasite on the same host crab, and also with what was found by Day (1935) who worked in the Mersey area on *Sacculina carcini* but parasitizing *Portunus holsatus*.

The length of life of the *Sacculina* externa and their ultimate fate are discussed. It is shown that in male crabs which act as hosts the liability of the secondary sexual characters to modification is correlated with size.

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ON THE SEASONAL ABUNDANCE OF YOUNG FISH. VII. THE YEAR 1939, JANUARY TO AUGUST

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(Text-figs. 1–4)

In a number of previous reports observations on the seasonal abundance of the pelagic young of teleostean fish in the plankton off Plymouth have been recorded for the years 1924 to 1938 inclusive. Owing to the outbreak of war the series for the year 1939 is unfortunately not complete. Collections were, however, made until the last week in August. Previous records have always shown that the numbers of young fish caught in the last four months of the year, September to December, are insignificant and in consequence it is desirable that the results for 1939 should be published since they cover fully the period of production of almost all species of fish. It is, also, essential that these records should not be lost as the year 1939 has been the worst yet recorded and sets a new low limit to the production of fish. It is much to be deplored that the sequence of observations may be broken, so that we may never know what point the trough of the decline may reach.

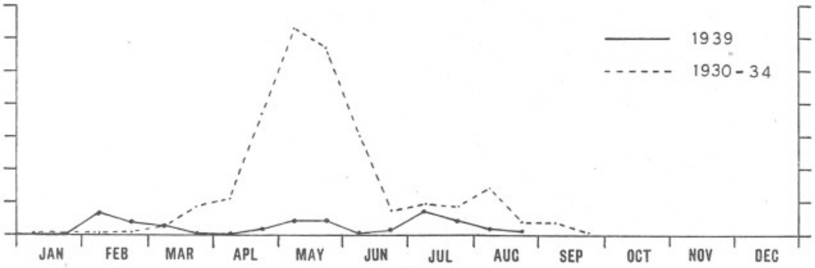

Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2 m. ringtrawl for each fortnight for all young fish, excluding clupeids, in 1939 (——) and the same averaged over the period 1930–4 inclusive (-----).

The results are published in the same form as in previous reports. The dates on which collections were made with the 2 m. stramin ringtrawl are given in Table I, and the monthly average catches of the young fish per half-hour oblique haul in Table II. In Fig. 1* is given the curve for the average catches for each fortnight of all young fish, excluding clupeids, and

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* In the corresponding Fig. 1 for 1938 in Russell, 1939, p. 381, the point for the second fortnight in June was omitted from the curve for 1930–4 in error.

superimposed upon this the corresponding curve for the average catches over the period 1930–4 inclusive.

The results show a complete absence of the peak for the young of spring spawners and a disastrous state of affairs in general. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive, excluding clupeids, was 57 in 1939, as against 135, 174 and 114 in 1938, 1937 and 1936 respectively. If records had continued to the end of the year this figure might have been slightly higher, but in the light of the results for previous years it is doubtful whether it would have exceeded 70, unless some unusual change took place.

The sums of the average monthly catches of the more important species for the year 1939 divided by the corresponding average sums for the period 1930–4 inclusive are given below. In the second column are the figures for the best year divided by the worst year from 1930 to 1939 inclusive.

	1939 / Av. 1930–4	Best / Worst
G. merlangus	0·08	23·6 ('32/'39)
G. minutus	<0·13	>40·3 ('32/'39)
Onos spp.	0·08	29·3 ('30/'39)
Arnoglossus sp.	0·30	11·5 ('31/'34)
S. norvegicus	0·04	43·0 ('32/'39)
P. limanda	0·06	28·0 ('31/'39)
P. microcephalus	<0·04	>41·0 ('32/'39)
S. variegata	0·05	32·5 ('32/'39)
Callionymus sp.	0·07	15·7 ('30/'39)
S. scombrus	0·23	11·2 ('30/'35)
Gobiid sp.	0·05	119·0 ('30/'37)

Of the species shown above all except *Arnoglossus* are normally practically absent by September, and it can be seen that the year 1939 has been the worst for all except three species during the period 1930–9.

All species except *Arnoglossus* and *Scomber* were less than one-tenth of their average for the period 1930–4.

If the number of young of summer spawners (57) be subtracted from the total young fish excluding clupeids (215), we are left with 158 for the remaining young fish most of which are the young of spring spawners. This is far and away the lowest number yet recorded and is nearly one-ninth of the 1395 specimens recorded in 1931. The results for the years 1930–9 are summarized in Fig. 2.

It is of interest to record the unusual occurrence of young plaice in the catches in February and March. They have not been seen before during the long period of observations.

The evidence supplied by the plankton indicator species (Figs. 3 and 4) shows that until the end of the observations the conditions were very similar to those of 1938, although the numbers of *Sagitta* were on the whole even lower than in that year. In this respect the rather high proportion of *S. elegans* shown in the lower half of Fig. 3 is somewhat misleading since the numbers of both *S. elegans* and *S. setosa* were generally so small as to be almost insignificant. There were indications of a slight incursion of *elegans* water in January and February. No occurrence of unusual plankton organisms was recorded and *Muggiaea atlantica* was remarkably scarce. The total number of medusae of all species was even lower than in 1938.

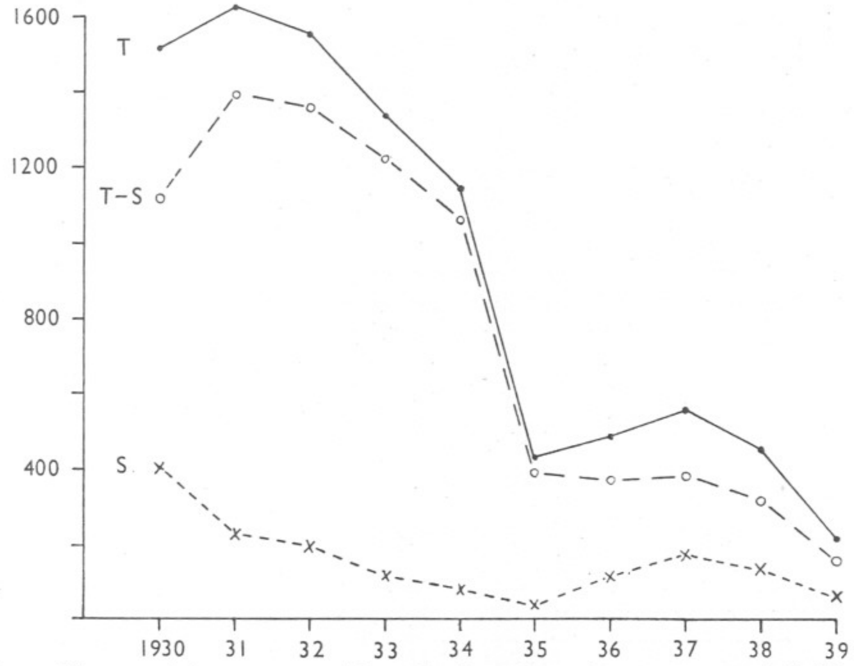

Fig. 2. The sums of the average monthly catches for each year from 1930 to 1939 in half-hour oblique hauls with the 2 m. ringtrawl for: *T*, total young fish (excluding clupeids); *S*, the young of summer spawners; and *T–S*, total young fish less the young of summer spawners.

There were again large numbers of pilchard eggs, which were present from April until the end of August when collections ceased. Their approximate numbers in the catches in which they occurred were as follows: April 17 (40), 25 (1370); May 1 (370), 8 (380), 15 (3890), 23 (2070), 31 (8020); June 2 (2940), 19 (19,480), 26 (19,340); July 4 (4820), 10 (680), 17 (1260), 24 (280), 31 (560); August 15 (10), 21 (620), 28 (20).

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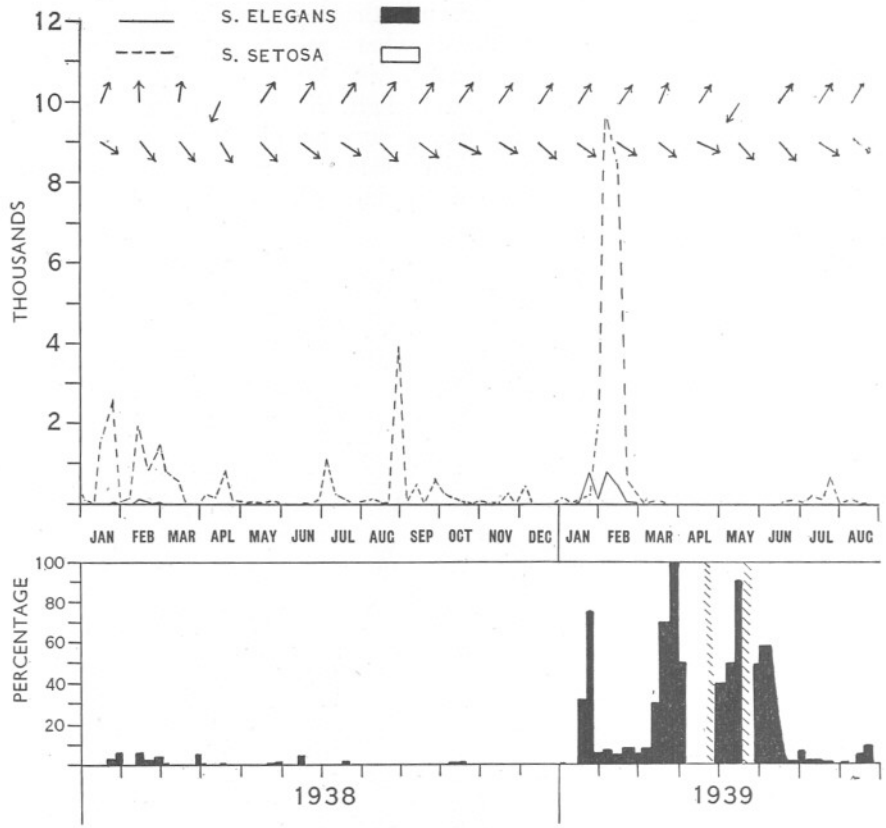

Fig. 3. Above, curves showing the actual abundance of *S. elegans* (——) and *S. setosa* (-----) in half-hour oblique hauls with the 2 m. ringtrawl during the period January 1938 to August 1939. Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched. At the top of the diagram the arrows indicate the mean directions (true) of the flow of water past the Varne Lightship (above) and the Royal Sovereign Lightship (below) from data kindly supplied by Dr J. N. Carruthers. (Continued from Russell, 1939, p. 383, Fig. 2.)

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1939

All 2 miles east of Eddystone unless otherwise stated

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
2	8	6	3	1	2	4	8
9	13	14	12	8	19	10	15
17	21	20	17†	15	26	17	21
24	27	27	25	23		24	28
30*				31		31	

* Off Stoke Point. † 6 miles W.S.W. of Rame Head.

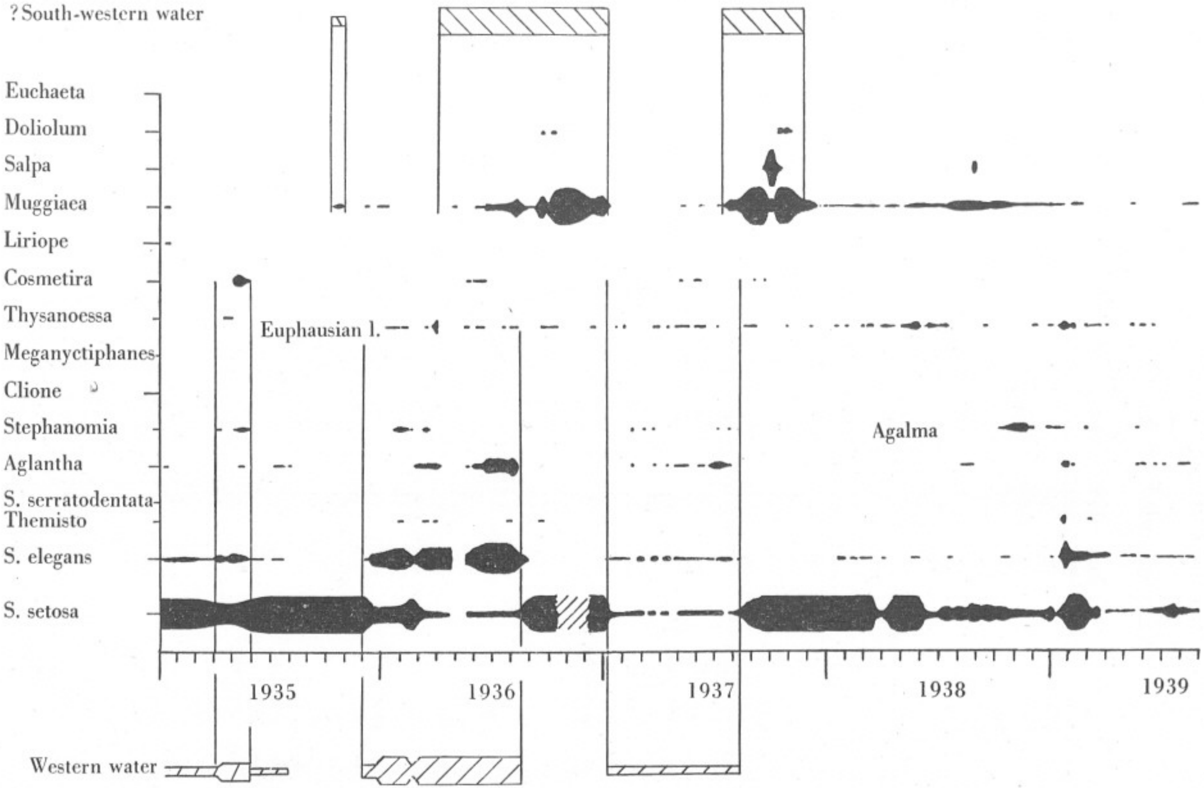

Fig. 4. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the years 1935 to 1939 inclusive. (Continued from Russell, 1939, p. 384, Fig. 3.) The *Muggiaea* species were *M. kochi* up to January 1937, and thereafter *M. atlantica*; the salps were *S. fusiformis*, and the doliolids *D. nationalis*.

TABLE II. AVERAGE MONTHLY CATCHES OF POST-LARVAE PER HALF-HOUR

Oblique hauls with 2 m. ringtrawl, 1939

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Σ
Total young fish	83	204	46	15	46	46	260	32	732
Ditto, less Clupeids	2	54	19	11	41	13	57	18	215
All Clupeid spp.	81	150	27	4	4	33	203	13	515
Clupea harengus	80	47	..	..	..	..	..	..	127
Gadus pollachius	..	+	..	..	1	..	..	..	1
Gadus merlangus	..	1	..	+	15	+	..	..	16
Gadus minutus	..	..	..	..	+	..	..	..	+
Gadus luscus	+	2	..	..	1	..	..	+	3
Gadus callarius	..	..	..	..	..	..	..	..	..
Onos spp.	..	..	..	+	3	1	+	..	4
Molva molva	..	..	..	..	..	..	..	..	..
Merluccius merluccius	..	..	..	..	..	..	..	..	..
Raniceps raninus	..	..	..	..	..	..	+	..	+
Capros aper	..	..	..	..	..	..	..	+	+
Zeus faber	..	..	..	..	..	..	..	..	..
Arnoglossus sp.	..	..	..	..	..	3	5	2	10
Rhombus spp.	..	..	..	..	..	+	..	1	1
Scophthalmus norvegicus	..	..	..	..	1	..	1	..	2
Zeugopterus punctatus	..	..	..	..	1	..	1	..	2
Zeugopterus unimaculatus	..	..	..	..	..	..	+	..	+
Pleuronectes platessa	..	18	1	..	..	..	..	..	19
Pleuronectes limanda	..	..	..	1	2	..	..	..	3
Pleuronectes flesus	..	..	+	1	..	..	..	..	1
Pleuronectes microcephalus	..	+	..	..	+	..	..	..	+
Solea vulgaris	..	..	+	..	1	..	..	..	1
Solea variegata	..	..	..	..	1	..	3	..	4
Solea lascaris	..	..	..	..	..	..	+	+	+
Solea lutea	..	..	..	..	..	+	+	..	+
Serranus cabrilla	..	..	..	..	..	..	..	..	..
Caranx trachurus	..	..	..	..	..	..	+	1	1
Mullus surmulletus	..	..	..	..	..	..	+	..	+
Morone labrax	..	..	..	..	..	..	..	..	..
Ammodytes sp.	1	31	12	1	..	..	+	..	45
Ammodytes lanceolatus	..	..	..	3	+	2	3	+	8
Cepola rubescens	..	..	..	..	..	..	..	3	3
Callionymus sp.	..	..	..	2	15	1	13	6	37
Labrus bergylta	..	..	..	..	..	+	..	..	+
Labrus mixtus	..	..	..	..	+	1	+	..	1
Ctenolabrus rupestris	..	..	..	..	..	+	20	3	23
Crenilabrus melops	..	..	..	..	..	1	1	+	2
Centrolabrus exoletus	..	..	..	..	..	..	1	..	1
Trachinus vipera	..	..	..	..	..	..	+	+	+
Scomber scombrus	..	..	..	..	..	..	3	2	5
Gobius spp.	+	+	..	..	+	+	2	..	2
Lebetus scorpioides	..	..	..	..	..	..	..	1	1
Blennius ocellaris	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	..	1	..	1
Blennius gattorugine	..	..	..	..	..	3	2	1	6
Chirolophis galerita	..	2	2	1	..	..	..	..	5
Agonus cataphractus	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	+	..	+	+	+
Cottus sp.	..	+	4	2	+	..	..	..	6
Liparis montagui	..	..	..	..	..	..	..	..	..
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	..	..	..	..	..	..
Pipe fish	..	..	..	..	..	..	..	..	..

A CUBICAL PHOTOMETER FOR STUDYING THE ANGULAR DISTRIBUTION OF SUBMARINE DAYLIGHT

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The variation in the angular distribution of light at different depths under water has been studied by Pettersson (1938) and his co-workers, Johnson & Liljequist (1938). Their methods, one of which enables a complete polar diagram of the illumination at any point to be obtained, are, however, scarcely suitable for use on our ship in the comparatively rough water so often experienced off Plymouth, and we felt that some measurements with simpler apparatus might be of interest.

We have accordingly constructed a cubical photometer case in each face of which is a toughened glass window 6 mm. thick and 66 mm. clear aperture, behind which is mounted an "Electrocell" selenium rectifier cell 40 mm. aperture. These cells are connected by a seven-core insulated cable to a set of switches, so that any cell or combination of cells may instantly be connected to the measuring apparatus.

For the latter we have sometimes used a Tinsley box-type light-spot portable galvanometer (resistance 10 ohms, sensitivity 16·5 scale divisions per microampere) whose suspended coil had been specially balanced for us by the makers so as to reduce as far as possible the zero shift caused by tilting. A pair of shunt boxes, each with × 5 and × 10 ratios, enabled the galvanometer to be shunted in convenient stages up to × 2500, the effective resistance remaining at 10 ohms. This arrangement proved convenient and satisfactory in comparatively calm water, but when there was a considerable swell we found it best to revert to our original potentiometer telephone method, with the Campbell-Freeth zero-resistance circuit (1929, 1934, 1937); the latter method is also quicker in use and less tiring.

The photometer case is made of cast gun-metal, and is about 12·7 cm. each way, or about 15 cm. to the outside of the collars holding the windows. Flanges cast on a pair of opposite vertical edges are drilled near their upper ends to receive the pins of the shackles of the supporting bridle, and also near their lower ends for the attachment of a bridle to carry a sinker, should that prove necessary. The weight of the case, about 17 kg. seems, however, to be sufficient to prevent appreciable tilting under ordinary conditions. The cable enters through a gland in one of the upper corners away from the supporting bridle, and in the remaining unoccupied upper corner a hole is drilled and tapped for the attachment of a tube to test the airtightness of the vessel, windows, and cable gland.

As some difficulty was experienced in making the rubber gaskets under the window staunch, the joints were eventually made by heating the gaskets in "Sira" wax, and clamping the windows down on them while still hot. The outer parts of the joints were then filled with Chatterton's compound, which in turn was covered with Berry's compound so as to give a non-adhesive surface. When the vessel had been proved to be airtight the testing tube was replaced by a solid screw plug, which was then sealed with Chatterton's and Berry's compounds. No further leakage troubles occurred down to a depth of 70 m.

Outside each window is mounted a VG 9 Jena colour filter 2 mm. thick covered by an opal-flashed diffusing glass, both being 76 mm. in diameter. As the filter rests on a thin flange of the surrounding metal collar, the window aperture being only 66 mm., there is no danger of light reaching the cell past the edge of the VG 9 filter, which limits the sensitivity mainly to the spectral region between 480 and 580 mμ. The outer surface of the diffusing glass is approximately flush with the edge of the surrounding brass collar (the glasses being held in place by means of clips) so that each cell is exposed to a complete hemisphere, the six cells measuring the light from the upper and lower hemispheres and four hemispheres with horizontal axes in rectangular azimuths, respectively.

It is often difficult to ensure that azimuths do not change between readings or at different depths, but when the ship is drifting owing to the action of the wind, approximate constancy can be ensured by the simple method of attaching a light horizontal rod with a vane at the end to one of the vertical flanges of the case. If the motion of the case through the water is sufficiently rapid it keeps the vane pointing approximately up-wind, so that the azimuth of each vertical window is nearly constant.

The six photocells were obtained from the makers in one batch, and, before mounting in the case, were tested on the photometer bench for curvature of the light/current characteristic. One of the cells showed appreciably less curvature than the rest, its sensitivity for green light falling by about 5·6% per milliampere for currents up to 4 mA. This was used for the top window. A second cell, whose curvature correction was much larger—about 11·7% per mA. was used for the lower cell to measure the small amount of light passing upwards. The corrections for the other four were sufficiently close to 7·0% per mA. for this value to be used for each of them. They were mounted behind the side windows. Unfortunately, there seems to be little doubt that while the weak-light sensitivity of these selenium cells may remain approximately constant their curvature correction may increase with time, thus causing their sensitivity for strong light to decrease very considerably.

Some cells seem to be immune to this effect, and it appears to be small or absent in our standard Weston, but all the cells in this photometer showed it strongly. When tested against our standard Weston cell in May and June, 1939, 7 months after the marine measurements Series C 1 to C 9, in daylight whose intensity was varied by means of additional opal glasses, they showed corrections ranging from 12 to 42% per mA. the changes in the weak-light sensitivity being small.

Fortunately the cell used to measure the downward vertical light still showed much the smallest correction, and these corrections are not very important in the weak light generally experienced by the other cells under water. It seems improbable, therefore, that any change of correction that may have occurred during the period of 7 or 8 weeks between the original standardizations and the dates of Series C 1 to C 9 could have had any important effect on the results. For Series C 10, obtained within a few days of the later determinations of "curvature" the revised corrections were used.

Further work on the increase of correction with time is desirable, and also on an effect that we came across during the bench tests, namely that the curvature depends on the colour of the light, being much greater for all cells with deep red light. This is probably due to increased leakage of current in bright light owing to the photo-conductivity of selenium, which has a maximum of sensitivity near the red end of the visible spectrum.

The relative sensitivities of the bare cells for weak light were found during the initial bench tests, but as differences might also occur in the filters, or diffusing glasses, the relative sensitivities of the cells as mounted in the case were found by daylight comparisons. A number of comparisons were also made between the top cell, as mounted, and our standard Weston mounted behind a VG 2 filter and opal glass (the VG 2 and VG 9 filters are very similar). These comparisons revealed certain irregularities, some of the ratios obtained differing by some 10% from the mean value. Comparisons made under the best conditions were, however, considerably closer, and by taking the mean it is probable that the error in the percentage illuminations due to this cause are not very serious. In one instance (Series C 6) the percentages have been reduced by 5% in order to reduce the value found just above the water surface to 100. Such errors in the percentages would be common to all the percentages in a given series (unless the errors were due to faulty curvature correction) and so would not affect the values found for the extinction coefficients. It seems possible that the intensities as measured by the deck cell were low in this series, since it was found that the gimbals mounting of the deck photometer was not functioning freely. This mounting has since been overhauled and an additional lead casting added so that the restoring force has been much increased; a more nearly level position is thus maintained.

In view of the irregularities in the behaviour of the cells used in this photometer the results given below are likely to be inferior in accuracy to those obtained, for vertical light only, with our Weston cell photometer, but it seems most unlikely that any errors which may occur are large enough to invalidate the general conclusions reached.

Only a few series of determinations have been made as yet, and in some of them the absence of drift allowed the photometer to rotate, and rendered it difficult to interpret the readings of the side cells. Thus in series C 1, the results of which are shown in Table I, the ship was anchored inside Plymouth breakwater, and there evidently was not sufficient tide to keep the photometer steady. As there was bright sunlight, the light under water was very highly directive, so that rotation of the photometer between readings rendered the results obtained with the side cells quite unreliable, and they have been omitted from the table, which only shows the results for the top and bottom cells, which of course are unaffected by rotation.

TABLE I

d m.	p %	μ_v	U/V %
SERIES C 1. 20. x. 38, 1.18 to 3.4 p.m. Anchored inside Plymouth breakwater. Sun and high wispy clouds. Wind fresh, E. Secchi disk seen to 7 m.			
A.W.	87	..	9·9
1	56	..	5·8
5	23·3	0·219	5·2
10	9·0	0·190	5·5
15	3·45	0·192	8·5
A.W.	89·5	..	8·2

Here d is the depth in metres, A.W. meaning that the photometer was suspended about 1·5 m. above the surface, in a position where some shading by the ship may have occurred. p is the percentage of the surface illumination, the latter being measured by our standard Weston cell with green VG 2 filter mounted on the roof of the deckhouse. μ_v is the vertical extinction coefficient for the depth interval between that opposite which it is printed and that next above. U/V is the ratio of the upward to the downward illumination, expressed as a percentage.

It will be noted that above water the mean value of U/V is near 9%; at intermediate depths it is about 5·5%; and at 15 m. reflection off the bottom, which was not far below, had raised it to 8·5%. The extinction coefficient, near 0·20, is considerably higher than that found out at sea a few days later, and we will see that in the clearer water the percentage of back-scattered light is considerably reduced. Clarke (1936) also found 4–6% for similar inshore water at Provincetown Harbour and Buzzards Bay.

If the sun is not shining the differences between the readings of the four side cells are far less marked, though it is not uncommon for one or two of them to give values some 50% higher than the others. This may partly be due to the greater brightness commonly found in the southern part of the sky, and partly to the large area of water darkened by the shadow of the ship, but unless the drift is sufficiently rapid to keep the photometer azimuth constant it is hard to disentangle the two effects.

It is probably best under these circumstances to read the sum of the currents through the four cells, remembering when correcting for curvature that, on the average only one-quarter of the current flows through each cell. This involves an under-correction, as the more strongly illuminated cells passing the larger currents should have larger correction factors applied to them. Moreover, the effective resistance of the galvanometer is increased, which would also slightly raise the factor. The error is not likely to be serious, however, unless the sun is shining, when each cell should be treated separately.

It is evident that, in the absence of direct sunlight, the mean horizontal illumination (as measured by a photometer with a plane vertical window set successively in all azimuths) is approximately equal to one-quarter of the sum of the four horizontal readings in rectangular azimuths. It would not, however, give a true picture of the average obliquity if we were to measure it by the ratio of this mean to the vertical illumination on the upper horizontal window. Almost all the light comes from above, the percentage of back-scattered light being generally from 2 to 5, and every oblique ray, no matter what its azimuth, contributes to the vertical illumination, whereas about half of them will fail to contribute to the horizontal illumination on a vertical window set in any given azimuth.

If we could replace our photometer having one horizontal and four vertical windows, each of area A suppose, by one, with a vertical cylindrical surface, area πA, to measure the horizontal light, it would obviously have an effective vertical area A to measure the horizontal component of a single ray in any azimuth. Thus the ratio of the light falling on the cylindrical surface to that on the horizontal plane surface would give the tangent of the obliquity of the ray. The actual illumination contains rays of all azimuths and obliquities, but still the mean value of the ratio would be the mean tangent of the obliquity, or we may say without serious error, the tangent of the mean obliquity. For any distribution not including a comparatively narrow beam, as would be produced by direct sunlight, the average efficiency per square centimetre of our four vertical windows would be very close to that of the cylindrical surface, thus, as their area is $4/\pi$ times as large, we should take $\pi/4$ times the sum of their readings as a measure of the total horizontal component of the light. The ratio of this to the vertical illumination gives the mean value of the tangent of the obliquity. It is worth noting that in air under a uniform hemispherical sky this ratio would have the value $\pi/2$, i.e. 1·57, corresponding to an obliquity of 58°, i.e. an altitude of 32°.* Beneath a smooth water surface the combined effects of refraction and of enhanced surface reflection of oblique rays greatly reduce the ratio, which falls to 0·60, corresponding to an obliquity of 31°, so

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* In view of the fact that the mean value of H/V is used as a measure of the angular distribution under water it seems to be more natural to describe this by the obliquity (i.e. the angle between the light and the vertical) rather than by the complementary angle of altitude, although we have hitherto used the latter for both aerial and submarine illumination.

we may take this angle as the average obliquity to be expected under a smooth water surface with a uniform sky. This obliquity is the same as that for a ray of sunlight with the sun at a zenith distance 43°·4, i.e. at an altitude of 46°·6, so for altitudes near that value the presence of direct sunlight should not have much effect on the average under-water obliquity.

Table II shows the results of three series obtained with an overcast sky and very light breeze near stations L 5, L 4, and L 3, situated 9, 5, and 1·5 miles south-south-west of Plymouth breakwater, respectively. The water surface was glassy, and the light dull, falling to about 3·7 kilolux at the end of series C 4 (as measured with standard Weston without colour filter), and becoming very weak by the time the C 5 measurements were made. These readings were made with the galvanometer. H/V is the ratio of the "total horizontal component" (as already defined) to the vertical component of the light, and $\theta = \tan^{-1} H/V$ is the mean angle of obliquity, namely the angle with the vertical. The other symbols have the same meaning as before, and all measurements refer to green light.

TABLE II

	d m.	p %	μ_v	U/V %	H/V %	θ
SERIES C 3, 25. x. 38, 11.27 a.m. to 12.45 p.m. At L 5, depth by sounding 56 m. Secchi disk visible to 15·5 m.						
	1	67·5	..	2·36*	58*	30°*
	5	39·5	0·133	3·08	71	35°
	10	22·4	0·114	3·25	77	38°
	15	13·4	0·103	3·03	78	38°
	25	4·8	0·103	3·08	72	36°
	40	0·94	0·109	2·67	70	35°
	55	0·18	0·110	5·6*	70	35°
Means	..	..	0·110	3·02	73	36°
SERIES C 4, 25. x. 38, 2.38 to 3.5 p.m. At L 4, Secchi disk visible to 11 m.						
	1	56·5	..	3·17*	71*	35°*
	10	20·6	0·112	3·29	84	40°
	20	6·05	0·122	3·31	85	40°
	30	1·87	0·117	2·91	76	37°
	40	0·62	0·110	..	77	37°
Means	..	..	0·115	3·17	80	39°
SERIES C 5, 25. x. 38, 3.45 to 4.6 p.m. At L3, Secchi disk visible to 12·5 m.						
	1	62	..	2·73*	64*	33°*
	5	35·5	0·139	3·07	70	35°
	10	18·6	0·129	3·45	78	38°
	20	5·1	0·129	3·85	84	40°
	30	1·23	0·142	3·0*	90	42°
Means	..	..	0·135	3·45	80	39°

* Disregarded in finding averages.

It is evident that on this day the water was fairly clear and very uniform, the opacity increasing slightly as one moved inshore. The percentage of upward light remained close to 3 throughout, neglecting a low reading at

1 m. and a high reading near the bottom, both in series C 3. The former is probably not very reliable, as readings so near the surface are difficult, and the latter is almost certainly raised by reflection off the bottom. The average obliquity was in general rather greater than that for the ideal case of smooth water and uniform sky. This was to be expected, as the sky is usually brighter at comparatively low altitudes, especially with the low, though completely obscured, sun of an October afternoon, and such waves as occurred in the comparatively smooth surface would further increase the average obliquity. It is somewhat surprising, however, that there is no evidence of a decrease of average obliquity with depth, due to enhanced absorption of oblique rays. Even in this clear water scattering appears to have been sufficient to maintain or in some cases even increase, the obliquity. The *U/V* ratio was found by us previously to be as low as 1·3 and 1·8 % (1928, 1933) with potassium cells (blue sensitive). Utterback (1936) reports about 1 % for green (5300 A.) and 2 % for blue (4800 A.).

When the sun is shining the differences between the readings of the side cells become very large, and it is no longer sufficient merely to take the sum of their readings. Under these circumstances, as has been pointed out, the disentangling of the results for horizontal light becomes difficult and unsatisfactory unless there is sufficient drift to keep the orientation of the photometer approximately constant. This was the case on October 26 at International Station E 1 20 miles south-south-west of Plymouth breakwater, when series C 6 was obtained, the results being set out in Table III. With the sun shining and the ship lying beam on to the wind, her head is always turned in whichever direction is most remote from the sun. Thus the photometer over the stern is safe from all shading of direct light, and as this forms the greater part of the total illumination the effect of the ship's shadow is much reduced. It affects chiefly one of the two side cells turned away from the sun, and on this we can base an attempt to disentangle the relative effects of sunlight and diffuse light from the readings of the four side cells.

Thus on October 26 1938 there was a strong north-west wind and rising sea. The ship lay with her head to the north-east, so that the sun, whose mean bearing during the series must have been about south-south-west to south-west by south (Magnetic), was astern and somewhat to starboard. The photometer vane in line with an edge between two cells presumably pointed upwind, i.e. north-west. This would bring the four side cells, which we designate *A*, *B*, *C*, and *D*, into positions facing approximately north, east, south, and west, respectively. We should expect that *A* would give the lowest reading, as it was the most remote from the sun, and partly faced the ship and the area of darkened water along her port side. *B* was also partly directed toward the ship, but on her starboard side where there was no shading of direct sunlight. *C* and *D* must both have received direct sunlight, and were entirely unshaded by the ship.

These expectations were, in the main, realized, though on two occasions—

at 20 and at 70 m.—the photometer appears to have swung round slightly so that B and not D received a share of the sunlight, and on the second of these with the photometer close to the bottom D actually received slightly less light than A. In working out the results we have assumed that the cell giving the lowest reading (A for all depths except 70 m.) was affected by shading, that the cell giving the reading lowest but one (B for most depths, D for 20 m., A for 70 m.) might be taken as a measure of the diffuse horizontal light, and that the excesses of the readings of the remaining two cells (C and either D or B) above this value were due to the horizontal component of the direct sunlight. Thus if c is the reading of cell C (always the greatest), and so on, and taking b as the diffuse light we have $c-b$ for the horizontal sunlight on C, and $d-b$ for that on D. Hence, if H_s is the horizontal component of the sunlight making an azimuthal angle ϕ with the normal to C, we have $c-b=H_s \cos\phi$, and $d-b=H_s \sin\phi$ hence $\tan\phi=\dfrac{d-b}{c-b}$. Hence we can find ϕ, and so H_s, the horizontal component of the sunlight as would be measured by a vertical window set in azimuth perpendicular to that of the rays. A cylindrical photometer area of curved receiving surface πA would only offer an area A to this directed light, but its area for the diffuse light would be πA, so that H_d, the total horizontal component of the diffuse light, is πb, and H, the total horizontal component of all the light, is H_s+H_d.

TABLE III

d m.	p %	μ_v	U/V %	H_s/H_d	H/V %	θ
SERIES C 6, 26. x. 38, 12.52 to 1.51 p.m. Sun's altitude 26–22°, mean 24°. Obliquity of sun's rays beneath smooth surface 42–44°, mean 43°. Obliquity for diffuse sky light 31°. At Station E 1, depth by sounding 71 m. Strong north-west wind and swell becoming heavy. Clear sun and blue sky.						
1	95·5	..	2·15*	2·30	63·5*	32°*
5	48·5	0·170	2·68	2·07	88·5	42°
10	25·8	0·126	2·98	0·67	88·5	42°
20	6·8	0·133	3·28	0·805	118·5*	50°*
40	0·96	0·097	3·34	0·254	79·5	38°
55	0·183	0·110	2·60	0·178	77·5	38°
70	0·041	0·100	3·75*	0·063	79·5	38°
Means ..	..	0·112	2·98	..	83	40°
SERIES C 10, 30. v. 39, noon to 2 p.m. Sun's altitude 62–53°, mean 58°. Obliquity beneath smooth water surface 20–27°, mean 23°. At Station L 4, depth about 50 m. Strong east-south-east wind, heavy swell with breaking waves. Clear sun and unclouded sky.						
1	59	..	1·91*	3·39	64*	33°*
5	42·5	0·082	2·02	3·48	71	35°
10	30·5	0·065	1·80	2·21	77	37°
15	23·5	0·052	1·89	1·94	69	35°
20	16·1	0·075	2·07	1·70	76	37°
30	5·95	0·099	2·72	1·59	90	42°
40	2·52	0·086	4·05*	0·94	89	42°
Means ..	..	0·076	2·10	..	79	38°

* Disregarded in taking averages.

We cannot measure separately the vertical components of the sunlight and diffuse light, since we cannot perform shading tests under water. It would seem, therefore, that the most convenient method of expressing the results at any depth is to give as before the value of H/V and also the value of H_s/H_d, the latter giving a measure of the persistence of direct sunlight at different depths, and hence of the scattering.

The table also shows the results obtained at L 4 on May 30 1939, with a cloudless sky, high sun, fresh wind and heavy swell with breaking waves. As the wind on this day was east-south-east cell *A* always received most of the direct sunlight.

With sunlight and rough water surface the readings at 1 m. must have been rather unreliable, so that no special significance need be attached to the very low surface loss in series C 6 nor to the rather high loss indicated in C 10. The readings at 20 m. in series C 6 are somewhat anomalous and those at 70 m. show the effects of reflection off the bottom. In finding the averages shown for each series the readings marked have been disregarded.

It would seem from the above figures that when the surface is rough, at least, the presence of either low or high sunlight makes little difference in the average obliquity of the light under water as compared with that found in the series with overcast sky. There is no evidence of reduction of average obliquity with depth; in fact in C 10 it apparently increased somewhat, which may be connected with the increase in the extinction coefficient found below 20 m.

The most remarkable feature of series C 10 is the exceedingly clear water in which it was carried out. The average extinction coefficient from 1 to 20 m. was only 0·068 which is rather smaller than any value that we have previously found for such an interval of depth. Below 20 m. there was a slight increase. It is possible that the depths may have been slightly over-estimated, as owing to the rapid drift the supporting wire made an angle of some 15° with the vertical when the photometer was at 40 m. This would cause the depth to be over-estimated by some 2 or 3 %, with a corresponding reduction in the value of μ_v. At the smaller depths, where the lowest values of μ_v were obtained, the relative error would be less, as the wire would be more nearly vertical.

This very clear water was similar to that found by Utterback & Jorgensen (1934) in the North Pacific. It was accompanied by a low value for the upward light, and the increase in this near the lower limit of the series may be due to the slight increase found in the opacity, since the bottom was too far below to reflect an appreciable amount of light. The low value of μ_v recorded above may be compared with that given by Oster & Clarke (1935), 0·049, for the Sargasso Sea, and Clarke's (1938) even lower value, 0·038, for the Cayman Sea, the most transparent part of the ocean as yet examined.

SUMMARY AND CONCLUSIONS

Preliminary observations have been made in the English Channel off Plymouth on the average obliquity of illumination under water, and on the relative intensity of light reflected upwards at various depths, the readings being made with a cubical photometer containing six "Electrocell" selenium rectifier cells mounted behind opal glasses and Jena VG 9 (green) filters. The cells measured the light of wave-lengths about 480–580 mμ falling on upward- and on downward-turned horizontal surfaces, and on four vertical surfaces in rectangular azimuths.

The average angle with the vertical or of obliquity was from 36 to 40°, and no significant difference could be detected between that for smooth sea and overcast sky, and that for rough sea and either high or low sun. Figures for smooth sea and sunlight are more difficult to obtain, as in the absence of drift due to wind the photometer may rotate.

No decrease in average obliquity with depth was found, in some cases there was evidence of a slight increase. This is in accordance with our previous results, and accords well with the constancy of extinction coefficient so often found throughout a series. It is not, however, in agreement with the careful work of Johnson & Liljequist, so further determinations would seem to be desirable.

The percentage of the light which was scattered back so as to fall on a downward-turned surface varied from 5·5 for comparatively opaque water (extinction coefficient 0·20) inside Plymouth breakwater, to 2·1 for very clear water (extinction coefficient 0·076) some miles off at sea. The presence or absence of sunlight had little effect, values close to 3·0 being obtained with and without sun for water having a coefficient close to 0·110.

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THE ECOLOGY OF THE TAMAR ESTUARY

VI. AN ACCOUNT OF THE MACROFAUNA OF THE INTERTIDAL MUDS

By G. M. Spooner, M.A. and H. B. Moore, Ph.D.

From the Plymouth Laboratory

(Text-figs. 1–12)

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INTRODUCTION

As pointed out in the Introduction to this series (Hartley & Spooner, 1938), a large part of the ground occupied by the estuaries of the Tamar and its confluent rivers, the Tavy and Lynher, consists of deposits of soft mud exposed at low water. A general account of the mud banks and flats, and their relation to tidal levels and position in the estuary, has already been given. Of the extensive intertidal zone (see 1938, Plate XVIII) by far the greater part provides a substratum of soft mud.

Owing to the extent of the intertidal muds, the fauna which they harbour must be regarded as one of the main elements of the fauna of the estuary as a whole. Supplying food for bottom-feeding fish* on the flood, and for various shore and wading birds on the ebb tide, its quality and quantity are likely to affect the numbers and distribution of the more conspicuous and economically important vertebrate population. Investigation of this particular element of the fauna was further prompted by the deficiency of information relating to it. While the main species frequenting this type of habitat in Britain are tolerably well known (though, as was discovered, not by any means completely), there is but little quantitative data of any sort relating to them. The difficulties presented to the investigator by the nature of the habitat are

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* Lists of food organisms for the various estuarine fish are given by Hartley (1939) in this *Journal*, pp. 1–68.

considerable, and probably explain why estuarine mud-dwelling faunas have been comparatively neglected.

This account deals essentially with the fauna permanently associated with the mud deposits, embracing species which are not dependent on the vegetation, deposits of weed, or other extraneous objects which may be lying on the surface of the mud. In the Tamar estuary the greater part of the surface of the muds is bare. In places, and at certain seasons, a thin coating of matted filamentous alga may be present, while locally there are growths of *Zostera hornemanniana* (see Tutin, 1936) and *Z. nana*. *Zostera* grows over large stretches of St John's Lake above the half-tide level, and thinly in restricted patches elsewhere. Ground supporting these limited types of natural vegetation is far from completely covered with the growths when the water rises over it, and the general facies of the burrowing fauna is unaltered. Surface-living forms are to some extent favoured by the additional surface and cover which the plants provide, but the species concerned are the same as those which are distributed over bare ground. It is another matter, however, where objects occur which provide close cover: for instance, clumps of brown algae, either loose or attached to scattered stones. These harbour a considerable population of Crustacea, etc., which evidently concentrate in them as the tide recedes. The cover provided by casually distributed stones, tin cans, etc., is similarly utilized. The fauna associated with such objects is here ignored, and will be dealt with on a future occasion.

Another group of species which fall outside the scope of this paper include forms such as mysids, shrimps, prawns, and gobies, which, though they sometimes occur in mud sievings, belong naturally to the free-swimming animal population. They occur only because they are liable to be stranded in shallow depressions as the tide recedes and to seek cover in the surface of the mud if the water drains away.

The microfauna of the muds, which includes small copepods, nematodes, etc., is being separately investigated by Mr P. R. Crimp as part of a more general survey of the microfauna of bottom deposits in the Plymouth area. Other types of littoral fauna in the Tamar also have been, or are being, studied. Population counts of the beach mollusc fauna at Torpoint, including some species dealt with here, are given in the second part of the work on the biology of *Littorina littorea* (Moore, 1939).

In so far as the salinity gradient of the estuary is considered in this paper, reference is made to the recent investigations by Milne (1938). In assessing the effect of the salinity changes on the fauna of the bottom, especially those species which are able to retreat into burrows, it must be remembered that water retained in the mud is subject to less fluctuation than the supernatant river water, and is likely to be of an appreciably higher salinity (see Reid, 1930; and Alexander *et al.*, 1932).

Information relating to the tidal levels is given in the Introduction to this series (Hartley & Spooner, 1938, pp. 504–6). It will be noted that Ordnance

Datum (O.D.), the zero standard to which levels are measured, is here nearly equivalent to the mid-tide level, being a little below mean sea-level and slightly above mean tide at Devonport. The mean range of the tide, measuring between 2·34 m. (neaps) and 4·73 m. (springs), is high compared with several districts in which attempts have been made to correlate fauna distribution with tidal level. This is a great advantage, since secondary fluctuations (resulting from varying winds, etc.) in the periods during which ground in the tidal zone is exposed are relatively small.

The primary object at the start of this work, after establishing what species were present, was to obtain some representative figures for their population density at different tidal levels and at different positions in the estuary. It proved possible to work a sufficient number of stations to give an indication expressed in quantitative terms of the way the various species are distributed in the tidal zone, as well as of their relative degree of penetration up-river.

MATERIAL AND METHODS

A series of localities was chosen as representative of the intertidal mud-flats as a whole, from St John's Lake, near the mouth of the estuary, to North Hooe at 18 km. from the datum line at the mouth. At each locality a series of stations was selected to give as representative as possible a sampling of the transect down the entire shore from the salting edge to low water. In most places the upper levels of the tidal zone were occupied by saltings, but at St John's Lake and Thanckes Lake the traverse could be carried to high water. The sampling unit was a square of 0·25 sq. m. area. The ground, marked out with a wooden frame, was dug to a depth which varied with the nature of the ground, but was usually from 15 to 30 cm. The earliest samples worked, including most of those at St John's Lake and Clifton Flat, were not dug sufficiently deep to include quite all the burrowing fauna, but thereafter all samples were dug to a depth which appeared to include all animals. The ideal practice in work of this kind is to take a number of small samples at each station, and combine them for obtaining a fair sample of the area. In the present work the time and labour available for collecting, transporting the samples to the boat, and dealing with them subsequently, only permitted that at most a total of $\frac{1}{2}$ sq. m. of ground could be taken at each station of a traverse. But in dealing with soft muds there proved to be a limit to the size to which the unit sample could be reduced. If the area is much less than $\frac{1}{4}$ m.^{2} (the unit adopted), the difficulties of digging a clean edge are increased, and errors introduced by the caving-in of the sides of the excavation may become large. Consequently the best that could be managed was to take one or two samples of $\frac{1}{4}$ sq. m. surface area at each station. The mud was dug into a large sack, which was then tied up, labelled, and slid over the mud to the boat, where it was hoisted on board for sieving. If the sacking is new the risk of loss from the sample is negligible, and this method of transport of heavy masses of mud for a distance over soft mud-flats proved as practicable a method as could be devised.

The sieve used was made of perforated zinc with round holes 0·8 mm. in diameter. A layer of the zinc formed the bottom of a wooden box a foot square in area and a foot deep. Sieving was found to be greatly facilitated when a window of fine gauze (of comparable mesh) had been fitted into the side of the sieve. When mud is being handled containing much vegetable matter, which easily clogs the bottom of the sieve, the larger particles tend to fall clear of the side window, thus allowing an exit for the muddy water; and though it also is found in practice to clog, the side window is much more easily kept clear than the bottom.

The mud from the sack was transferred in portions into a small bath standing inside a larger bath. In the former it was mixed by hand with water until it reached a soup-like consistency. Water was continually added to this bath and the mud suspension allowed to overflow into the larger bath, from which it drained through a plug over the side of the boat into the sieve. The fine washings collecting in the sieve were removed at intervals. Heavy objects, such as larger molluscs, stones, gravel, shells, etc., settled to the bottom of the baths, and were collected separately as "coarse" washings. This method of sieving has several advantages. The most important is that the more delicate animals are mostly undamaged, and do not get crushed to pieces as inevitably happens if the lumps of mud are broken in the sieve itself. Several people can work together round the bath, but even with only two a larger amount of mud can be handled in a given time than with any simpler method.

The samples of sieved material were washed clean in the laboratory, and spread out in flat dishes. The larger animals were picked out and the full number in the sample counted, while for the smaller sizes (typically the most numerous) it was necessary to have recourse to subsampling. Subsamples varied from one-sixth to one-third of the total matter, depending on the nature and bulk of the sieved material. These were worked through in detail. The coarse washings usually required a greater degree of subsampling than the fine washings.

An attempt was always made to reduce the additional error of estimation due to subsampling to a minimum. Every time as many animals as practicably possible were picked out of the whole sample, so that by far the greater *bulk* of animals, including all the larger, most of the medium-sized, and even many of the smallest individuals, were removed before the remainder was subsampled. For species still present in the subsamples the estimate of the total number, N, is simply obtained as follows:

$$n_1 + an_2 + bn_3 \ldots = N,$$

where n_1 is the number first removed from the whole sample, n_2 that removed from a portion of the sieving which had been divided to $1/a$ of the total, n_3 that removed from another portion divided to $1/b$, and so on. It is easily shown that the greater the value of n_1, that is to say the greater the number of individuals picked out of the whole sample, the smaller is the sampling error of N. Except for the very smallest sizes (e.g. *Cardium* spat), or abundant small species such as *Hydrobia ulvae*, the contribution made by n_1 was always the largest.

The catches were sorted within one or two days, before the animals had time to die and decay. There was thus no difficulty in distinguishing the living *Hydrobia ulvae* from the empty shells which were often present in great numbers, and which give great trouble in the sorting of preserved samples. The numbers of polychaetes, when the specimens were fragmented, were determined from the numbers of heads present.

The levels of the stations were determined at the time the samples were taken by means of a dumpy level, being referred to a fixed point on the shore or salting. At the same time the distance between the stations was measured either directly with a tape or by means of a range finder. The levels are not of any great accuracy on account of the difficulty of finding any firm foundation for the level. The levels of the fixed points on the saltings, to which all station levels were temporarily related, were themselves related to Ordnance Datum by a series of measurements taken in August 1937. At low tide the water in the estuary slopes down very considerably from the upper part of the estuary towards the mouth, but at high tide, when the whole width of the estuary is full of water, it may be assumed that the level is practically constant throughout. The measurements were made on a comparatively windless day, and in summer, so as to avoid any large flow of fresh water. During the low-water period a series of gauges were set up to record the highest point reached by the water at each locality on the next high tide. The gauges consisted of a length of about a metre of glass tubing coated inside with gelatine containing silver chromate, which changes colour in contact with sea water. The tube was lashed to a stake driven into the mud, and its lower end fitted with a short length of capillary tubing to damp out any wave action, the capillary tubing itself being protected from clogging with any floating mud by a piece of muslin tied over the end. The open top of the tube was protected from any possible rain by a small glass cap. The recorded heights of high water on each gauge were correlated with the fixed datum at each locality, and with Ordnance Datum through a measurement made at high water at a datum mark on the shore below the laboratory at Plymouth.

The greater part of the work was carried out during the summer months, when weather conditions and the temperature of the water were not too adverse. As a check, however, one traverse was worked on St John's Lake in February. The results, as will be seen, indicate no essential differences between the summer and winter population.

We wish to express our indebtedness to Messrs W. Searle and C. Haughton for their ready co-operation in the field work, and to several visitors to the

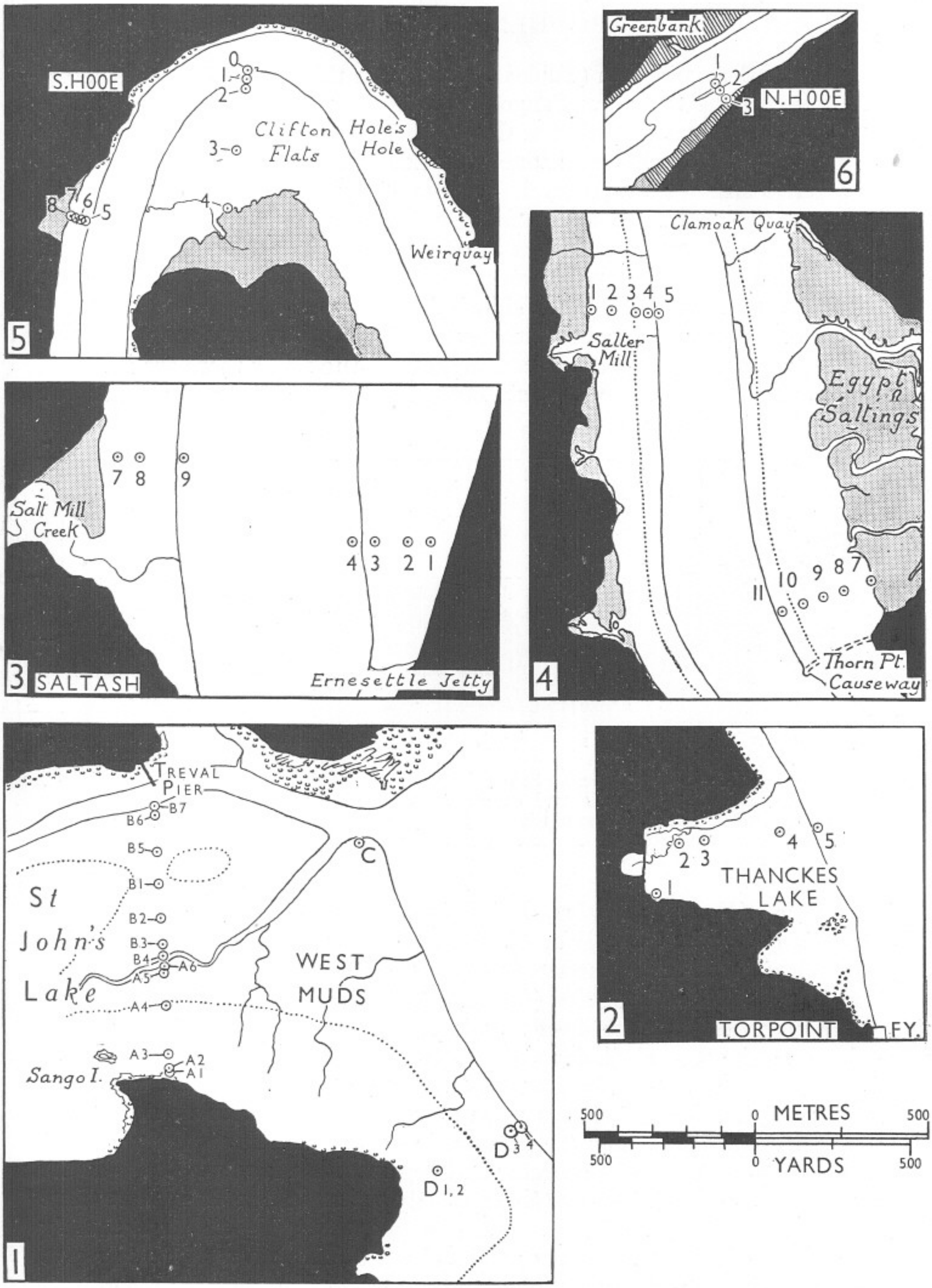
laboratory who at one time or another helped in the collection of the material; to Mr P. H. T. Hartley who gave much valuable help at various times in dealing with the samples and in the surveying work; to Miss M. V. Lebour for assistance in naming the Mollusca, and to Mr D. P. Wilson for confirming the identification of polychaete species.

RESULTS OF ANALYSIS OF THE SAMPLES

The animal populations of all the stations worked, with estimates of the population density of each species present, are given in a series of Tables (I–VIII). The stations are grouped naturally, for the greater part, into traverses across the intertidal zone at different positions in the estuary. The actual positions of the traverses and the stations are shown on maps (Figs. 1–6), which can be readily related to the plan of the estuary given in the Introduction to this Series (Hartley & Spooner, 1938). In the Tables as much essential information as available is given for each station, e.g. tidal level, a general indication of the nature of the ground, and any noteworthy character of the solid material held in the mud. While the latter has not been studied in any detail, some note has been taken of the presence of excessive amounts of broken shells, stone fragments, vegetable fragments, leaf remains, etc.; and it may be pointed out that both the relative composition and total bulk of such solid matter held in the mud was found to vary greatly both in different localities, at different tidal levels, and even in adjacent positions at the same level.

The estimates of population density are expressed in number of individuals per square metre, since this has become an established standard in ecological literature. The use of this unit, as often happens, involves the somewhat unsatisfactory procedure of multiplying the original count or estimate by a figure ranging from $1\frac{1}{3}$ to 4, and the approximate nature of the figures must therefore be strongly emphasized. In attempts to make comparisons it must be further remembered that the effects of marked patchiness of distribution could not be overcome by the sampling methods employed. The sort of differences that are shown between a number of stations worked on St John's Lake near the mid-tide level might have been expected on other traverses had more samples been taken at given levels. Full weight being given to these considerations, it is yet concluded that sufficient counts have been made to give, when taken in combination, a fairly clear picture of the order of population density attained by at least the more widely distributed species. As measures of the total macrofauna population, or for use in estimating the total bulk of animals, the total counts for each station are evidently good close approximations.

The areas investigated are dealt with in succession, progressing up-river. Twenty-four stations were worked on the broad flats of St John's Lake



Figs. 1–6. Maps showing the positions of stations at which sample population counts were made (Tables I–VIII). Land marked black; high grass saltings hatched; typical saltings marked in stipple; the permanent river and other channels marked by the M.L.W.O.T. line. The dotted line indicates approximate mid-tide level. 1. St John's Lake area (Tables I–III). 2. Thanckes Lake (Table IV). 3. Flats above Saltash Bridge (Table V). 4. Flats between Cargreen and Weirquay (Table VI). 5. Clifton and South Hooe area (Table VII). 6. North Hooe area (Table VIII).

(Fig. 1): of these nineteen (Tables I and II), in thirteen positions, lie along a traverse passing from near Sango Island to the channel at Treval landing-stage. A diagrammatic section of this traverse is given in Fig. 7, showing its drop to a narrow secondary channel, and rise to a wide "flat" lying between the levels 0 and −1 m. At levels between +1·0 and −0·25 m. the surface of the ground is covered with a fairly continuous growth of *Zostera hornemanniana*.* The traverse crosses a moderately productive winkle ground. Some additional stations were worked on the "West Muds" adjoining the main river channel (Fig. 1 and Table III).

The total number of species listed is considerable, but some are not typical of soft mud habitats and others are irregular. Altogether there are included (i) true burrowing forms which are hidden below the surface when the tide has receded (*Nereis*, *Nephthys*, *Heterocirrus*, *Ampharete*, *Mellina*, *Scoloplos*, *Corophium*, *Cardium*, *Macoma*, *Scrobicularia*, *Abra*, etc.); (ii) forms which live freely exposed on the surface, though at times may retreat into the mud far enough to be hidden from view (*Cereus*, *Hydrobia*, *Littorina* spp. and *Carcinus* in part); and (iii) surface dwellers which make use of any available cover such as algal mats, shell deposits, vegetation debris, or growing *Zostera* (*Sphaeroma*, *Gammarus*, *Carcinus*, *Idothea*, and *Littorina* in part). The third group of animals is particularly liable to include species which are not strictly characteristic of soft muds: the occurrence of even the most regular species of the group is likely to be sporadic and dependent on local variations in the surface of the ground. Thus *Sphaeroma* only occurs in numbers where there is a thick deposit of old mollusc shells, and young *Mytilus* are entirely dependent on some solid object for attachment. The leaves of *Zostera* give an extra area of substratum to *Littorina*, *Cereus*, and *Hydrobia*, but the growth

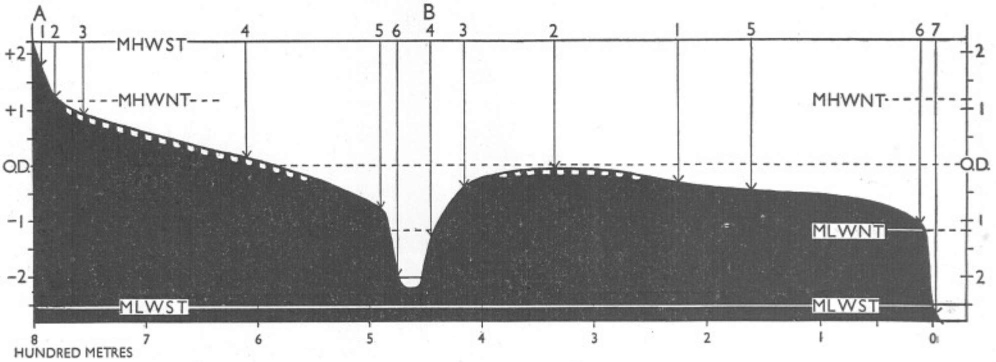


Fig. 7. Section of main traverse across St John's Lake (Fig. 1 and Tables I and II). Horizontal distances in metres from Treval channel. Vertical scale in metres from Ordnance Datum (O.D.). The positions of the stations (A 1–6 and B 1–7) are indicated by vertical lines, labelled along the top of the diagram. The broken white line indicates the extent of the *Zostera* growth.

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* St John's Lake (Treval shore) is the type locality for this plant (Tutin, 1936).

TABLE I. ST JOHN'S LAKE, MAIN TRAVERSE, MAY TO AUGUST 1936. Numbers of animals per square metre

Station no.	A 1	A 2	A 3	A 4	B 2	B 1	B 3	B 5	B 5	A 5	B 6	B 4	A 6	B 7
Date	21. vii. 36	21. vii. 36	21. vii. 36	21. vii. 36	6. viii. 36	6. viii. 36	6. viii. 36	5. v. 36	6. viii. 36	21. vii. 36	6. viii. 36	6. viii. 36	21. vii. 36	6. viii. 36
Level, in m. from O.D.	+1·79	+1·25	+0·95	+0·15	−0·05	−0·33	−0·35	*ca.* −0·4	−0·45	−0·75	−1·05	−1·25	−1·95	−2·65
Area sampled	0·5 m.^{2}	0·5 m.^{2}	0·5 m.^{2}	0·75 m.^{2}	0·5 m.^{2}	0·5 m.^{2}	0·5 m.^{2}	0·75 m.^{2}	0·5 m.^{2}	0·75 m.^{2}	0·5 m.^{2}	0·5 m.^{2}	0·75 m.^{2}	0·5 m.^{2}
Surface of ground	Some stones	Bare	Some *Zostera*	Some *Zostera*	Thick *Zostera*	Some green alga	Some green alga	Many shells	Many shells	Bare	Bare	Some green alga	Bare	Bare
Species														
COELENTERATA														
Cereus pedunculatus	..	10	..	3	32	..	..	..	58	..	..	..	..	..
NEMERTINI														
Nemertine spp.	..	..	..	1	..	10	..	..	6	..	..	..	..	..
POLYCHAETA														
Leptonereis glauca	..	..	..	..	..	16	..	..	..	..	..	..	..	..
Nephthys hombergi	..	..	..	..	..	..	288	207	130	264	278	158	125	82
Scolecolepis fuliginosa	..	2	..	..	..	..	..	..	..	..	..	..	..	..
Ampharete grubei	..	..	..	..	..	70	1290	4033	2640	1400	260	176	128	76
Mellina palmata	..	..	..	..	..	..	..	5	..	..	..	..	..	..
Scoloplos armiger	10		64	..	152	..	..	..	..	..	..	..	..	..
CRUSTACEA														
Sphaeroma serratum	..	..	..	..	..	..	..	279	310	..	..	..	..	..
Idotea viridis	..	..	..	..	26	2	2	1	..	..	..	..	..	..
Gammarus spp. imm.	..	..	..	..	..	..	..	4	..	..	..	..	..	..
Melita palmata	..	..	..	..	..	..	16	132	162	..	..	30	..	..
Carcinus maenas juv.	2	2	34	49	200	10	28	19	168	52	..	16	7	..
INSECTA														
Dipterous larvae	10	2	..	..	..	..	..	..	..	..	..	..	..	..
MOLLUSCA														
Hydrobia ulvae	2140	8200	14,160	24,660	28,420	1420	3150	1008	3240	1180	20	200	192	70
Littorina littorea:														
Over first year	..	10 } 26	..	21 } 60	54 } 74	2 } 2	..	4 } 156	346 } 480	26 } 26	..	..	..	..
First year		16		39	20	..		152	134	..				
L. saxatilis	10	420	580	360	88	..	..	1	10	..	..	..	..	..
Cardium edule:														
Over 2 cm.		10	38	76	16	..	14	15	46	29	..	4	1	
1–2 cm.	..	24 } 44	12 } 146	17 } 164	12 } 144	14 } 64	6 } 44	.. } 383	28 } 114	11 } 128	6 } 6	2 } 8	3 } 24	..
0·5–1 cm.		..	} 96	} 71	12	2	..	} 368	16	} 88	..	..	} 20	
Below 0·5 cm.		10			104	48	24		24		..	2		
Macoma balthica:														
Over 1·2 cm.	..	14 } 20	12 } 28	11 } 11	4 } 4	..	24 } 30	} 4	12 } 36	5 } 13	4 } 6	8 } 12	3 } 3	..
Below 1·2 cm.		6	16	..	..		6		24	8	2	4	..	
Scrobicularia plana:														
Over 3 cm.	..	..	} 4	} 1	..	..	..	?	2	..	..	..	..	..
2–3 cm.	..	..			..	..	..	?	..	..	..	..	..	..
1·2–2 cm.	.. } 50	.. } 46	} 1094	} 34	.. } 158	.. } 160	2 } 178	? } 75+	.. } 50	.. } 173	.. } 150	.. } 14	.. } 8	.. } 10
0·6–1·2 cm.	..	..	..	..	..	10	2	..	..	..	..	..	..	..
Under 0·6 cm.	50	46	1090	33	158	150	174	75	48	173	150	14	8	10
Abra prismatica	..	..	..	..	..	..	..	..	..	..	..	12	3	..
A. nitida	..	..	..	..	..	..	..	..	..	..	10	..	..	..
Mytilus edulis juv.	..	10	28	11	12	..	..	..	..	..	..	..	..	..
Chiton sp.	..	..	2	3	..	..	..	5	24	..	..	..	..	..

Notes on nature of ground, and material retained by the sieve. All stations on soft mud. A 1, on edge of the mud flat, much admixture of stony matter (shillet) and mollusc shells. A 2, sievings with some gravel and fragmented shillet, but more vegetable matter. A 3, growth of *Zostera*, sievings typical. A 4, thick growth of *Zostera*, sievings typical. B 2 and B 1, some green alga, sievings typical. B 3 and B 5 (May 5), unusual amount of shelly material. B 5 (August 6), extra amount of gravel admixture. A 5, typical bare soft mud residues. B 6, B 4, A 6, A 7, very soft ground on channel slopes.

Depth to which samples were dug. At station B 5 on May 5 1936 the sample was dug only to 4 cm., being originally designed to estimate the fauna living at or close to the surface. Some of the larger individuals of polychaetes and *Scrobicularia* would have been left behind. Other stations were dug to about 15 cm., but it is still possible that a few large *Scrobicularia* escaped detection.

Note on fauna. Small Oligochaetes occurred in considerable numbers in some stations: these, however, are not included among the macrofauna. The absence of *Nereis diversicolor*, *Corophium volutator*, and some other species which are listed in Tables II and III is noteworthy. The size-measurements of the groups into which the populations of bivalves are divided refer to lengths. The population of *Littorina littorea* is divided into year groups, of which the first is clearly separable from the rest.

TABLE II. ST JOHN'S LAKE, MAIN TRAVERSE, FEBRUARY 10 1937

Numbers of animals per square metre

Station no.	B 2		B 1		B 3		B 5		B 6	
Approx. level, in m. from O.D.	−0·05		−0·30		−0·35		−0·45		−1·05	
Area sampled	0·5 m.^{2}		0·5 m.^{2}		0·5 m.^{2}		0·5 m.^{2}		0·5 m.^{2}	
Surface of ground	Bare		*Zostera*		Bare		Bare		Bare	
Species										
COELENTERATA										
Cereus pedunculatus	..		10		..		..		..	
Other Anemones*	..		12		..		..		..	
POLYCHAETA										
Nereis diversicolor	..		..		8		8		2	
Nephthys hombergi	184		..		212		176		134	
Heterocirrus zetlandicus (?)	..		..		32+		..		..	
Ampharete grubei	..		..		..		..		..	
Mellina palmata	6		..		..		..		..	
Scoloplos armiger	6		..		..		..		..	
Phyllodoce maculata	4		..		10		..		..	
CRUSTACEA										
Sphaeroma serratum	6		..		12		..		2	
Idotea viridis	54		..		10		..		..	
Corophium volutator	..		..		2		..		..	
Carcinus maenas juv.	2		36		2		10		..	
MOLLUSCA										
Hydrobia ulvae	10,890		8130		2260		..		30	
Littorina littorea:										
Over first year	16	16	68	178	..		8	8	..	
First year	..		110				..			
L. saxatilis	32		..		..		..		..	
Cingula sp.	6		..		..		..		..	
Cardium edule:										
Over 2 cm.	4	4	2	32	4	104	6	10	2	2
1–2 cm.	..		24		4		..		..	
0·5–1 cm.	..		6		4		..		..	
Under 0·5 cm.	..		..		92		4		..	
Macoma balthica:										
Over 1 cm.	4	16	1	2	10	10	..	2	..	4
0·5–1 cm.	12		1		..		2		4	
Scrobicularia plana:										
Over 3 cm.	..	138	4	6	..	26	..	40	..	2
2–3 cm.	..		..		..		..		..	
1·2–2 cm.	20		..		..		4		..	
0·6–1·2 cm.	32		2		12		14		2	
Under 0·6 cm.	86		..		14		22		..	
Abra nitida	..		..		..		..		4	
Mytilus edulis (juv.)	..		24		..		..		..	

Note. All stations on soft mud; B 2, sievings contained much vegetable detritus; B 1, growth of *Zostera* and shelly matter in sievings well above average; B 3, sievings typical; B 5, much vegetable detritus; B 6, on top edge of channel slope, much vegetable detritus. The samples were dug to a depth of at least 15 cm.

* Probably *Halcampa chrysanthellum*.

TABLE III. ST JOHN'S LAKE, WEST MUDS, MISCELLANEOUS SAMPLES

Numbers of animals per square metre

Station no.	D 1		D 2		C		D 3		D 4	
Date	22. x. 37		22. x. 37		19. viii. 36		22. x. 37		22. x. 37	
Level, in m. from O.D.	*ca.* +0·6		*ca.* +0·6		*ca.* −1·8		*ca.* −1·8		*ca.* −2·2	
Area sampled	$\frac{3}{8}$ m.^{2}		$\frac{3}{8}$ m.^{2}		$\frac{1}{2}$ m.^{2}		$\frac{3}{8}$ m.^{2}		$\frac{3}{8}$ m.^{2}	
Depth of sample	8 cm.		4–6 cm.		10 cm.		10 cm.		9 cm.	
Species										
NEMERTINI										
Nemertine sp.	..		5		..		..		..	
POLYCHAETA										
Nereis diversicolor	..		..		27		..		56	
Nephthys hombergi	11		75		98		187		32	
Heterocirrus zetlandicus (?)	64+		..		10+		+		3000+	
Ampharete grubei	..		..		86		64		158	
Mellina palmata	..		..		20		189		40	
Lanice conchilega	..		..		..		..		20	
Arenicola marina	..		3		..		..		..	
Phyllodoce maculata	67		3		..		..		51	
Sthenelais boa	..		..		..		..		3	
CRUSTACEA										
Sphaeroma serratum	13		3		..		..		3	
Idotea viridis	3		5		..		..		3	
Jaera albifrons (*marina*)	..		..		..		..		3	
Gammarus locusta	11		40		2		..		85	
Melita palmata	..		45		..		..		37	
Amphipod sp.	..		..		..		..		16	
Corophium volutator	11,000		53		6		..		254	
Carcinus maenas juv.	8		43		7		..		13	
INSECTA										
Dipterous larvae	3		..		..		..		..	
MOLLUSCA										
Hydrobia ulvae	4000		13,800		96		104		32	
Littorina littorea:										
2nd year class and over	3	3	13	48	..		+*		+*	
1st year class	..		35							
L. saxatilis	80		1101		..		..		..	
Gibbula cineraria	..		..		10		..		..	
Cardium edule:										
Over 2 cm.	11	51	6	174	†2	2	..	40	‡16	33
1–2 cm.	29		80		..		..		11	
0·5–1 cm.	11		21		..		..		5	
Under 0·5 cm.	..		67		..		40		1	
Macoma balthica:										
Over 1·2 cm.	..		..	5	4	4	..	3	..	
Below 1·2 cm.	..		5		..		3			
Scrobicularia plana:										
Over 3 cm.	..	13	..	51	..	10	..	5	..	16
2–3 cm.	..		..		..		..		..	
1·2–2 cm.	5		8		..		..		..	
0·6–1·2 cm.	5		11		..		2		..	
Below 0·6 cm.	3		32		10		3		16	
Montacuta bidentata	..		..		..		..		43	
Abra prismatica	..		..		37		..		..	
A. nitida	..		..		11		5		..	
Mytilus edulis (small)	..		5		..		..		..	
ECHINODERMATA										
Ophiothrix fragilis	..		..		..		..		3	

Notes on nature of the ground and material sieved. D 1, patch of bare mud in *Zostera* zone; sievings typical. D 2, damp depression with thick growth of *Zostera*; sievings, apart from *Zostera* plants, typical. C, bare mud near main channel with surface ripples; sievings nearly all vegetable detritus. D 3, black soft mud, sievings typical. D 4, bare mud with heavy content of coarse shelly material; ground rather firm.

* Adult specimens present on ground with a density of 1 or 2 per m.^{2}

† Large specimens occurred freely on this ground. A number were hand-collected close by.

‡ A high density of large-sized specimens.

on St John's Lake is not sufficiently dense to bring in a new population of animals which concentrate in thick cover. It may be further noted that though *Littorina littorea* is often distributed in the open, concentrations are liable to occur round solid objects, clumps of weed, or where other cover exists: their distribution, as actually observed, is liable to be sporadic.

The true burrowers are of more regular occurrence over the area investigated, and it is among them that the effects of tidal level can best be tested. They include, however, a few irregular species, such as *Arenicola marina* and *Lanice conchilega*, which appear to find the substratum generally unsuitable, and *Corophium volutator*, which is probably exceptionally sensitive to disturbance of the ground by tidal currents (see p. 327). The most regularly distributed worms are *Nephthys hombergi*, from about mid-tide level downwards (see p. 304), and *Ampharete grubei*, also below mid-tide (see p. 307). Among molluscs, *Cardium edule* (see p. 317), *Macoma balthica* (see p. 322), and young *Scrobicularia plana* (see p. 318) occur in nearly every station worked.

Within the zone it occupies perhaps the most uniformly distributed species and most independent of the nature of the ground is the surface-living *Hydrobia ulvae* (see p. 311). As readily seen by inspection of the ground, this mollusc is extremely abundant over many acres of mud-flat with its maximum density between +0·5 m. and just below O.D. The density distribution shown diagrammatically in Fig. 11 shows a clear zoning in relation to tidal level.

The salinities to which the main part of St John's Lake flats are exposed, excluding only the steeper slopes on the edges of the channels, may be taken as normally ranging between 35 and 30% in winter and almost marine conditions in drier periods of summer (see Milne, 1938). That there is definite estuarine influence is evident from the occurrence of *Scrobicularia plana*, *Nereis diversicolor*, and *Idotea viridis*.

A comparison of Tables I and II shows that there is little reduction of the fauna in winter. The polychaete *Ampharete grubei* is the only annual species which dies down in the autumn (see p. 307). The numbers of *Hydrobia ulvae* are significantly smaller, but the zone of maximum abundance may have been missed or not quite reached.

Table IV gives the results of a single traverse on Thanckes Lake, 3·4 km. from the river mouth (Fig. 2). The paucity of species here as compared with St John's Lake is mainly due to the lack of variety in the types of ground sampled, and to the small number of the samples. There are however some other indications of an increase in estuarine conditions: namely a decrease in numbers of *Cardium* and *Hydrobia*, with the appearance of *Nereis diversicolor* in fair quantity above the half-tide level. Excepting the slope at the edge of the river channel, the salinities to which this stretch of mud is exposed are estimated as only slightly below those affecting St John's Lake.

Two traverses were worked, one each side of the river, a little above Saltash Bridge (Fig. 3 and Table V). On the Cornwall shore, at the level of Salt Mill (7·8 km. from the river mouth), the high water zone is occupied by an expanse of saltings, which gives place to bare mud at 1·0 m. above O.D. The Devon shore is here a stone railway embankment which artificially limits the mud flat at a level just below O.D. The seven stations worked appeared well representative of the area, and the reduction in the number of species as compared with St John's Lake is certainly significant. Those which do not range up the estuary to this level include *Ampharete*, *Scoloplos*, and some other polychaetes; *Chiton* spp., *Abra* spp.; and *Cereus pedunculatus*. Of brackish-water species, *Nereis diversicolor* and *Scrobicularia plana* are well established, while *Cyathura carinata* and *Gammarus zaddachi* make their first appearance. A picture of the salinities prevailing in this locality has been given by Milne (1938), who studied the daily variation in detail on May 24 and June 3 1937. On the first date the salinity to which the low-water stations were exposed

TABLE IV. THANCKES LAKE TRAVERSE, AUGUST 8 1937

Numbers of animals per square metre

Station no.	2	3	4	5
Level, in m. from O.D. ...	+0·13	+0·13	−1·20	−2·20
Area sampled	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}
Ground	Bare mud	Bare mud	Bare mud	Bare mud
Species				
POLYCHAETA				
Nereis diversicolor	40	350	+	..
Nephthys hombergi	310	260	510	50
Heterocirrus zetlandicus (?)	..	..	..	1150+
Ampharete grubei *Mellina palmata*	20	+	+	295
CRUSTACEA				
Gammarus locusta	..	+	90	..
Corophium volutator	..	..	..	20
Carcinus maenas juv.	..	..	35	+
MOLLUSCA				
Hydrobia ulvae	204	790	60	..
Cingula semicostata	..	..	..	+
Cardium edule (below 0·5 cm.)	..	..	..	+
Macoma balthica:				
Over 1·5 cm.	..	..	..	
1·0–1·5 cm.	..	.. } 76	.. } 12	..
0·6–1·0 cm.	..	40	12	
Below 0·6 cm.	..	36	..	
Scrobicularia plana:				
Over 3 cm.	4	..		
2–3 cm.	..	4		
1·2–2 cm.	.. } 44	.. } 64	..	..
0·6–1·2 cm.	..	56		
Below 0·6 cm.	40	4		
Abra prismatica	..	..	+	+

Note. Station 1, at +0·78 m., on gravelly mud, yielded no fauna. In this table a bare + indicates that one specimen only was found in the sample.

TABLE V. TRAVERSES ABOVE SALTASH BRIDGE, May 13 1937

Numbers of animals per square metre

	Salt Mill, Cornwall Shore			Ernesettle Flats, Devon Shore			
Station no.	S 7	S 8	S 9	S 1	S 2	S 3	S 4
Level, in m. from O.D.	+0·96	+0·26	−2·25	−0·43	−0·55	−1·35	−2·25
Area sampled	0·5 $m.^2$	0·25 $m.^2$	0·25 $m.^2$	0·25 $m.^2$	0·25 $m.^2$	0·25 $m.^2$	0·25 $m.^2$
Surface of ground	Bare	Bare	Bare	Bare. Stiff mud	Bare	Bare	Bare. Muddy gravel
Species							
NEMERTINI							
Nemertine sp.	2	..	..	..	..	..	..
POLYCHAETA							
Nereis diversicolor	90	56	..	770	4	..	12*
Nephthys hombergi	6	132	84	40†	264	128	96
Mellina palmata	..	4	..	..	..	..	16
Lanice conchilega	..	..	..	..	..	..	4
Arenicola marina	..	..	..	..	+‡	..	..
Heteromastus filiformis	..	..	..	40	..	..	..
CRUSTACEA							
Cyathura carinata	380	..	..	4	..	..	..
Sphaeroma serratum	..	..	..	20	..	..	..
Melita palmata	..	4	4	..	..	16	..
Corophium volutator	..	..	12	..	4	..	..
Gammarus zaddachi imm.	..	..	..	..	..	..	4
Carcinus maenas juv.	2	..	..	..	..	..	+‡
MOLLUSCA							
Hydrobia ulvae	1090	170	..	60	4	..	..
Littorina littorea:							
Above 1st year	..	..	..	+§ } +	4 } 4	4 } 4	} +§
1st year	..	..	..	..	..	..	
Cardium edule:							
Over 2 cm.	6	..	4	..		..	..
1–2 cm.	2 } 32	.. } 8	.. } 40	.. } 9	..	.. } 4	.. } 4
0·5–1 cm.	22	4	..	..		4	4
Below 0·5	2	4	36	9		..	..
Scrobicularia plana:							
Over 3 cm.	12	..		20	12		
2–3 cm.	..	..		4	..		
1·2–2 cm.	2 } 280	4 } 16	..	.. } 33	.. } 12	..	..
0·6–1·2 cm.	20	12		9	..		
Below 0·6 cm.	246	..		..	..		
Mytilus edulis	..	..	..	..	+‡	..	..
INSECTA							
Dipterous larvae	40	..	..	..	..	..	..

Note. All stations on mud, of varying softness, except S 4. S 7, sievings contained much shelly material, especially quantities of old shells of *Hydrobia ulvae*. S 8, also much shell content. S 9, very soft mud on channel slope; sievings contain stone fragments. S 1, stiff mud, with high content of vegetable detritus. S 2, rather soft mud, with high coarse shelly material content. S 3, soft mud, typical sievings. S 4, muddy gravel at low water springs; sievings contain unusual quantity of stone and shell fragments.

* Very large specimens.
† Very young individuals only.
‡ Noted present on ground, but none in sample.
§ Present on ground, about 1 per $m.^2$ At S 4 clustered locally.

was as low as 17 ‰, and may be expected to fall to about 10 ‰ in the winter. The highest intertidal salinity on June 3 was 32 ‰. Milne (1938, Fig. 3) further gives high- and low-water salinities at Saltash from October 1936 to June 1937. There is a marked seasonal variation: high-water value can be as low as 14 ‰ in winter and as high as 33 ‰ in autumn, and low-water values range from 32 ‰ to 8 ‰. To sum up, it can be said that the flats above Saltash Bridge, while subjected to wide daily and seasonal fluctuations in salinity, are never covered by "fresh" water below 1 ‰, and, though during dry spells the water may regularly rise above 30 ‰, are never under the influence of full salinity sea water.

The next series of stations, worked on the flats between Cargreen and Weirquay (Fig. 4 and Table VI), show a still further depletion of marine species. Apart from the small *Heteromastus*, polychaetes are now represented by two species only, *Nereis diversicolor* and *Nephthys hombergi*, the latter in small numbers only and nearing the limits of its range, the former attaining a marked dominance over other worms. Among Crustacea, juvenile *Carcinus maenas* still occur, but *Gammarus zaddachi* and *Sphaeroma rugicauda* almost completely replace *Gammarus locusta* and *Sphaeroma serratum*,* while *Cyathura carinata* becomes a dominant species. Four species of Mollusca persist, *Scrobicularia* attaining dominance, but *Cardium* and *Hydrobia* occurring in greatly diminished numbers even on the most suitable ground. The upper limit of the three species of *Littorina* has been passed at Cargreen. It will be noted that the density of *Nereis* and *Scrobicularia* is sufficient to maintain the numbers of the total worm and bivalve population and counteracts the reduction or disappearance of other species. Extensive saltings, bordered for most of their length by an abrupt salting cliff, fringe this part of the river. The *Nereis* and *Scrobicularia* population extend through the salting creeks, and *Nereis* and *Corophium volutator* settle in salting pools. *Hydrobia ulvae* is much more plentiful in the saltings than on the mud flats. Salinities in this region are considerably lower than at Saltash. Near low water in wet periods in winter the channel may run almost fresh at the surface, while the highest summer salinity is not likely to exceed 27 ‰.

The flats off Clifton and South Hooe (Fig. 5 and Table VII) show a still further reduction in species. The upper limit of *Cardium edule* has been passed, and *Hydrobia ulvae* has declined still further. *Nereis diversicolor* is the only polychaete, but attains a high population density. The highest salinity to which the flats may be subjected, though by far the greater part of their surface rises above the half-tide line, is not likely to exceed 25 ‰. Finally, off North Hooe (Fig. 6 and Table VIII), the fauna is virtually restricted to *Nereis* and *Scrobicularia*. While the latter has started to decrease, the density of *Nereis* at the top of the mud bank was the highest obtained at any station worked. The

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* Additional data relating to these species is being published in another contribution.

TABLE VI. TRAVERSES ON FLATS BETWEEN CARGREEN AND WEIRQUAY

Numbers of animals per square metre

	Salter Mill, Cornwall Shore, 12·3 km. from mouth, July 22 1937					South End Egypt, Devon Shore, 11·2 km. from mouth, May 26 1937				
Station no.	E 1	E 2	E 3	E 4	E 5	E 7	E 8	E 9	E 10	E 11
Level, in m. from O.D.	+0·48	+0·33	−0·12	−0·96	−1·90	+0·86	+0·45	+0·39	+0·33	−1·51
Area sampled	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·5 m.^{2}	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}
Species										
POLYCHAETA										
Nereis diversicolor	484	392	236	8	..	590	142	130	28	..
Nephthys hombergi	8	32	+	12	20	..	6	8	20	..
Heteromastus filiformis ‡	..	..	60+	..	..	..	90+	20+	8+	..
CRUSTACEA										
Cyathura carinata	304	204	88	..	..	64	282	100	+	..
Gammarus zaddachi	..	..	..	..	..	260*	..	30†+	..	150†+
Carcinus maenas juv.	+	+	+	..	..	..	+	+	..	..
MOLLUSCA										
Hydrobia ulvae	610	180	100	76	12	80	328	470	160	..
Macoma balthica:	36	32	8	16	20	..	16	20	8	..
Over 1·5 cm.	4	4	..	..	..		..	..	..	
1·0–1·5 cm.	28	16	4	4	12		2	..	4	
0·6–1·0 cm.	4	12	4	12	4		14	20	4	
Below 0·5 cm.	..	..	..	..	4		..	..	..	
Cardium edule:	32	36	4	4	..	4	..	..	..	..
Over 1 cm.	..	..	..	..		4				
0·5–1 cm.	16	4	4	..		..				
Below 0·5 cm.	16	32	..	4		..				
Scrobicularia plana:	104	148	196	8	..	12	84	108	12	..
Over 3 cm.	28	56	48	..		..	34	28	4	
2–3 cm.	56	28	20	..		..	8	..	4	
1·2–2 cm.	12	20	36	..		12	26	12	..	
0·6–1·2 cm.	8	36	40	8		..	16	68	4	
Below 0·6 cm.	..	8	52	..		..	..	..	..	

Notes on the nature of the ground and of the material sieved. All stations on soft mud with no superficial growth. E 1 and E 7 are 4 m. from the base of the respective salting "cliffs". E 1–E 5, bare soft mud, sievings typical. E 7–E 9, bare mud, rather stiff and clayish below surface; sievings with increasing content of vegetable detritus. E 10, softer mud; sievings with very little shelly material and large quantity of vegetable detritus. E 11, very soft mud, rich in leaf deposit ("point stuff"); sievings with large quantity of dead leaves and twigs. All samples dug to at least 15 cm. A bare plus sign indicates only one specimen in the sample.

* Mostly small immature. † All small immature; identity confirmed by rearing to maturity.
‡ A species too small to have been adequately sampled.

TABLE VII. TRAVERSES IN CLIFTON AND SOUTH HOOE AREA, APRIL 27 1937

Numbers of animals per square metre

	Clifton Flats, Cornwall Shore, 14·2 km. from mouth				South Hooe, Devon Shore, 14·8 km. from mouth		
Station no.	F 4	F 3	F 2	F 1	F 7 & 8	F 6	F 5
Level, in m. from O.D.	+0·73	+0·58	−0·07	−0·79	+0·92	−0·39	−1·11
Area sampled	0·25 m.^{2}	0·5 m.^{2}	0·5 m.^{2}	0·25 m.^{2}	1·0 m.^{2}	0·5 m.^{2}	0·5 m.^{2}
Species							
POLYCHAETA							
Nereis diversicolor[*]	824+	1020+[†]	22+	..	950	1024	..
CRUSTACEA							
Cyathura carinata	288	68	..	..	61	12	..
Corophium volutator	..	..	..	..	..	2	..
Gammarus zaddachi imm.	20	..	..	..	..	..	..
Carcinus maenas juv.	..	2	..	..	1	..	..
MOLLUSCA							
Hydrobia ulvae	36	82	..		21	2	..
Macoma balthica:							
Above 1·0 cm.	20 } 20	2 } 4	2 } 2	..	..	..	..
Below 1·0 cm.	..	2	..				
Scrobicularia plana:[‡]							
Over 3 cm.	16	2+	+?		49	16	
2–3 cm.	8	2+	2+		25	2	
1·2–2 cm.	20 } 48	12 } 80+	12 } 26+	..	22 } 136	.. } 42	..
0·6–1·2 cm.	4	64	12		40	24	
Below 0·6 cm.	..	..	..	..	..	..	

One other station on the Clifton shore, F 0, at −1·85 m. level (0·5 m.^{2} area sampled) yielded no fauna.

Notes on the nature of the ground and material in sievings. All stations on bare mud. F 4, relatively firm ground, and sievings with little coarse material. F 3, relatively firm ground, sievings normal. F 2, soft ground; considerable quantity of vegetable detritus. F 1, soft mud with dense deposit of leaves and twigs ("point stuff"). F 0, firm muddy sand at edge of channel, well scoured; sievings with large quantity of fine sand, and much "point stuff". F 6–8, soft mud, with extremely little solid matter. F 5, very soft mud, with extremely little solid matter.

[*] The figures for stations F 4, F 3, and F 2 should be a little higher, as the samples were dug only to 10 cm.: some of the largest *Nereis* were therefore missed.

[†] The great majority were small immature.

[‡] In stations F 2–F 4 a few of the largest sizes may have been missed, owing to depth of sampling.

TABLE VIII. TRAVERSE AT NORTH HOOE, SEPTEMBER 22 1937

Numbers of animals per square metre

Station no.	G 3	G 2	G 1
Level, in m. from O.D.	+0·22	−0·54	−1·60
Area sampled	0·25 m.^{2}	0·25 m.^{2}	0·25 m.^{2}
Ground	Soft mud, below embankment	Soft mud, slope to channel	Muddy sand of bank rising from river channel
Species			
POLYCHAETA			
Nereis diversicolor	3030	400	..
MOLLUSCA			
Hydrobia ulvae	8	..	..
Scrobicularia plana:			
Over 3 cm.	32		
2–3 cm.	.. } 32	..	..
Below 2 cm.	..		

absence or scarcity of fauna in the lower levels of the tidal zone in the upper traverses is too striking to be disregarded. The cause is attributable to the scouring effects of the river channel, the evidence for which is discussed on p. 327.

List of Species and their Distribution

In summarizing the information on the various species encountered, it is usually possible to draw on additional data to those presented in the foregoing section, as general observations have been made in various parts of the estuary on occasions apart from those on which the quantitative samples were taken. Reference is also made (1) to certain other observations on neighbouring estuaries, and brackish-water habitats in Dorset; (2) to previously published records from the Tamar and other South-western estuaries; and (3) to published quantitative data referring to the species under consideration from whatever habitat. Species which have occurred casually, or which are more appropriately considered in connexion with habitats other than the intertidal mud-flats, are omitted. The names, unless otherwise indicated, follow the *Plymouth Marine Fauna* (1931).

COELENTERATA

Cereus pedunculatus (Pennant).

This anemone, which often occurs in great numbers in muddy estuaries as well as in a variety of other habitats, apparently finds conditions in the Tamar much less suitable than in the Salcombe estuary and Poole Harbour. On St John's Lake it occurs patchily, the highest density found being 58 per m.^{2} at a place where old mollusc shells were particularly numerous in the mud. It inhabits only the lower reaches of the estuary: Rat Island (Percival, 1929) is the highest position recorded. At one station on soft mud in Poole Harbour there were 770 per m.^{2}

POLYCHAETA

Phyllodoce maculata (L.).

This species is one of several polychaetes which occur at the marine end of the estuary. It is more general on St John's Lake than the sample counts may suggest, though evidently patchy. Rat Island (Percival, 1929) appears to mark its upper limit.

Nereis diversicolor O. F. Müller.

This characteristic species of estuaries and brackish waters occurs abundantly in some part or other of all Devon estuaries, inhabiting intertidal flats, salting creeks, salting pools, and brackish ditches. At Weymouth, Dorset, it is plentiful in the mud of Radipole Lake and Lodmoor, in brackish lagoons of standing water.

In all estuaries for which there are published fauna lists the general features of the distribution of *N. diversicolor* are the same. It is scarce or absent at the marine end, but becomes plentiful in the middle reaches of the estuary, where it is customarily reported as by far the most plentiful polychaete, and nearly, but not quite, reaches the upper limit of estuarine influence. It flourishes best in muds, and is partly replaced by other species in cleaner ground. In the Tees Survey Report (Alexander *et al.* 1935) some data of comparative abundance are given, based on counts of sample patches of ground through a 2 mm. sieve, showing a steady increase up-river to a maximum abundance in the middle of the estuary, after which a steady decline follows.* Hitherto, however, it has not been clear to what extent this increase to a maximum in the middle reaches is simply the result of an increasingly favourable substratum, since in most estuaries the intertidal deposits are predominantly sandy at the sea end, and do not attain the consistency of soft mud for some distance from the mouth. This complication does not arise in the Tamar, and, as will be seen, the data secured seem to give a definite answer on this point.

In the Plymouth district the status of *Nereis diversicolor* as a marine species is doubtful. Though recorded occasionally from the Sound, it probably never establishes itself in permanent full salinity sea water. Passing into the Tamar Estuary, one finds it occurring patchily in the muds of St John's Lake adjoining the Hamoaze, apparently here confined to the lower tidal levels. Becoming more plentiful in Thanckes Lake, it steadily increases up-river, becoming an outstandingly dominant member of the fauna, and reaching its greatest density—over 3000 per m.^{2}—at the highest station worked, North Hooe. Distribution diagrams are given in Fig. 8. Its upper limit in the river was not reached, but is given by Percival (1929) as half a mile above Calstock. Since in the Tamar a suitable substratum of soft mud is provided as low down as St John's Lake, it is clear that the progressive increase to the upper middle estuarine reaches is independent of substratum requirements.

As regards the optimum tidal level, Fig. 8 further demonstrates a clear preference for the upper half of the tidal zone, and an evident contrast in this respect with *Nephthys hombergi* (Fig. 9). Thamdrup (1935), investigating an area subject to comparatively high salinities and so near the seaward limit of this worm, records the species from all tidal levels over a wide stretch of muddy sand, the optimum (maximum density 320 per m.^{2}) rather above (once at) mid-tide level. Wohlenberg (1937) found it well distributed on various types of ground in a bay at the north end of Sylt, but predominantly in the upper part of the tidal zone; several counts of $1/20$ m.^{2} samples indicate that the maximum density falls well short of 1000 per m.^{2} In the Isle of Man, generally on muddy sand, the worm can occur at all levels, but is generally

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* The significance of these counts is impaired, as the authors of the Report emphasize, by the fact that variation with tidal level could not be taken into account, and successive samples may not have been strictly comparable: nevertheless a maximum *somewhere* in the middle reaches of the estuary is quite evident.

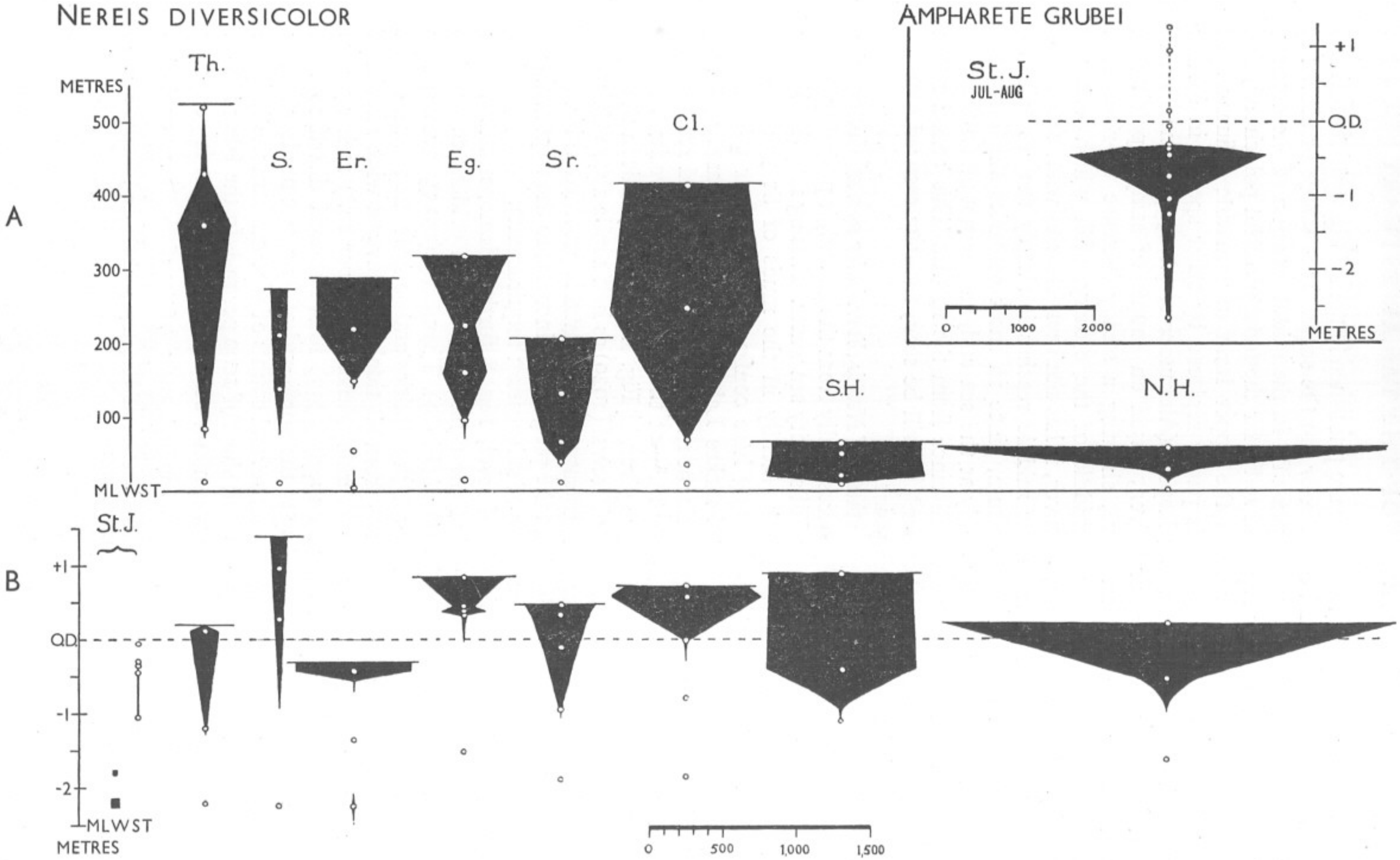
NEREIS DIVERSICOLOR
Th.
METRES
500
400
300
200
100
MLWST
S.
Er.
Eg.
Sr.
Cl.
S.H.
N.H.
A
B
St.J.
+1
O.D.
-1
-2
MLWST
METRES
0
500
1,000
1,500
AMPHARETE GRUBEI
St. J.
JUL-AUG
+1
O.D.
-1
-2
0
1000
2000
METRES

Fig. 8.

most abundant between mid-tide and high-water neaps (Moore, 1937*b*). Again, in Scotland Stephen (1929, 1930) records it from various more or less sandy localities as closely restricted to high-water mark, with a decided preference for places where the salinity is lowered by a stream. It is noteworthy that at the seaward end of its range in the Tamar, the worm has been found only in the lower half of the tidal zone, the region—perhaps significantly—in which the daily salinity fluctuations are greatest and in which the lowest salinities are encountered.

Such figures as have been published on population density fall well short of the higher values obtained in the middle reaches of the Tamar, but with one exception they all apply to habitats which clearly do not provide the optimum conditions for the species. Only in the Tees (Alexander *et al.* 1935) have counts been made in the middle reaches of an estuary. Here, however, a 2 mm. sieve was employed and an allowance must be made for the smaller individuals which would have escaped collection. Judging from the size distribution of populations we have collected, we conclude that to multiply the Tees' figures by 3 is a generous allowance: the maximum (at section IX of the river) of 230 thus becomes 690 per m.^{2} In other sections of the river the densities were much less than this, and it is evident that the worm flourishes better in the Tamar than in the Tees. It only remains to mention the figures given by Nicol (1935) for another type of habitat, namely small salting pools. Averages of five counts of one square foot of ground for each of five pools give values ranging from 32 to 645 per m.^{2} In four other pools the estimates do not exceed the highest of the above counts. The typical densities of the more suitable intertidal habitats are therefore not reached. But in one pool on one occasion, presumably immediately after a spat-fall, 8890 young were counted in one square foot of mud, representing the extraordinary density of 95,700 per m.^{2}

The fact that it attains its maximum density above mid-tide level shows that *Nereis diversicolor* suffers no disadvantage in habitats which are exposed to the air for longer periods than they are submerged. That exposure is not essential to the species, or conveys some possible advantage, is shown by its general occurrence in muds of brackish ditches and lagoons which are

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Fig. 8. *Nereis diversicolor*: distribution diagrams for successive traverses, showing population density (numbers per m.^{2}) in relation (A) to position on the shore, and (B) to tidal level. The base-line of the top row (A) is mean low-water mark of spring tides, from which the distances of the stations and the upper boundary of the mud-flat are measured in metres. The bottom row (B) shows the same population counts plotted against tidal level, each diagram corresponding to the one above it. White dots or circles indicate positions of stations. A horizontal line across the top of a diagram marks the upper boundary of the mud-flat. The series, passing from left to right, represents the order of the traverses in an up-river direction. *St.J.* St John's Lake (Fig. 1, Tables I–III); *Th.* Thanckes Lake (Fig. 2, Table IV); *S.* Salt Mill; *Er.* Ernesettle (Fig. 3, Table V); *Eg.* Egypt; *Sr.* Salter Mill (Fig. 4, Table VI); *Cl.* Clifton; *S.H.* South Hooe (Fig. 5, Table VII); *N.H.* North Hooe (Fig. 6, Table VIII). Inset: *Ampharete grubei*: distribution diagram for St John's Lake on main traverse in summer (Table I): numbers per m.^{2} in relation to tidal level.

permanently covered. It can be said that the worm is completely adapted to tolerate the necessity of remaining passively inside its burrow for long periods. With regard to its ability to withstand lowering of salinity, Ellis (1933) has shown that it is also well adapted in this respect, but seems to require a certain minimum of calcium salts in the water.

Nephthys hombergi Lamarck.

This is another widely spread burrowing polychaete, occurring in company with the above, but, as the data presented show (Fig. 9), with a decidedly different range. Occurring on the seashore, both intertidally and below low water, it penetrates some distance up estuaries in sands and muds. In the Tamar it is generally plentiful up to the flats at Saltash, from which point its numbers steadily decrease until it disappears altogether at about Weirquay. It occurred so regularly in samples in numbers ranging between 100 and 300 per m.^{2} (once over 500 per m.^{2}) that its normal density on average suitable ground appears to fall in this range. But at its zone of maximum abundance, encountered at Thanckes Lake (Table IV and Fig. 9), the greatest density obtained is far short of that reached higher up the river by *Nereis diversicolor*. Another contrast with the latter species is seen in its distribution within the tidal zone. Fig. 9 shows that this worm is regularly concentrated below the mid-tide line. In the estuary it is evidently better adapted than other animals associated with it to living in soft mud which is liable to constant disturbance by river currents.* In St John's Lake it was entirely absent from the upper stations of the main traverse, and its upper limit suspiciously abrupt: possibly it tends to avoid ground where there is a growth of *Zostera*, or where the surface is coated with a mat of filamentous green algae. The relative proportions of *Nephthys* and *Nereis* show a progressive change up-river, and might well prove useful as a biological indicator of the general conditions at different levels of an estuary.

The picture that may be drawn from the Tamar data of the distribution and abundance of these two widely distributed polychaetes, and of the contrasts which emerge between them, evidently represents a typical state of affairs. The penetration of the *Nephthys* into the lower reaches of estuaries is evidently general. In a locality such as Salcombe Estuary, in which no main river flows, and in which high salinities prevail well up into its narrow parts, this species may be expected to predominate. This was in fact found by Allen & Todd (1900) who surveyed the fauna up to Garston Point, at which level the zone of predominance of *Nereis diversicolor* had still not been reached: the *Nephthys* was found to be about equally distributed from the mouth of the estuary to this point, and appeared to be one of, if not quite, the commonest polychaetes over the whole area investigated. In the Exe the same investigators (1902) found the *Nephthys* present generally in all types of ground, except the very

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* The suspected reason is that it is comparatively active for a burrowing polychaete, and, unlike *Nereis*, does not occupy a permanent burrow.

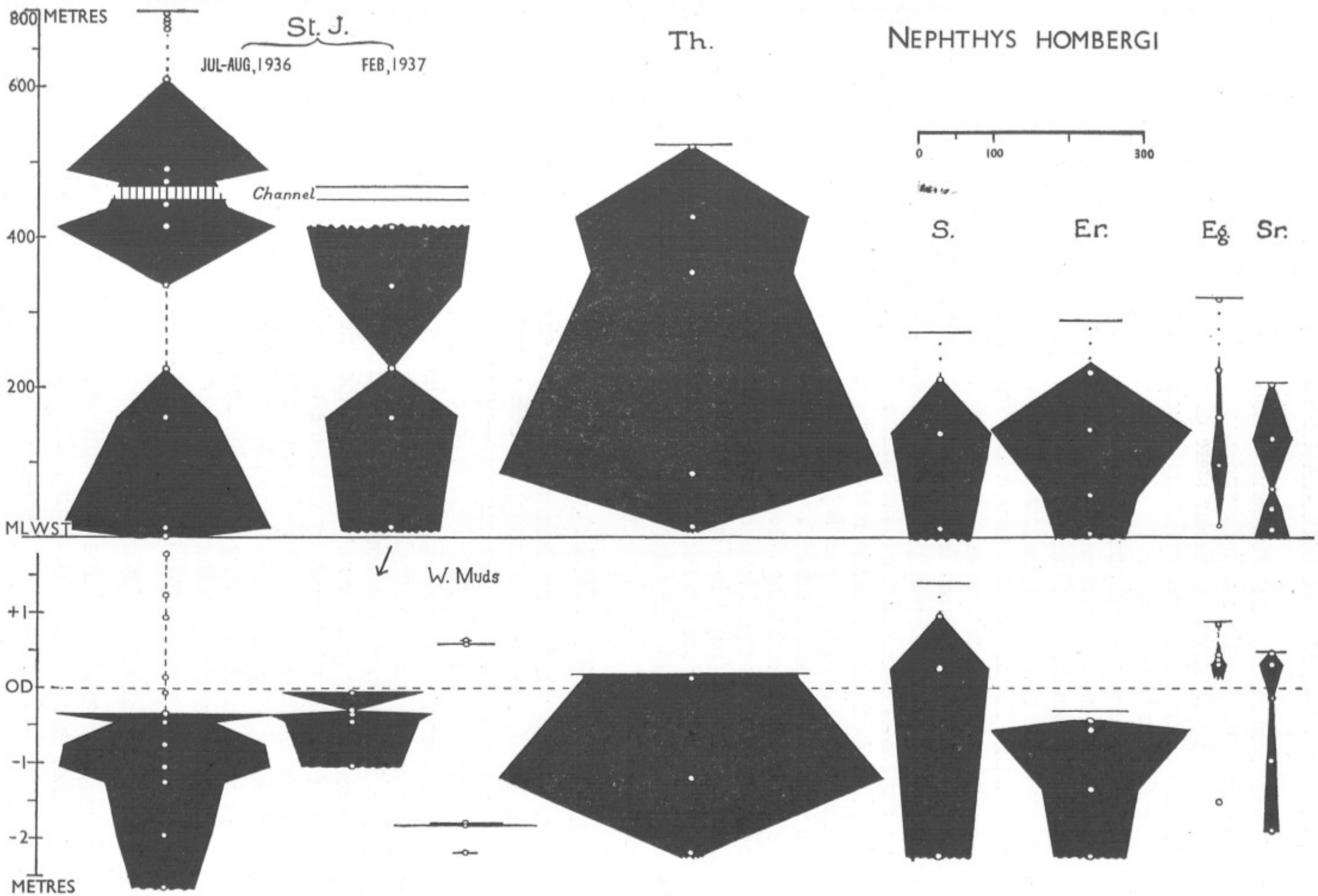

Fig. 9. *Nephthys hombergi*: distribution diagrams. Explanation as in Fig. 8.

muddiest, from the mouth to Powderham, the *Nereis* being absent in the lower part of the estuary and becoming abundant towards Topsham. In the Mersey, Bassindale (1938) shows a similar state of affairs: the *Nephthys* does not penetrate the first narrows, while the *Nereis* is a dominant species in the "Inner Estuary" to Runcorn.

The Tees Survey Report, besides defining the complete range of the two species in that estuary, presents some quantitative data, to which reference has already been made. When the ranges, optimum zones, and relative densities of the two species, indicated by this data, are compared with those found in the Tamar, the agreement is striking. In both rivers *Nephthys hombergi* attains its maximum a little way from the seaward end of the estuary, as though it found its optimum in water of appreciably reduced salinity rather than in a purely marine environment. As it then declines up-river, the *Nereis* increases to a dense maximum in the middle reaches of the estuary. In both rivers, in the respective optimum zones of the species, the population density of the *Nereis* is greatly in excess of the other.

As regards its relation to tidal level, Thamdrup (1935) and Moore (1937*b*) have recorded it as occurring chiefly about low water or below, and Wohlenberg (1937) found it to fail towards high-water levels. In the Severn Estuary, however, Purchon (1937) has recently recorded it as plentiful in the zone between high-water springs and neaps at Portishead. It is variously recorded from dredgings below the tidal zone. No population counts have hitherto been published.

Scoloplos armiger (O. F. Müller).

This species, which is sometimes plentiful at the lower end of estuaries, e.g. the Tees (Alexander *et al.*, 1935), but does not penetrate any great distance up-river, occurred in moderate numbers—up to 152 per m.^{2}—in some of the samples from St John's Lake. Here it appears to be restricted to the upper tidal levels in the *Zostera* zone, though polychaetes as a whole were scarce in this region. Thamdrup (1935) found it common on his main traverse at Skalling, Denmark, with an optimum well in the upper part of the tidal zone (maximum density 460 per m.^{2}). In other localities it has been recorded at all tidal levels, as was found by us at the seaward end of Poole Harbour; with its optimum at varying positions, sometimes near low water (Stephen, 1929; Moore, 1937*b*). It also occurs below the level of tidal influence, in shallow water at least. It may be significant that St John's Lake is close to the limit of estuarine penetration, towards which limit a narrowing of the worm's vertical zone upwards may be expected.

Heterocirrus zetlandicus (MacIntosh) (?).

A small cirratulid which has been attributed to this species (e.g. Percival, 1929), though doubt may be expressed as to its true identity, occurred in several samples from the lower traverses. Owing to its small size and delicacy the species was imperfectly estimated. Only the larger individuals would have been retained by the sieve. It appears to occur in dense patches on suitable ground, and to reach a maximum in the region of low water. Neal Point appears to mark its upward limit of penetration.

Arenicola marina L.

The presence of the common lug worm is readily detected from its familiar castings, and the general scarcity of the worm in the intertidal zones of the Tamar Estuary can be confirmed by inspection of the ground. Patches of it have been noted here and there from West Muds to Thorn Point, and the lower end of the Tavy branch. The scarcity of this species may be due to the fact that it requires a considerable admixture of sand in its substratum. In the River Yealm, however, it colonizes a bank of extremely soft mud near Steer Point.

Ampharete grubei Malmgren.

This little-known tubicolous polychaete proved quite abundant on St John's Lake, in numbers up to 4000 per m.^{2} In the traverse stations (Table I) it occurred regularly from about mid-tide downwards, with a sharply defined maximum between this level and low-water neaps (Fig. 8, inset). On West Muds it occurred at all three lower stations, but not at the two higher (Table III). It was present in smaller numbers on Thanckes Lake, but nowhere higher up the river. Though a marine species, it is unrecorded from the sea around Plymouth. But it proved to be abundant intertidally in the mud at the seaward end of Poole Harbour, Dorset. In none of the published faunas of British estuaries (quoted under other species) is this worm recorded, but possibly sometimes it is overlooked among young stages of the allied *Mellina palmata*, or escapes capture owing to its somewhat small size. Wohlenberg (1937) records the species occurring intertidally at Sylt, and restricted to near low water.

The fact that it was completely absent in the winter (Table II), and that samples in the summer were composed of specimens of a uniform size which progressively increased from May to October, shows that, unlike other species dealt with here, *Ampharete* is an annual. It appears to have a limited breeding season in the autumn.

Melinna palmata Grube

This ampharetid, similar in habit and general appearance to the last, but attaining larger sizes, occurred in some stations in the lower part of the estuary. Up to Thanckes Lake it was always found in company with *Ampharete*, being most abundant at low water at the edge of West Muds, where 189 per m.^{2} is the highest recorded density. But it was also present on the flats above Saltash, while Percival (1929) records it from the lower end of the Lynher up to Wivelscombe Lake: it evidently penetrates higher up the estuary than the other species. Unlike the latter, it is plentiful in Plymouth Sound (*Plymouth Marine Fauna*). Allen & Todd (1900) record it, under the name of *M. adriatica*, as extremely abundant in the very finest mud in the Salcombe Estuary; but by contrast very scarce in the Exe (1902). No figures for population density have hitherto been published. The allied *Mellina cristata* was not encountered.

Lanice conchilega (Pallas)

In the lower 10 km. of the estuary this familiar terebellid occurs here and there on the fringes of the mud banks where the substratum near low water is noticeably of a gravelly consistency. Among the stations worked it occurred in two only, both at extreme low water, and where the ground was atypical—containing an excessive content of shelly or stony matter. The normal types of soft mud appear entirely unsuited to it.

CRUSTACEA

Cyathura carinata (Kröyer).

First recorded from the Plymouth district by Crawford (1936, 1937), this peculiar isopod proves to be a dominant species of the mud-flats in the middle reaches of the estuary. Like the amphipod *Corophium volutator* it inhabits burrows in the mud, an exceptional mode of life for an isopod. It ranges in the Tamar from Saltash at least to the region of Pentillie Quay. Percival (1929), recording it as *Anthura gracilis*,* found it on the mud-flats above St German's Bridge, while Crawford gives additional localities in Sconner Creek and the upper end of the Tavy estuary.

Fig. 10 shows the regular occurrence of the species in the traverses from Salt Mill to South Hooe, where the dwindling numbers perhaps indicate that the upper limit is being approached. All traverses are consistent in showing a marked concentration above mid-tide level. The maximum densities from Salt Mill to Clifton Flat were respectively 378, 282, 304, and 288 per m.^{2}—very consistent values which may with some confidence be taken to represent the order of maximum density reached in the Tamar in the optimum part of its range. The species was also found in the mud of Poole Harbour, where two stations yielded 200 and 34 per m.^{2} respectively.

Sphaeroma serratum (Fab.).

The species of *Sphaeroma* only barely qualify for inclusion in the mud fauna, as the main habitat of these partly cryptic and partly free-swimming isopods comprises the cover provided by clumps of weed, stones, and various casual extraneous objects lying on the surface of the mud. It is proposed to

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* Crawford (*loc. cit.*) pointed out that this identification was obviously an error: this opinion has since been confirmed from examination of Percival's actual specimens.

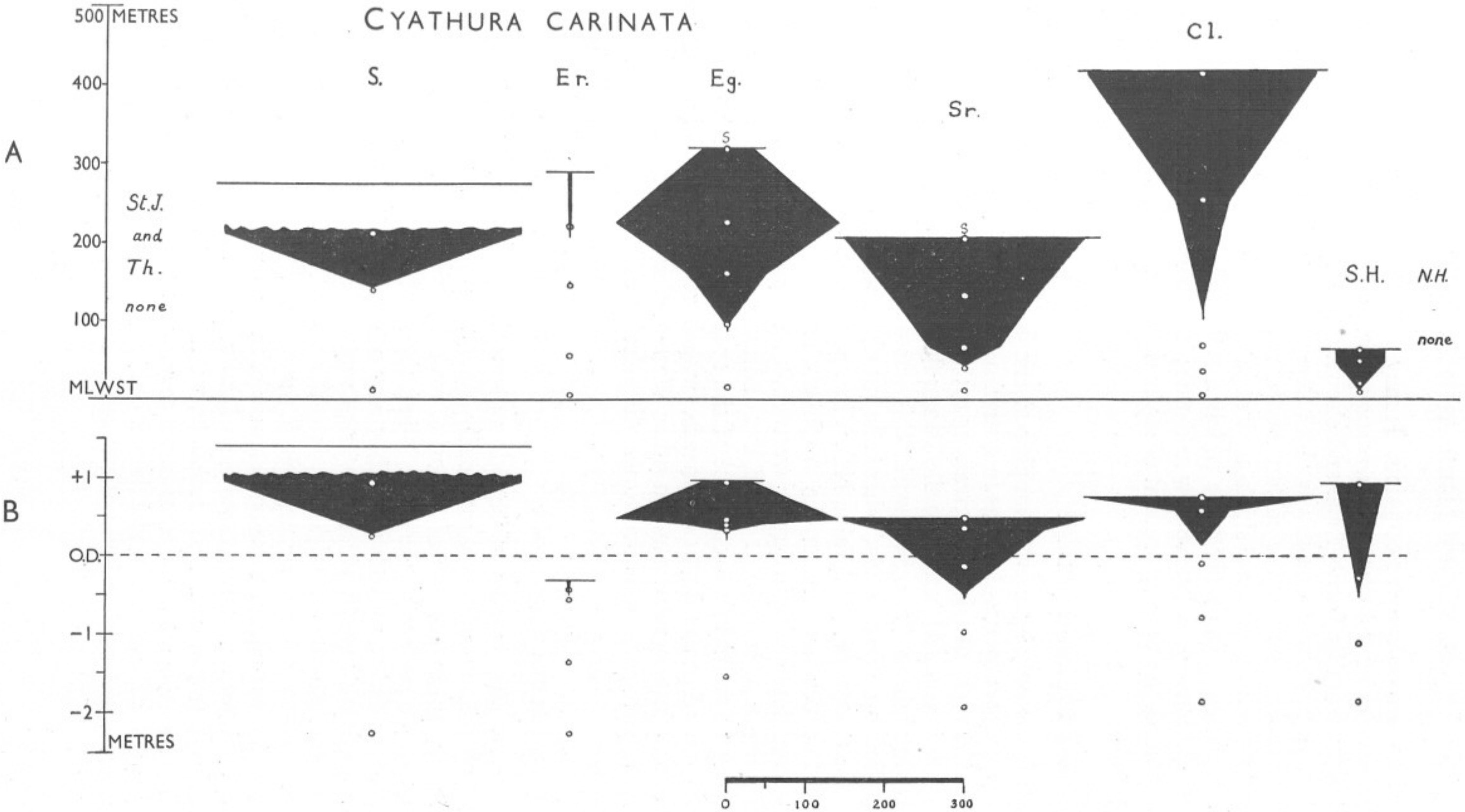

Fig. 10. *Cyathura carinata*: distribution diagrams. Explanation as in Fig. 8.

deal with them on another occasion. It may be noted, however, that the most marine species of the genus, *S. serratum*, figures in several samples, though irregularly, from St John's Lake and elsewhere. It occurred in any numbers only where there was a relatively thick deposit of old mollusc shells, among which it takes cover, at the surface of the mud—in two stations there were about 300 per m.^{2} As these shells are a regular component of the substratum, this *Sphaeroma* is probably quite widely distributed on the flats in the lower part of the estuary, at least below mid-tide; but its numbers must be mainly dependent on the varying amount of cover the surface of the ground happens to provide.

Corophium volutator (Pallas).

This is the only burrowing amphipod encountered. Though often present in vast numbers over wide areas in estuaries, and found abundant in the mud in the Calstock district (Percival, 1929; Crawford, 1937), it proved unexpectedly scarce and patchy on the Tamar flats up to North Hooe. Occurring almost throughout the region worked, it was only found in high numbers in one station on West Muds, where the number of all sizes retained by the sieve was 11,000 per m.^{2} (Table III). The species was seen to occur in plenty over a considerable area in the neighbourhood of this station, but failed almost completely a little farther westwards on the site of the main traverse. A comparison of stations D 1 and D 2 indicates that a growth of *Zostera* is unfavourable to it. The occurrence of the species in abundance in soft mud of salting pools, as at Egypt Saltmarsh, in sheltered brackish ditches, and in firmer sand-impregnated mud in other West-of-England estuaries, indicates that it is particularly sensitive to the disturbance of its substratum by water currents.

Other Isopoda *and* Amphipoda

The remaining species of isopods and amphipods which are included in the sampled fauna counts are essentially dependent on the presence of growths of *Zostera*, green algae, leaf deposits, or other vegetation which may be present at the surface of the mud. When the mud is bare over a wide area, these species fail completely; but they may occur casually on bare patches in the proximity of ground which provides a more suitable habitat. The numbers obtained indicate the sort of density in which these Crustacea may be expected where the cover is not dense, and where they are accessible to avian predators. *Idotea viridis* may occur in sparse clumps of filamentous alga, or in very thin growths of *Zostera*. A few *Gammarus locusta* or *zaddachi* may be present in the very sparsest of cover. *G. zaddachi*, which replaces *locusta* in the middle estuarine zones, occurs in some abundance among leaf deposits near low water, and young stages can exist where there is only a moderate deposit of fragmented vegetation in the surface layer of the mud. *Melita palmata*, which becomes abundant on stony ground, makes use of the shelter of old mollusc shells rather than of vegetation.

Carcinus maenas (Penn.).

It is probably because of their abundance in the estuary as a whole that the juveniles of the common shore crab figure so regularly in the fauna counts. Numbers are usually found under the cover of weeds and stones, but to some extent they also scavenge over the open mud (as can be observed in tidal pools), and take partial cover in the mud itself. To some extent the *Carcinus* population recedes with the tide (this has actually been observed), but the fall of the tide finds a number of individuals sparsely, but fairly regularly, distributed over the mud flats. The presence of any sort of object that can in any way provide cover tends to favour their occurrence. The highest population densities, of between 100 and 200 per m.^{2}, were found in St John's Lake where there was a growth of *Zostera* or a surface deposit of shells.

MOLLUSCA

Hydrobia ulvae Peringia Pennant.

This very characteristic inhabitant of estuarine muds is more readily studied than most species dealt with here, owing to its habit of exposing itself freely on the surface after the tide has receded. The data secured from the sample counts are but a fraction of the information now available on the occurrence and habits of the species in the south-west counties. The references to it in the literature are also considerable. Only some of the more relevant facts can be dealt with here.

In the Plymouth district *Hydrobia ulvae* occurs in at least one locality on the shore of Plymouth Sound, but its occurrence in marine habitats is probably dependent on local freshwater influence. The estuaries, however, provide habitats in which it occurs in typical profusion. On the mud-flats of St John's Lake it is densely spread over many acres from West Muds to the very head of the "Lake" near St John. The population densities given in Tables I–III, and shown diagrammatically in relation to position on the shore and to tidal level in Fig. 11, are noteworthy not only for their size but also for their regularity. A maximum concentration about the mid-tide level is indicated, with a rapid decline from the maximum during the first half-metre below O.D. The decline upwards towards mean high water is more gradual, and the bulk of the population comes to be concentrated between the levels of O.D. and + 1 m. The density appears to be increased by the presence of growths of *Zostera*, etc., which provide an additional effective area of substratum, but the molluscs are conspicuously densely spread over wide areas of bare mud completely devoid of macroscopic vegetation. Inspection of the ground when the tide has receded long enough to allow the mud to settle and the *Hydrobia* to emerge to the surface shows that, at any given

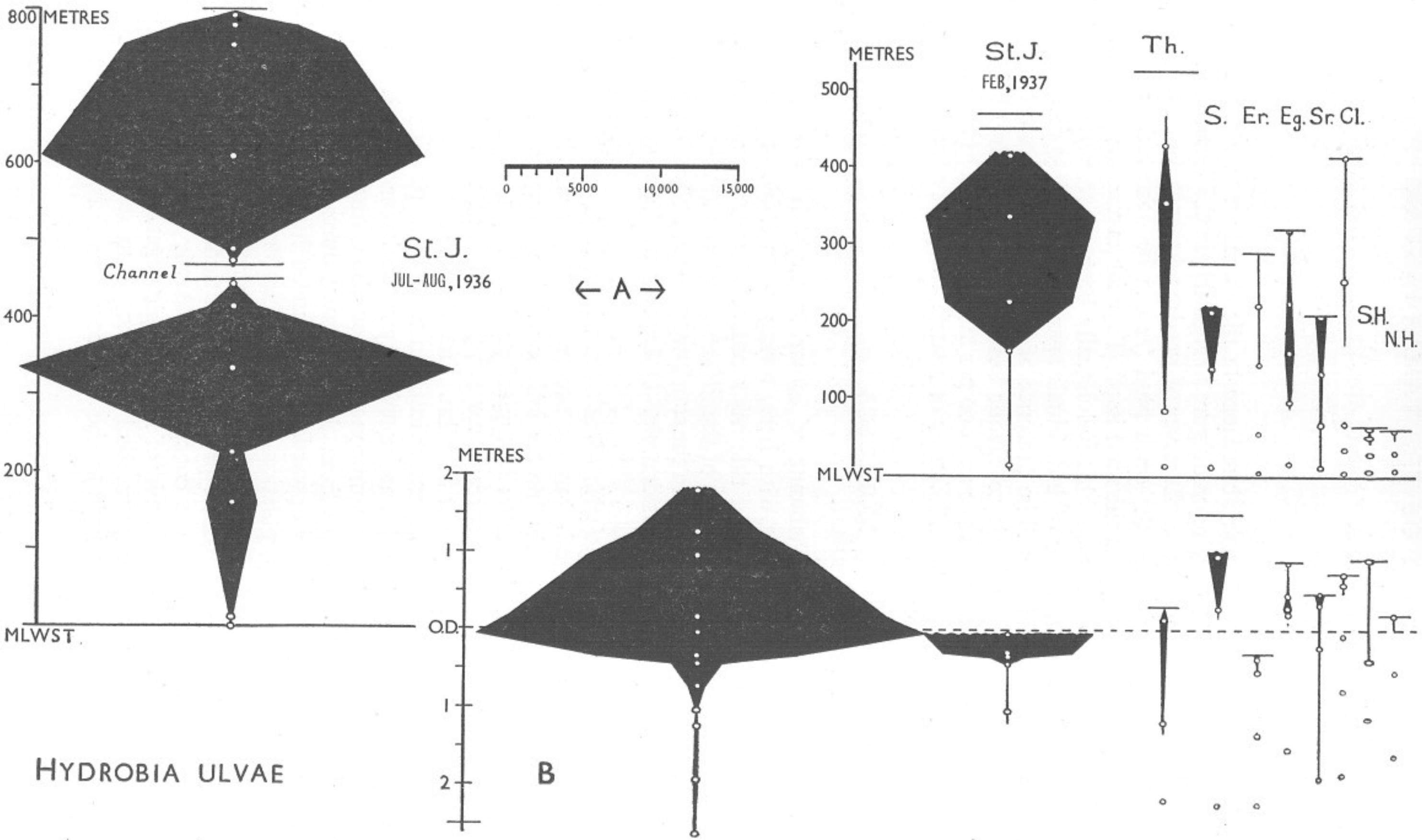

Fig. 11. *Hydrobia ulvae*: distribution diagrams. Explanation as in Fig. 8. Note that, owing to space requirements, the left-hand pair of diagrams are not in alignment.

level, the animals are remarkably uniformly distributed and almost independent of the nature of the surface of the ground. This may range from fragmented shillet*, provided silt is mixed freely with it, to bare soft mud.

At St John's Lake *Hydrobia* reaches its maximum abundance, and nowhere higher up the river were anything approaching the higher population densities encountered. The diagrams in Fig. 11, however, exaggerate the extent to which the species declines up-river, as locally, in sheltered bays particularly, moderately dense populations occur. An example is Salt Mill Creek, where most of the mud-flat is occupied by a much denser concentration than the 1000 per $m.^2$ obtained at the top station on the river side of the salting. Relatively high numbers also occur on the flat south of Cargreen. North of Weirquay, however, inspection of the ground confirms the indication given by the traverse figures that the species is nearing the upper limit of its range on the mud-flats.

The distributions on the traverses from Thanckes Lake upwards all agree in showing a concentration above the mid-tide level, even though the population densities are small. The species was evidently scarcer above Cargreen than near Saltash, and scarcer still in the region of Clifton and South Hooe. At North Hooe, the highest limit previously recorded, only a bare indication of its presence was obtained. Sheviock Wood is given by Percival (1929) as its upper limit in the Lynher, and on the Tavy branch it reaches Gnatham.

The upper limit, however, has been observed to fluctuate from one year to another. In 1938, after a long period of deficient rainfall early in the year, with resulting decrease of freshwater influence in the estuaries, definite signs of up-river extension of range were noted in three localities:

(i) River Tamar: on the mud-flats bordering Egypt Saltmarsh, much more numerous in 1938 than 1937 (and marked decline in 1939). (ii) River Tavy: in June 1937 none above Bere Ferrers and still very sparse 1 km. distant below, whereas in summer 1938 it colonized the flats at least up to Gnatham. (iii) River Yealm: none seen in Cofflete Creek above Steer Point in 1937, but quite numerous up the creek in 1938.

The account of the distribution of *Hydrobia ulvae* would not be complete without reference to its partiality for a habitat which differs in many respects from the intertidal mud-flats. The extent to which it dominates in salt-marshes is apparently not generally realized. In salting "meadows" (typically a closed association of grasses, sea-plantain, etc.) it may be collected in large numbers from the damp mud around the bases of the grasses, etc., and is apt to congregate thickly in the damper, but more open, depressions. During 1937 the species was observed in salting "meadow" habitats in West Sussex, Norfolk, Lincoln, and Cornwall (River Camel), as well as in the Tamar Estuary, as for example at Egypt Saltmarsh (see also Rothschild, 1938). The animals

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* A local term applied to the clay-slate of which the geological strata mainly consist.

here are subject to long periods of exposure to the air, as salting meadows are typically only covered by spring tides. Conversely, their abundance and flourishing condition in many salting pools shows that they are capable of tolerating permanent immersion. In the course of her studies on its trematode parasites, Rothschild (1936, 1938, and 1939) has brought to light several interesting features of the biology of this mollusc. Of these it may be noted here that in salting pools and damp hollows in saltings much greater average sizes are attained than on the mud-flats: in both situations infection by trematode parasites tends to increase growth above the normal for the habitat. The growth conditions amongst the grass of saltings also appear to be superior to those on the mud-flats. Analysed samples from St John's Lake and Egypt Saltmarsh show this contrast well; but when specimens from the two localities were reared in the laboratory under similar favourable conditions, the growth-rates were found to be identical, proving that the environment is wholly responsible for the difference (A. and M. Rothschild, 1939).

The tendency for *Hydrobia ulvae* to concentrate in the upper part of the tidal zone is apparently a general phenomenon. It is shown, for instance, in a traverse of eight stations worked by Stephen (1930) across the shore of Loch Gilp. Lambert (1930) remarks on the long periods of exposure to which the species is subjected on the mud of the Thames Estuary, and goes so far as to express the opinion that it requires exposure to the air for at least 20 out of the 24 hours. The precise data given by Thamdrup (1935) for a traverse at Skalling, Denmark, over a period of years, show a regular and usually very high maximum about mean high water, between +0·5 and 0·6 m., and an abrupt diminution between that level and half-tide. Wohlenberg (1937), in his survey of a bay in the north of Sylt, records *H. ulvae* generally distributed in the upper third of the tidal zone. Similar conditions to those observed at St John's Lake—dense concentration above half-tide and disappearance towards low water—have been observed by inspection of the ground in other English localities, among which the upper part of the Salcombe Estuary and the mud-flats near Blakeney (Norfolk) deserve particular mention.

The higher population densities found on St John's Lake seem to be fairly typical for the optimum intertidal environment. A summary of other figures for comparison is listed below (Table IX). Especially useful data are given by Nicol (1935) and Thamdrup (1935). The very high maximum densities found by the latter are confined to a narrow zone in the region of high water. No attempt was made at St John's Lake to seek out the densest patches at the most favourable season, and it is not improbable that densities approaching the maximum recorded may occur. Nicol's figures are the only ones available for salting pools; but the concentrations which have been observed in favourable pools suggest that counts would have compared closely with those from optimum zones on intertidal muds.

TABLE IX. POPULATION DENSITIES OF *HYDROBIA ULVAE*

Author	Locality	Habitat	Particulars of estimate	Mesh of sieve mm.	Population density per sq. metre
Thamdrup, 1935	Skalling, Denmark	Wide flat of muddy sand	Maximum in thickest patches discovered	0·9	*ca.* 60,000
,,	,,	,, ,,	Maximum on traverse, March 1934	,,	46,300
,,	,,	,, ,,	Do. July 1932	,,	37,000
,,	,,	,, ,,	Do. July 1933	,,	24,500
,,	,,	,, ,,	Do. Oct. 1933	,,	18,200
,,	,,	,, ,,	Do. July 1931	,,	17,000
,,	,,	,, ,,	Do. Aug. 1934	,,	15,300
Stephen, 1930	Loch Gilp, West Scotland	Muddy sand	Maximum on traverse	2·0	3,060
,,	Tynninghame, Firth of Forth	Soft estuarine mud	One sample of $\frac{1}{4}$ m.^{2}	,,	*ca.* 1,400
Nicol, 1935*	Aberlady, Firth of Forth	Bare estuarine mud	—	? 1·0 or less	32,500
,,	,, ,,	Tidal sandy pools	Selected dense patches, maximum	,,	27,650
,,	,, ,,	,,	Normal high counts	,,	6,300–3,900
,,	,, ,,	Clean estuarine sand	—	,,	8,930
,,	,, ,,	Salting pools	Highest figure obtained	,,	11,620
Spooner & Moore (unpublished)	Poole Harbour, Dorset	Soft mud	One station at + 1·09 m., probably above optimum zone for species	0·8	3,940
Serventy, 1934	Scolt Island, Norfolk	Brackish muds	Estimate of highest density	—	*ca.* 16,000
,,	,, ,,	,,	Estimated normal high density	—	*ca.* 8,000

* Nicol's figures are given in numbers per square foot and have been converted.

Littorea littorea (L.).

The Common Winkle frequents various intertidal habitats in estuaries as well as on the seashore, among which mud-flats are included. Though inclined to cluster round clumps of algae, or other objects which provide cover, it is often to be seen well scattered over open bare mud. At best, however, its distribution is patchy, and sampling on a wider scale would be necessary for population counts which could be related to tidal level irrespective of other factors.

On the grounds sampled it was found in abundance only on St John's Lake, ranging almost over the whole tidal zone from high-water neaps even down to low-water springs on suitable ground. The range of population densities of 0–480 per m.^{2} gives an indication of its patchiness, the two highest figures being obtained from ground which contained the highest admixture of old mollusc shells. At the station with 480 per m.^{2} no fewer than 346 belonged to the larger sizes (second and higher year groups). The biology of this species on St John's Lake, where until the recent restrictions it was regularly collected by fishermen, has been dealt with independently (Moore, 1937*a*). Population counts have also been made at known levels on the alga-covered shore near Torpoint opposite West Muds (Moore, 1939). In this habitat the species is more evenly distributed, from high-water neaps to low water, and shows the same maximum concentration between mid-tide and low-water neaps as is typically found on the sea coast. If allowance is made for patchiness, the data for the St John's Lake flats (Tables I–III) indicate a similar distribution.

Higher up the estuary *L. littorea* is mainly restricted to the local patches of stony ground, but on the flats along Ernesettle embankment it was observed to be generally, though sparsely, distributed. The traverse figures here indicate a density of the order of 1 or 2 per m.^{2} Its upper limit in the estuary is not far above this point: while still numerous near high water at Neal and Lime Points on stony ground, it occurs regularly, though sparsely, under the cover of weeds on Thorn Point Causeway, but has never been found in the Weirquay district or above. Many empty shells are washed up along Egypt saltmarsh, but very few higher up. Antony Creek is given by Percival (1929) as its upper limit in the Lynher. A comparable degree of penetration up-river is evident in the Exe (Allen & Todd, 1902), Tees (Alexander *et al.* 1935), Mersey (Bassindale, 1938), and other estuaries.

Among the numerous scattered papers which deal with the ecology of *L. littorea*, estimates of population density are sometimes included. The density on open ground appears usually to be of an order of 1/10 of that attained where fucoids, mussels, stones, or other objects provide suitable cover. Investigating the mud-flat winkle grounds of the Blackwater Estuary (Essex), Wright (1936) made four sample counts of patches amounting to $2\frac{1}{2}$–3 m.^{2} The average total numbers per m.^{2} of all sizes above 3 mm. lay between 12 and 39. Thamdrup (1935) records a density of 330 per m.^{2} on a mussel bed below mid-tide, but much lower numbers, when the species occurred at all, on barer ground. In a series of counts along the sea-wall of the River Tees (Alexander *et al.* 1935), in which the average of six counts of one $\frac{1}{4}$ m.^{2} at each station was taken, the highest figure derived was just on 300 per m.^{2} Fraser's data (1932, Table VIII) for a locality in the Mersey Estuary indicate the usual kind of patchiness: about half the samples of $\frac{1}{16}$ m.^{2} patches contained none, others several *L. littorea*, up to 32 (=512 per m.^{2}).

Littorina saxatilis (Olivi) [=rudis (Maton)].

This species occurred in company with the above on St John's Lake, in numbers up to 1100 per m.^{2} Here it appears almost confined to levels between high water and mid-tide, its usual optimum zone on the shore (see, e.g. Moore, 1939). The low level of Ernesettle flats probably accounts for its absence on that traverse, for its upper limit in the estuary appears almost identical with that of *L. littorea*. Though not recorded from Cargreen, it is fairly plentiful at Lime Point. Published data on the occurrence of *L. saxatilis* in estuaries are extraordinarily scanty: even if scarcer on the whole, it is liable to be overlooked when mixed with the young of the larger species. In spite of having an optimum high up the tidal zone, it tolerates permanent immersion. Thus it abounds in the shallow brackish waters of the Fleet, Dorset; and Howes (1939) records it swarming on *Ruppia* in a saline Essex creek.

Cardium edule L.

The Common Cockle occurs regularly in muds in the seaward half of the estuarine zone, inhabiting all levels from mean high water to the permanent river channel. Like other species already considered which occur only in the seaward half of the estuary, it showed a maximum density at St John's Lake. In this region it is a dominant member of the fauna. Though apparently more consistently plentiful between high-water neaps and mid-tide, it shows no marked optimum that can be related with any confidence to tidal level (Fig. 12). The variation among the population densities of different stations seems attributable mainly to the nature of the ground. Thus a growth of *Zostera* seems favourable, as well as a high admixture in the surface layer of the mud of dead mollusc shells; while on the other hand *Cardium* is scarcer on soft slopes which are scoured by tidal currents. No greater regularity of distribution is shown by the larger sizes (1 cm. length and over) when the obviously irregularly distributed young are deducted. The population densities found for larger sizes vary up to 93 per m.^{2} For all sizes retained by the sieve, that is from *ca.* 0·15 mm. length and over, 383 per m.^{2} was obtained at one station where there was an unusual number of young, but between 100 and 200 per m.^{2} was more usual for typical "good" grounds. A comparatively dense concentration of very large specimens on the edge of West Muds (station D 4) is noteworthy.

In succeeding traverses up-river very small numbers of cockles were obtained. From Thanckes Lake to Salter Mill sizes above 1 cm. length appear either absent or rarely present above one individual per m.^{2} Smaller sizes are somewhat more frequent: 40 per m.^{2} occurring at low water at Salt Mill, and 36 per m.^{2} in one station at Salter Mill. The species appeared entirely absent on Clifton Flats and above. That Weirquay marks the upper limits of its range in the Tamar is confirmed by other observations, and in the Lynher it occurs at least up to Sheviock Wood. These limits coincide with those of *Nephthys hombergi*. Compared with other dominant species, *Cardium edule* penetrates somewhat farther than *Littorina littorea*, but not so far as *Hydrobia ulvae*.

It is of interest to enquire whether the population density of the cockle on St John's Lake approaches the maximum attained by the species. In none of the stations worked on various types of ground in different localities on the Scottish coast by Stephen (1929, 1930, 1932) was a density found which, making full allowance for his use of a 2 mm. sieve, exceeds the higher values for St John's Lake. Thamdrup (1935), however, found much higher densities on his traverses at Skalling, where *Cardium edule* proved the most abundant of all animals by weight, and was only exceeded by *Hydrobia ulvae* in numbers. One traverse, worked by him on seven occasions between July 1931 and November 1934, gave population curves which consistently show a scarcity of cockles at the highest levels (the zone of maximum abundance of *Hydrobia*), but regular high numbers over the rest of the traverse with a maximum nearly always just above mid-tide level. The maximum densities found, which do not include the 0-year-group, vary from 4675 to 1360 per m.^{2} As Stephen (1931) found in Scotland, the average size tended to increase towards low water. On the second traverse cockles were scarcer, but even here a density of 1500 per m.^{2} was obtained. Evidently, then, the conditions on St John's Lake fall well short of the optimum for the species.

Scrobicularia plana (da Costa).

Abundant generally in estuaries in the south and east of England (but scarcer and more local in the north), in varying types of ground, this lamellibranch is particularly characteristic of intertidal brackish muds. Unrecorded from the open shore in South Devon, it occupies a wide range in estuarine zones. In the Tamar it occurs from St John's Lake up the main river to North Hooe, up the Lynher branch to above St Germans (Percival, 1929), and up the Tavy to Maristow. In the Salcombe Estuary the species begins to appear sparsely at Salcombe, becoming more common near Snape's Point (Allen & Todd, 1900), and is plentiful higher up. In the Exe, Allen & Todd (1902) found it in abundance, mainly in stiff mud, with a lower limit very near the mouth. In estuaries of the Plym, Yealm, Erme, Avon, and Camel, it has been noted as extending well above the limits of *Cardium edule*. Unlike *Cardium*, it appears more or less intolerant of permanent immersion.

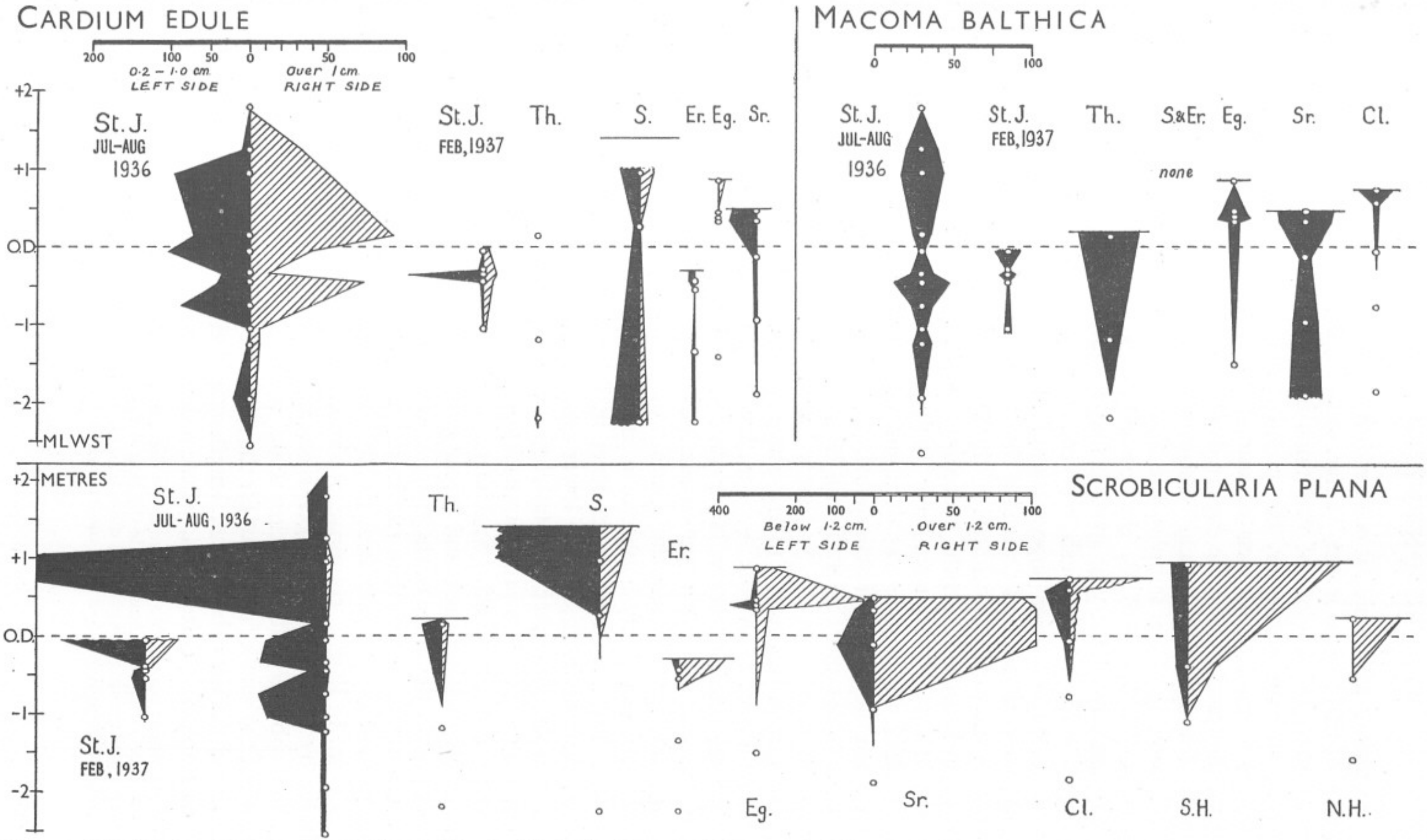

Fig. 12. Distribution diagrams for *Cardium edule*, *Scrobicularia plana*, and *Macoma balthica*, population density shown in relation to tidal level only (row B in previous figures). With *Cardium edule* and *Scrobicularia plana* the numbers of the smaller sizes are plotted on the left-hand side of each diagram (black) and the larger sizes on the right (cross-hatched). With *Macoma balthica* the usual total numbers are plotted. Remaining explanation as in Fig. 8.

The regularity with which it occurred in the mud samples emphasizes the prevalence of this species in the Tamar. Since it seems improbable that it is greatly affected by the sort of variations in the substratum that were encountered; and since, further, the population seems to contain sufficient year-groups to mask the effects of annual fluctuations in recruitment, the data from the traverses may be expected to show up more clearly than usual the general features of the species' distribution.

In the counting of the samples, the *Scrobicularia* were separated into five size groups (Tables I–VIII), the lowest group of below 0·5 cm. length consisting entirely of first-year spat. It may be noted that these smallest sizes have fragile shells which crush very easily if sieving operations are at all drastic: it would have been impossible to have obtained the whole population of young *Scrobicularia* intact without the "souping" methods employed for dealing with the mud. Specimens of the two larger size-groups (2–5 cm. in length) often burrow to depths exceeding 10 cm. Where pointed out in the tables specimens of these sizes were liable to be lost owing to the shallow depth to which the sample was dug, and due allowance must be made for this fact when the results are compared.

From the tables and Fig. 12 it will be seen that *Scrobicularia* occurred in every station worked on the St John's Lake grounds, showing that here it ranges from mean high-water to low-water springs. The mollusc, however, is consistently absent below the −1·0 m. level on all other grounds up-river. Whether total numbers, or the larger sizes alone, are considered, the species tends to be concentrated in the upper half of the tidal zone down to just below mid-tide level. Where the presence of saltings limits the extent of the mud-flat, the species may be traced in salting creeks well up into the high-water zone. The actual optimum level may vary somewhat. There is an indication that the decline at the lower range of the intertidal zonation sets in at an increasingly higher level up-river.

A remarkable feature is brought out when the distributions of the different size groups are compared. Specimens of below 1·2 cm. length (which approximately includes the 0 and 1 year groups) occur in highest numbers in the lower part of the range of the species, especially on St John's Lake, where six stations produced more than 100 per m.^{2}, and one actually over 1000 per m.^{2} On this ground these small sizes, chiefly composed of the smallest group of below 0·5 cm. in length, comprise the bulk of the *Scrobicularia* population. For here, by contrast, the larger sizes are relatively very scarce.* The populations obtained at Thanckes Lake and Salt Mill were still mainly composed of the smaller sizes, but for the first time at Salt Mill and Ernesettle the density of the sizes above 2 cm. length exceeded 10 per m.^{2} The optimum zone was reached at Salter Mill, where a dense population was encountered

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* This statement makes due allowance for the inadequate sampling of the largest sizes in several stations. Tests have been made digging deeper in the mud; the scarcity of burrows can be seen by examining the ground; old shells are considerably less plentiful than up-river; and the middle size-group (1·2–2 cm.), most of which would have been collected, is very scarce.

in which all sizes were well represented. There the larger, above 2 cm., reached 84 per m.^{2} in two stations; and an average density, for these sizes, of at least 75 per m.^{2} is indicated for the whole flat from the salting edge to the $-0{\cdot}5$ level. In this part of the river the star-shaped impressions which mark the burrows are conspicuously numerous on the surface of the mud. The mud at South Hooe appeared on inspection to be another good *Scrobicularia* ground, and here another well-balanced population was obtained in the samples. At North Hooe only some large specimens of over 3 cm. were obtained in the upper sample: this locality is at, or very near, the upper limit of the mollusc's range.

The indications, then, are that the conditions for settlement of the spat are most favourable at the lower limit of the range of the species, but that growth conditions are at an optimum much higher up the estuary. This optimum zone coincides with the very upper limit of penetration of *Cardium edule* and *Nephthys hombergi*, and approximately coincides with the optimum for *Cyathura carinata*.

It would appear that the great majority of the spat which settle on St John's Lake die off naturally at an early age. A more striking example of this phenomenon has been observed in the Fleet, Dorset. In the Langton Herring district vast numbers of spat settle in shallow water on mud-bearing growths of *Zostera hornemanniana* and *Ruppia*. Though sizes of below 0·6 mm. length can be collected in great abundance, not a single larger specimen could be found. Every year the tide marks of the Fleet are strewn with myriads of the small-sized valves, but the valves of larger sizes do not occur. The tidal zone is for the most part gravelly and unsuitable for settlement, and if it is indeed true that intertidal conditions are necessary for the survival of the spat and growth of the adult, a partial explanation is provided. If this is so, a different factor must be operating on St John's Lake: the high salinity seems by far the most probable.

The literature relating to the biology of this abundant species is surprisingly meagre. In Britain at least it is essentially an intertidal species of waters of reduced salinity, and typically fails in permanent standing water or below the tidal zone. Few estimates of population density have been made. Stephen (1930) records 136 per m.^{2} retained by a 2 mm. sieve in one mud sample from Firth of Forth; while Thamdrup (1935) throws some light on its behaviour at the very seaward end of its range (in West Denmark). On one of his traverses the species occurred very sparingly about mid-tide level in 1931 and 1932, and then somewhat more plentifully in 1933, when it was distributed from just above mid-tide level to low water (only small specimens below mid-tide). In 1934 there was a bigger spat-fall still. The complete absence of the species, even in the latter year, from the higher tidal levels, across 200 m. of flat, may be noted.* Evidently the salinities were still too

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* Wohlenberg's (1937) data from Sylt shows agreement: in 1932 the species was very scarce on the area surveyed, but in 1934–6 became common on suitable ground. No precise data, however, are given on densities or tidal levels.

high to enable the *Scrobicularia* to colonize the upper part of its normal intertidal range, as it is already just able to do in the Tamar at St John's Lake.

A density of 58 per m.^{2}, of which 24 were below 0·5 cm. length, was found in one sample of sheltered soft mud near the mouth of Poole Harbour.

Macoma balthica (L.).

In the south-west of England this species is typically greatly outnumbered by the above, and appears never to attain a dominance comparable with that in some localities in North England and Scotland. In the Tamar, though very widely distributed, it is everywhere relatively scarce. On St John's Lake it was absent from only five out of twenty-four stations, but never exceeded a density of 36 per m.^{2} The highest density recorded was 76 per m.^{2}, of smaller sizes below 1 cm. length, at Thanckes Lake. Still present at Salter Mill, where it occurred in all five stations with a maximum of 36 per m.^{2}, it reached an upper limit on the Clifton flats.

The species proved to be fairly uniformly distributed through the tidal zone (Fig. 12), and distinctly more tolerant of low-water conditions than *Scrobicularia*, especially in up-river localities.

At the time this work was carried out there was an almost complete absence of the spat of this mollusc. Specimens collected tended to fall in groups of similar size, with marked gaps between the groups. The evidence indicates that appreciable recruitment of the population occurs only in favourable years.

Conditions in the Tamar are evidently adverse for *Macoma*. The sizes attained, judging both from living material and cast-up valves, are well below those which the species is known to attain elsewhere. Also far higher densities occur where the species thrives. Thus, in the Firth of Forth, Stephen (1929, 1930, 1931) found that the denser populations reached 150–200 per m.^{2} (highest sample 288); Thamdrup (1935) found up to 1000 per m.^{2} and a maximum of no less than 6325 g. per m.^{2} by weight; while in the Mersey (Fraser, 1932; Bassindale, 1938) it is the commonest bivalve, occurring at great abundance in places, especially in thick mud, almost completely displacing *Scrobicularia*, and attaining densities as high as 5900 per m.^{2} (2·5 mm. sieve).

Abra nitida (Müller) and Abra prismatica (Montagu).

Both of these species occurred in small numbers near low water only, at the seaward end of the estuary. *A. nitida* occurs along the edge of West Muds, where it has been collected on several occasions, following the main St John's Lake Channel at least as far as B 6. *A. prismatica* appears restricted to the edges of the tributary channel (having occurred at A 6, B 4, and C) (Fig. 1), at the mouth of which it mixes with other species. It was also present at the two lowest stations at Thanckes Lake.

Both species are essentially marine, but evidently able to tolerate a lowering of salinity which might enable them to penetrate considerably farther up the estuary in the upper tidal levels. But their distribution in purely marine habitats shows them to be intolerant of intertidal conditions. It may be noted that much of the zone they inhabit—soft unstable mud on the channel slopes—supports a very sparse fauna.

DISCUSSION

By way of summarizing the main features of the distribution of the principal species encountered Table X has been drawn up. The species are conveniently separated into three groups. Group A includes those which thrive in marine habitats where the salinity of the water is more or less full strength, but have a greater or lesser toleration of water of reduced salinity, and penetrate to varying extents into estuaries. Group B includes species which, though occurring freely in marine habitats, have a decided preference for water of reduced salinity, and are on the whole better known as estuarine than marine animals. In the Tamar only two species (possibly three, if *Heterocirrus* sp., omitted from the table owing to imperfect information, can be included) fall in this group, and for one of these, *Nephthys hombergi*, there is evidence that its optimum zone is not in the sea, but where the salinity is appreciably reduced (p. 306). Group C includes species which are predominantly estuarine, and which, if they occur in more or less purely marine habitats, do so irregularly in much reduced numbers. Of the five species of this group encountered in the Tamar, *Hydrobia ulvae* is most nearly connected with the previous group.

The first two columns in Table X refer to the extent and degree of penetration into the Tamar Estuary. It is not surprising to find all the species of Group A occurring in greatest numbers at the lower end of the estuary—St John's Lake—and either disappearing or steadily decreasing above this point. The majority, if not all, may be expected to find their optimum environment in the sea or at least in more truly marine conditions than those which hold for St John's Lake. In Group B, *Nephthys hombergi* appears to find its optimum a little way inside the estuary; and in Group C optimum conditions are of necessity found somewhere in the estuarine zone—one (*Hydrobia*) low down, at St John's Lake, one (*Corophium*) apparently diffused over a very wide stretch of river in which dense patches occur as far apart as West Muds and Calstock, and three others with a definite optimum well up the river. As regards extent of penetration, Group A species disappear somewhere in the lower half of the estuary, with the exception of the juveniles of *Carcinus maenas*; Group B reach to about half the length of the estuarine zone (15 km.); and Group C pass beyond 15 km. into the upper half.

It is not proposed to discuss further the subject of up-river penetration, as this is best deferred until other sections of the fauna can be surveyed. It must be emphasized that the marked tendency for most species to concentrate

TABLE X. SUMMARY OF DATA RELATING TO SPECIES WHICH INHABIT MUD-FLATS OF THE RIVER TAMAR

Species	Approximate position of maximum abundance in Tamar Estuary	Relative penetration up Tamar Estuary (in km. from mouth)*	Usual vertical distribution, as far as known + = present o = absent		Intertidal distribution found in River Tamar
			Occurrence in intertidal zone	Occurrence where permanently immersed, *a* = known to occur well beyond tidal zone	
			A. ESSENTIALLY MARINE SPECIES		
Abra prismatica	St John's Lake	2	Not typically intertidal	+ *a*	At low water only
Abra nitida	St John's Lake	4	Not typically intertidal	+ *a*	At low water only
Ampharete grubei	St John's Lake	4	Lower part of tidal zone†	+ *a*†	Lower half of tidal zone (Fig. 8)
Mellina palmata	St John's Lake	8	Lower part of tidal zone‡	+ *a*	Lower half of tidal zone
Phyllodoce maculata	St John's Lake	6	+	+	? Scattered
Cereus pedunculatus	St John's Lake	6	Greater part of tidal zone‡	+	? Scattered
Lanice conchilega	St John's Lake	*ca.* 9	At and near low water	Shallow water	Around low water only
Scoloplos armiger	St John's Lake	2–6	Throughout tidal zone (p. 306)	Shallow water only (?)	Where occurs, only known from above mid-tide
Carcinus maenas juv.	St John's Lake	*ca.* 28	Throughout tidal zone	Mainly shallow water	Scattered
Littorina littorea	St John's Lake	11	Through tidal zone, maximum below mid-tide	Usually o (see Colman, 1933)	Through tidal zone, with indications of maximum below mid-tide
Littorina saxatilis	St John's Lake	10	Maximum mid-tide and above	Not in sea, but in shallow brackish waters and tidal pools	Concentrated above mid-tide line
Cardium edule	St John's Lake	13·5	Throughout tidal zone	Mainly shallow water	Scattered (Fig. 12)
			B. MARINE AND ESTUARINE SPECIES		
Nephthys hombergi	Thanckes Lake	13·5	Usually in lower part of tidal zone	+	Mainly in lower half of tidal zone (Fig. 9)
Macoma balthica	No marked maximum	15	Relatively uniform through tidal zone, sometimes maxima about mid-tide	General below tide-marks, but chiefly shallow water	Scattered through tidal zone (Fig. 12)
			C. MORE OR LESS STRICTLY ESTUARINE SPECIES		
Hydrobia ulvae	St John's Lake	18·5	Typically concentrated in upper half of tidal zone (pp. 311–14)	In shallow salting pools, and sometimes in small numbers below tidal zone	Marked concentration mid-tide upwards (Fig. 11)
Corophium volutator	?	*ca.* 27	Usually concentrated near high water	In shallow pools and sheltered ditches, etc.	(As far as known, maximum in upper half of tidal zone)
Cyathura carinata	Salter Mill	15+?	+‡	+‡	Concentrated, and almost confined, above mid-tide (Fig. 10)
Scrobicularia plana	Salter Mill	18·5	General intertidal, but no precise data on optimum levels	Usually o	Concentrated above mid-tide (Fig. 12)
Nereis diversicolor	North Hooe	*ca.* 24		In various types of permanent (brackish) waters	Concentrated above mid-tide throughout range except at extreme seaward end (Fig. 8)

* The complete range of estuarine influence is 30·5 km.

† Indicates as far as known from limited data.

‡ Indicates precise data lacking.

at certain tidal levels, found here to apply even to the mud fauna, shows how essential it is to consider tidal levels when the faunas of successive localities up the river are compared.

The other aspect of distribution studied (and the rest of the data in Table X) refers to the "vertical" range of the species, that is to say their relation to tidal level. The tendency for many shore animals to show preference for certain regions of the tidal zone is elementary knowledge. Some species maintain their relation to tidal level irrespective of changes in the substratum. Such zoning of *Littorina* spp., for instance, appears well established. But as a rule it is by no means clear, when intertidal zoning is found, to what extent it is due to changes in the substratum which more often than not accompany changes in tidal level. This consideration applies more especially to the fauna of bottom deposits, particularly burrowers. It is not often that such a uniform mud substratum from high to low water is found as provided by the flats of the River Tamar. The deposits of most estuaries contain a considerable content of sand particles, the presence of which results in a horizontal gradient between soft mud and clean sand down the length of the estuary, and also tends to produce a similar gradient vertically down the shore. The unusual lack of sand in the Tamar, making for a relative uniformity in the mud deposits, simplifies the study of intertidal zonation as well as of horizontal distribution.

It has been seen that most species for which there are sufficient data show some degree of concentration towards one part or another of the tidal zone. Tendencies of this kind which appear to be consistent are stated in the last column of Table X, the two previous columns giving for comparison a brief summary of the normal habits of the species, as far as is known. For the marine species of Group A, the normal distribution on the sea coast can be considered apart from the behaviour shown in estuaries. The list for this group includes species showing all types of vertical distribution. If the last column is examined, it is seen that, as far as the data go, the distribution found in the Tamar is in essential agreement with that normally found on the open shore. There is only one species (*Scoloplos armiger*) which may have a more limited vertical range than it has at its optimum (see p. 306). In Group B, *Nephthys hombergi*, which at the marine end of its range is rarely found except at or below low water, maintains its preference for lower levels up the estuary. Similarly *Macoma balthica*, which appears normally to range fairly uniformly through the tidal zone on suitable ground (Stephen, 1929, 1930; Thamdrup, 1935), was found in the Tamar more evenly distributed between high-water neaps and low-water springs than most species.

For the five estuarine species of Group C, it is only possible to give a summary of their distribution in other brackish waters for comparison with that found in the Tamar. The data given are based on the discussion of the individual species earlier in the paper. For three of them there is almost nothing previously known of their optimum intertidal levels. The striking point about their vertical distribution in the Tamar is that all five species show a very marked preference for the upper part of the tidal zone, whereas of the fourteen species in Groups A and B only two at the most show a comparable preference. The three species in the latter groups which penetrate farthest up the river, and with which comparison is possible, behave otherwise: *Nephthys* is concentrated below half-tide, while *Cardium* and *Macoma* showing no marked optimum are at least more tolerant of the environment near low water than the five species of Group C. The contrasts between the former and *Nereis*, and between the two latter and *Scrobicularia*, may be noted. It is furthermore noteworthy that the species of Group C show this preference for levels above half-tide irrespective of their degree of tolerance of immersion. *Scrobicularia plana* is the only one of them for which there is any evidence that conditions approaching permanent immersion may be unfavourable.

Such are the data which present themselves for interpretation. There is evidently sufficient zoning shown by certain members of the estuary mud fauna to require explanation. It is impossible at this stage, and beyond the scope of this paper, to embark on an adequate consideration of ecological limiting factors. This will be more suitably done when a wider range of species can be considered, and when further laboratory and field observations have been carried out. But it is desirable to call attention to a few relevant points regarding this problem.

Since all intertidal species (with the exception of insect larvae, which are not dealt with on account of their scarcity) are aquatic organisms, the decrease and final absolute limit towards high water, at whatever levels these occur, are bound to depend partly, if not entirely, on the various adverse effects which accompany decreasing immersion and increasing emersion. Other influences which may also sometimes come into play—e.g. of the salinity, as mentioned on pp. 327–8, or lack of adequate currents for plankton or deposit feeders—will be detected with difficulty, and as likely as not be completely masked. But as regards a downward decrease, when this is shown, from a maximum within the tidal zone in the direction of low water, there is no causal influence which operates universally. The species which show this effect include several which are perfectly able to tolerate permanent immersion. Other causal factors have to be looked for, and probably several operate separately or in conjunction. The elucidation of these seems to us to be the most significant aspect of the problem raised.

Whatever other influences are at work in the Tamar, there is one which we have good grounds for believing to be of importance and to affect most species in varying degrees. This, namely, is the effect of tidal and river currents. Bottom deposits of soft mud are particularly susceptible to their action. The stronger the currents, the greater is the scouring effect at the surface of the mud, and so the greater the instability of the substratum even if its texture is substantially unaltered. Where the tidal zone is broad, as in most parts of the Tamar estuary basin, the narrowing of the channel on the ebb tide brings an accompanying increase in the flow of the water (and a corresponding decrease towards high water on the flood). Despite the fact that the tide is flowing more slowly at the low-water period than at half-tide, when these and other relevant phenomena are taken into consideration, it is clear that the scour must be much greater near low water than in the upper half of the tidal zone. The interplay of water currents, furthermore, creates the contours of the mud-banks: deposition of silt occurs where currents are weak and removal where they are strong. The form of the mud-banks in return reacts on the currents, until an approximate equilibrium appears to be reached. The effect normally attained is that the mud-banks have a very gradual slope above, which increases slowly at first, then sharply towards low water; and the result is further to accentuate the increased scouring effect on the edge of the channel. Finally it emerges that the slope of the mud-bank may be taken as a useful guide to the relative scouring effect to which the surface is exposed.

Sections have been drawn of all the traverses in the same manner as that figured for St John's Lake in Fig. 7, and from them an approximate measure of the surface gradient at each station obtained. The decrease of the total fauna in places where the gradient is steeper than about 1 in 50 is consistent in all traverses. Some of the steepest gradients are encountered on the channel slopes in the highest traverses worked, where the instability of the ground is apparent, and the fauna may be reduced to nil. Locally almost level ground is found at low-water springs, e.g. at the edge of West Muds (Fig. 1, D 2), and here the fauna is normally rich.

From such and other circumstantial evidence the suggestion is strong that the increased disturbance to which the ground is liable towards low water is an important factor in causing decline of population density in this direction.* Some species, it may be suspected, are affected more than others. Among those which will feel the influence first are small surface-living species (e.g. *Hydrobia ulvae*) and animals which occupy permanent burrows in the mud. It seems very significant that *Cardium*, *Macoma*, and *Nephthys*, which show the greatest tolerance of low-water conditions, do not occupy permanent burrows, in contrast to *Nereis*, *Cyathura*, *Corophium*, and *Scrobicularia* which do. The concentration of the latter species in the upper part of the tidal zone—a fact stressed above—may thus be explained. It can now also be understood why a species which ranges from moderate depths into the lower half of the tidal zone can come to show a maximum in that part of the tidal zone occupied, as, for example, *Ampharete grubei* (Fig. 8).

Another influence which might theoretically cause a decrease towards low water concerns the salinity conditions. As Milne (1938) has shown, in the Tamar Estuary there is a marked gradient from high to low water. Briefly,

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* It is not overlooked that increase in water currents may have a certain beneficial effect. *Balanus balanoides* notably flourishes where there is strong water action (e.g. Moore, 1935). Other plankton and detritus feeders—e.g. *Scrobicularia plana*—may quite possibly benefit from a moderate increase in current for the same reason.

at high water the range of daily fluctuation is small, but towards low water becomes considerable. At the same time the average salinity of the water covering the ground decreases down the shore. In every respect the conditions become increasingly unfavourable down the shore for a marine species whose range into an estuary is limited by salinity (or for an estuarine species at the upper end of its range). Conversely conditions on the whole become increasingly adverse towards high water for an estuarine species at the *lower* end of its range. If salinity were the only, or the primary, limiting factor, certain results might be anticipated. Thus a marine species should become increasingly restricted to the upper part of its intertidal range as it approaches its upper limit in an estuary. Similarly for a species of more extensive range in estuaries, the optimum level should steadily rise. For an estuarine species with a lower limit within the estuary, the vertical zone should, in a seawards direction, tend to narrow down towards low water. Effects of such kinds might be expected to show in the distribution diagrams of at least the more abundant species. But, in fact, there are only minor indications. The restriction of *Nereis diversicolor* below mid-tide, and of *Scoloplos armiger* above mid-tide, in St John's Lake are in accordance with expectations; but otherwise there is a noteworthy absence of anticipated effects. The inference is that the limiting effects of salinity conditions are masked by some more important factor, such as, for example, the influence of water currents discussed above.

Two possible factors limiting species towards low water have thus been brought to notice. An adequate treatment of the subject will have to deal with a third—the obscure and somewhat paradoxical adverse effect of prolonged immersion, which appears sometimes to operate (cf. *Chthamalus stellatus*, Moore & Kitching, 1939).

SUMMARY

The macrofauna of the intertidal mud-flats of the River Tamar have been investigated. Quantitative samples were taken by sieving the mud through a 0·8 mm. sieve. Traverses of series of stations were worked at successive intervals up the river, and the tidal level of each station ascertained.

The characteristic species which inhabit the mud-flats are listed and the data secured regarding (1) population density, (2) up-river penetration, and (3) vertical distribution, are summarized and related to previous information on these points.

While some species are more or less uniformly distributed intertidally, others show marked zonation, with maxima in one part or another of the intertidal zone. Marine species which penetrate into the estuary tend to show the same intertidal distribution as in marine habitats. All five of the more strictly estuarine species are concentrated in the upper tidal levels.

In considering the limiting factors which cause a decrease of population at lower tidal levels, emphasis is placed on the probable importance of the increase in strength of water currents towards low water.

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FLUCTUATIONS IN OYSTER PRODUCTION IN THE FAL ESTUARY

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INTRODUCTION

In the course of studies during the last five years on the breeding and spat-fall of oysters (*Ostrea edulis*) on the producing grounds, Blackwater and Roach Rivers, in the Thames Estuary, good spat-falls have been observed. In 1935 an exceptionally good fall occurred on these grounds at a period when adult stocks of oysters were at a very low ebb. Good spat-falls have also occurred since that time. It was therefore considered worth while to investigate whether comparatively good spat-falls had occurred also in the Fal Estuary and at the same time compare the existing conditions with those found in surveys in 1924 and 1926 (Orton, 1927 *a* and *b*). The Fal Estuary beds may be regarded as at least second in national importance to the Thames Estuary beds for the production of oysters. Moreover, as suggestions have been made that the oyster pest, the American slipper limpet, *Crepidula fornicata*, might become introduced and establish itself on the Fal beds, it was desirable to find out whether *Crepidula* had yet been found on the oyster grounds.

By the courtesy of the Truro Town Clerk, Mr L. J. Carlyon, and the River Committee, permission was given for the desired survey, which was carried out on February 23 1939. The expenses of the research were defrayed from a grant from the Durning-Lawrence Bequest, Liverpool University; acknowledgement is gladly tendered.

SURVEY OF THE BEDS

On the day of the survey only ten boats were at work. Most of the boats were visited in turn and their dredge-hauls scrutinized and recorded. The bailiff, Mr Tyache, reported that recently about 12 boats per day had been working. From figures of the daily catches of five sailing boats from February 24 to March 3 (kindly supplied along with other valuable assistance by the bailiff, Mr Tyache), the average daily catch per boat each using two dredges was 133 oysters of legally takeable size, i.e. with minimum span in any direction of $2\frac{5}{8}$ in. The daily catches ranged from 100 to 207. The price of these oysters at the time was very low, namely about 4*s*. 6*d*. per hundred. In the same period the average daily catch per man per rowing boat (haul on tow) was 99 oysters, the daily catches ranging from 79 to 123.

The state of the beds can be closely estimated from these figures of the daily catches and the detailed report on the examination of the dredge-hauls given in Table I.

Table I. Analysis of Dredge-hauls for Oysters, Truro Grounds, Fal Estuary, February 23 1939

Ten boats seen at work. Price of oysters 4*s*. 6*d*. per 100

		Small oysters		Large oysters 2⅝ in. and over	Remarks
		About 1 in.	1–2½ in.		
A. River above Turnaware Bar: rowing boats only					
Haul 1. Boathouse	Living	2	3	0	None of dead bored
Hauls made in absence: Haul 2	Living	36	10	0	None bored
From 9.30 to 10.45 only 7 large caught					
Haul 3. Clenhalls Flat	Living	14	11	1	2 *Carcinus* with *Sacculina*
Hauls at least 3: Totals	Living	52	24	1	
Average living per haul		17·3	8	0·3	Culch fairly clean and abundant
		25·3			
B. Truro Lake. Turnaware Bar: rowing boat only					
1	Living	17	5	2	Culch very dirty
C. Truro Lake: sailing boats. North and middle of East Bank: sailing boat, good breeze					
2, 3	Living	13	1	12	5 one inch dead, none bored
4, 5	,,	0	4	4	
6, 7	,,	30	2	19	Struck a bed inshore
8, 9	,,	20	2	6	6 spat on a stipes of *Laminaria*
One shell found February 22 carrying three 1938 spat about 1 in. Culch abundant but very dirty					
Parsons Bank: sailing boat, wind slight, one dredge					
10	Living	4	0	0	Good bag of culch
11	,,	3	0	4	,,
One shell found February 22 bearing seven 1938 spat about 1 in. Culch abundant, but very dirty					
Mylor Bank to Penarrow: sailing boat, fair breeze					
12	Living	4	1	5	Culch old and heavily overgrown with sponges and *Lithothamnion*. 2 pairs of *Archidoris* in copula; clump of *Buccinum* spawn
13	,,	0	0	5	
14	,,	2	0	0	
15	,,	0	0	1	
16	,,	0	0	2	
Note. No dumps seen in any hauls on any grounds					
Sums for 15 hauls		76	10	58	
Averages per haul		5·0	0·7	3·9	Approximate catch per man per day = 133 legal oysters
Average total per haul			9·6		

The river beds above Turnaware Bar, Table I A, are fairly well stocked with small oysters, the average haul working out at about 17·3 one year old and 8·0 two or more year old small. These beds, however, at the end of the 1938–9 season carried very few large (legal) oysters, only one large oyster being taken in three hauls. It is clear that there had been reasonable spat-falls in 1937 and 1938, but there were few survivors from previous years.

On Turnaware Bar (Table I B) a good supply of 1938 young and a few of previous years occurred; these were similar in amount to those found in the river.

On the banks (Table I C) the supply of small oysters is very poor, not more than four to six per haul being taken in the average haul. Hauls 2, 3, 6 and 7 on the East Bank are probably exceptional, as they were taken from a small patch of ground which could only be worked satisfactorily under the favourable conditions of tide and wind existing at the time. If, therefore, these hauls be excluded the average catch per haul on the banks is 3 one year old, less than 1 more than one year old small, and 2·4 large, with a total of 6·1 oysters per haul. When the presumed exceptional hauls are included the average rises to 5·1 one year old, 0·7 more than one year old small and 3·9 large, giving a total of 9·7 oysters per haul. Such a high average is seen to be improbable when a comparison is made with those results of extensive dredging in 1924 and 1926 given in the reports for those years. The comparison is given in Table II.

TABLE II. COMPARATIVE STATE OF THE BEDS ON THE BANKS IN 1924, 1926 AND 1939

As indicated by dredge-hauls in sailing boats only

Date	No. of hauls	Small per haul	Large per haul	All oysters per haul	Size of ring	Daily catch of large per man
Nov. 1924	237	6·4	4·2	10·6	2½	300–325
Dec. 1926	387	2·8	1·3	4·1	2⅝	About 100
Feb. 1939	11	3·7	2·4	6·1	2⅝	About 133

The results from the small number of dredge-hauls in 1939 in comparison with those for 1924 and 1926 can only be taken as indicative of the conditions on the beds at that time. Since in 1926 a man's daily catch was about 100 with an average of 1·3 oysters per haul, it is probable that in 1939 when the average catch was about 133 the average number of large per haul would be $\frac{133}{100} \times 1{\cdot}3$, i.e. about 1·7. It is reasonable to infer that the dredging on February 23 1939 was on the whole unusually good and this conclusion is supported by the fact that the sailing boat hauls were taken near the time of low water on a fair spring tide with mostly a good breeze. The figure for the average of small and large oysters per haul may be concluded to be rather higher than would be given by a large number of hauls in variable weather.

Bearing this in mind it is possible to compare the state of the grounds in the years 1924, 1926 and 1939.

The stocks on the beds in 1939 were rather better than in the slump period in 1926. With the ring at $2\frac{5}{8}$ in. 4·1 oysters per haul were taken in 1926 and rather more in 1939. In November 1924 when the beds were in a more flourishing state the average number of oysters per haul was 10·6, and 4·2 oysters per haul were legal with the ring at $2\frac{1}{2}$ in.

DISCUSSION

Although the beds are a little better than in 1926, the state must be regarded as unsatisfactory. With the favourable weather in recent years for oyster spat-falls the beds on the banks might be expected to show a recovery towards the condition in 1924. The river beds are probably stocked with more young oysters than were on the banks in 1924, and may be considered to be in a fairly satisfactory state. Too few hauls were taken on Turnaware Bar to determine the stock accurately, but the indications are that the stocks of young are very much less than in 1924, when an average of 56·4 young per dredge-haul were taken (Orton, 1927*a*, p. 31). As Turnaware Bar is a settling ground for spat, heavier stocks might reasonably be expected.

CONCLUSIONS

The poverty of the grounds at Turnaware and on the banks in comparison with the reasonable stocks of young in the river is correlated with the presence of clean culch in the river and dirty culch on the banks. In the view of the writer the condition of the culch on the banks is the main deterrent to the recovery of these excellent spatting grounds. In all the hauls seen the culch was abundant but either dirty or, as on the Falmouth North Bank, heavily overgrown with marine organisms, especially with sponges and *Lithothamnion*.

It was noticed that the dumpy oysters which formed rather more than 40% of the oyster population in 1924 and 1926 (Orton, 1927*a*, p. 32) were totally absent. In these years the bulk of the dumps were undersize for legal oysters. These dumps which were valuable as a stable spawning stock are not now present on the grounds, with the consequent loss of a real spawning asset to the beds. A fair proportion of older young oysters 1–$2\frac{1}{2}$ in. were found recently dead in the river, but few on the banks. None of these was bored by tingle. No indications of deposits of oil were seen. The American slipper limpet, *Crepidula fornicata*, was not found, and appears to be unknown.

RECOMMENDATIONS

The outstanding feature of the beds is the lack of sufficient clean culch on the banks. It is therefore recommended that culch be dredged from the edges of the banks and sides of the Channel (where it is mostly clean) and redistributed over the banks on the same day as dredged. There are other ways of supplying the culch necessary but the one suggested seems the simplest. As it will take many years in the economic conditions under which the beds are administered to supply all the culch which might be usefully employed on the banks, it would appear that there should be no delay in making a beginning.

It is suggested that twelve men working six sailing boats might be employed under the supervision of the bailiff for one or two weeks in the year in June catching culch from the edges and spreading it over the banks. In this way clean culch would be available on the banks at about the time the oyster larvae are ready to settle. Perseverance in this procedure may be expected to result in the ultimate recovery of the beds and their maintenance in good condition.

It is recommended that the bailiff be asked to report periodically to the River Committee whether the American slipper limpet has been seen on the beds. Samples of this limpet have been supplied to the bailiff, who will ensure that the dredgermen are also familiar with this important pest in oyster cultivation.

SUMMARY

A survey of the Fal Estuary Beds in February 1939 gave evidence that the stocks of oysters were only slightly better than in the slump period of 1926.

The failure of the beds to show the recovery expected in recent years is attributed largely to the absence of sufficient clean culch on the banks.

It is suggested that means be taken to scatter clean culch over the banks in June yearly to prevent further decline of the beds and assist in their more rapid recovery to a flourishing condition.

The American slipper limpet, *Crepidula fornicata*, was not found and appears to be unknown on the beds.

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THE REARING OF OYSTER LARVAE ON AN ALGAL DIET

By J. R. Bruce, Margery Knight and Mary W. Parke

From the Marine Biological Station, Port Erin

(Text-figs. 1–3)

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INTRODUCTION

The cultivation of the European flat oyster, *Ostrea edulis* L., has been the subject of numerous experiments on the Continent and in Britain. These experiments and their varying but usually ephemeral success, have been fully reviewed in several publications (Kändler, 1930; Gaarder & Bjerkan, 1934; Orton, 1937), and it is not proposed to go over this ground in the present report which deals purely with experimental work.

It is fair criticism of most of this previous work to state that ultimate failure, or at any rate only partial success, was associated with imperfect knowledge of one or other phase of the oyster's life history, and its special and varying requirements in the way of food and physical conditions at the successive stages of growth and development. Much greater significance therefore attaches to the most recent contribution to the oyster-breeding problem—that of the Ministry of Agriculture and Fisheries—an investigation in which the importance of a full knowledge of the biological and physical factors, and their incidence at all stages of the oyster's life is adequately realized, and applied so far as practical limitations permit; with the result that Cole (1938) is now able to claim, as the outcome of several years' success, that "the production of oyster-spat on a commercial scale in tanks may be reasonably expected".

Among the various factors recognized as significant, that of food and feeding, especially in the free-swimming larval stage, stands out pre-eminent; and some of the preliminary work undertaken in the course of the Ministry's experiments is described by Cole (1937). This work, carried out at the Conway Mussel Cleansing Station, was necessarily conditioned by the physical environment there obtaining, and it was realized by the Ministry's staff that certain aspects of the work, notably the detailed study of unicellular algal cultures as potential sources of food supply for the developing larvae, could better be studied at the Port Erin Biological Station, where facilities were available for small-scale experiments under the control of an algologist.

The experiments in the present series have extended so far over five seasons. It is not justifiable to apply to these experiments the criterion of percentage settlement alone, which on a commercial or semi-commercial scale, would naturally afford a measure of relative success. The work has been to a great extent exploratory, and the "success" of an experiment has been appraised on the total contribution which it has made to the solution of the general problem in view.

At the same time, certain positive, occasionally spectacular, results have been achieved; for example, in some experiments 90–99 % of the larvae initially introduced completed their metamorphosis. Side by side, however, with these encouraging successes there must be recorded a not inconsiderable number of unexplained failures—that is, failures to repeat results in consecutive and even occasionally in parallel experiments where all observable external conditions were as closely identical as possible. Such seeming inconsistencies appear to be a commonplace among the observations of oyster-workers, and lead to the conclusion that certain factors—some of them conceivably genetic—remain unrecognized, and may assume significant proportions under certain conditions.

The content of the report calls for brief notice. Primarily devoted to an account of a series of feeding experiments on oyster larvae on a laboratory scale, that aspect of the work and especially the results of the 1938 season, takes pre-eminence in point of amount and importance. At the same time, the production of the necessary larvae, whether on a large scale in the semi-natural ponds of the Station, or under controlled conditions in tanks and trays, calls for some description, since we have reason to believe that the viability of oyster larvae depends in some measure upon the factors influencing the adult breeding stock prior to spawning and liberation.

The final report must of necessity omit reference to much essential preliminary work.

The authors have great pleasure in placing on record their indebtedness to Dr R. J. Daniel, Director of the Port Erin Biological Station, 1933–9. Dr Daniel has been closely associated with the work here recorded. He was

largely responsible for its initiation, and throughout the whole period now under review has maintained a close interest. His critical advice and constructive suggestions have been of great value.

It is fitting to record here also our sense of appreciation of the willing co-operation and cordial good-will of those members of the Conway staff of the Ministry of Agriculture and Fisheries who are more directly associated with oyster culture—Mr H. P. Sherwood, Mr H. A. Cole and (during the earlier years of the work) Dr R. W. Dodgson, at that time Director of the Conway Laboratory. Throughout the investigation there has been a free interchange of experience and reciprocal personal contact between the two laboratories.

It is a pleasure to acknowledge the valued advice of Prof. J. H. Orton, D.Sc., whose specialized knowledge of oyster problems has been placed freely at our disposal.

The work has been financed throughout by H.M. Development Commission.

MAINTENANCE OF LARVAL SUPPLY

It is known that a female-functioning oyster may release anything up to a million larvae, but in the experiments under review, only relatively few could be used at a time. It was therefore a matter of some moment to extend the spawning period in order to have larvae available for as long a period as possible. It was of equal importance that the larvae should be of the highest viability.

To meet these needs the spawning stock was kept under the widest possible range of conditions.

The Spawning Stock. Four main sources of supply were used, namely: the Fal Estuary, the Yealm Oyster Fisheries, Lochryan and the Blackwater River. From these localities a sufficient stock was obtained in April of each year, and to this was added a number of "survivor" stocks which had spent the previous season in the Port Erin ponds and tanks.

The samples obtained through commercial channels contained no very small oysters, and were for the most part three years old and more, with occasional large specimens up to 11·5 cm. in diameter. These were augmented, in the last three seasons, by a number of oysters bred in the Port Erin Station; the numbers of these were never large but definite proof was obtained that some, at least, were female-functioning when two years old.

SPAWNING STOCK KEPT IN OUTDOOR "PONDS"

Three ponds used in winter and spring for other purposes, and known respectively as the "East", "West" and "Lobster" ponds, have been available during the summer for housing the oysters. In the first three or four seasons, they served also as the locus of large-scale experiments in the rearing of larvae, and in some years a moderate spatfall occurred in them. The ponds were, however, too readily subject to varying conditions to give consistent results, and latterly their use has been restricted to that of accommodating the parent oysters.

The ponds lie west of the Station, are rock-cut and sunk to the level of the ground in the Manx slate, but differ from each other in detail.

(*a*) "*Lobster*" pond, capacity 15,000 gallons, 50 ft. × 13 ft. × 5 ft. 6 in., floored by bare rock. This was the subject of an experiment in reducing illumination with the object of keeping the *p*H value of the water low, but it involved a serious temperature loss which negatived any possible gain from change in the light factor.

(*b*) "*West*" pond, capacity 51,000 gallons, 39 ft. × 30 ft. × 9 ft. Floor and walls cement-covered, but continuous use over a long period may be assumed to have made the cement innocuous to larval life.

(*c*) "*East*" pond, capacity 73,000 gallons, 52 ft. × 31 ft. × 8 ft. 9 in., part natural rock, part cement, used only in 1938.

All ponds are filled by pumping from Port Erin Bay and the water is delivered by wooden chutes. The spawning oysters in the ponds are accommodated on light wooden trays and covered by sheets of asbestos to reduce algal growth. The number of oysters was such as never to exceed 1 per 100 gallons of sea water. Whether destined for ponds or smaller vessels, all oysters were carefully examined and "cleaned" to avoid the introduction of undesirable organisms.

Physical Conditions in the Ponds

The physical conditions in the ponds are not susceptible to any considerable degree of control. In the one instance in which control of light was attempted, no useful result emerged. The usefulness of the ponds in any given season is largely dependent upon such meteorological conditions as temperature and sunshine.

Chemical factors such as *p*H, phosphorus content and oxygen content are intimately bound up with the phytoplankton. Some of these factors have been continuously observed, but in view of the relatively small share in the ultimate result played by the ponds, it is not proposed to discuss them in detail in this report. Abstracts of the data are given in Table I.

Biological Conditions in the Ponds

The biological conditions in the ponds and particularly the character of its included plankton are of some importance. Analyses of the number and nature of organisms present in the pond waters have been made at regular intervals.

During the first year of experiment, samples of pond water were examined by Mr H. A. Cole of the Conway Experimental Station, using the "Buwa"

Table I. Use of the Spawning Ponds during the Seasons 1934–8. With Notes on Conditions, Larval Count, Settlement of Spat, etc.

Year	Weekly mean temperature			Other factors	Maximum larval count	Spat-fall	Remarks
	10° or above	15° or above	Maximum				
				West pond			
1934	May 6–Oct. 18	June 8–Aug. 28	July 16, 19°·8	*p*H 8·4–8·8	July 9–July 31 885 per gal.	18,000	*Gymnodinium simplex* very abundant. Healthy larvae, of which the earlier liberated gave best spat-fall
1935	(June)*–Oct. 15	June 15–Aug. 29	Aug. 13, 18°·6	*p*H 8·6–8·8 O_2 94–110 % Sat. P. 4–5 mg./m.^{3}	June 28–July 28 236 per gal.	3,400	*G. simplex* again abundant in early July. Spat-fall confined to July. Green unicells dominant later
1936	May 7–Oct. 10	June 21–Sept. 24	July 4, 18°·2	*p*H 8·4–8·6 O_2 102–109 % Sat. P. nil	June 29 113 per gal. July 22–Sept. 30 259 per gal.	2,780	The earlier larvae included many prematurely spawned. Spat-fall mid-Aug. only, at 16°·5
1937	May 1–(Sept.)	May 29–Sept. 7	July 24, 17°·7 Aug. 7, 17°·7	*p*H 8·5–8·8 O_2 101–118 % Sat. P. 12·5 mg./m.^{3} in July, nil in Aug.	Mid-July and mid-Aug., few	Nil	Many larvae again premature. None reached "eyed" stage
1938	(May)–(Oct.)	June 18–Aug. 20	Aug. 13, 17°·5	*p*H 8·75–8·85 early, but 8·5 in Aug. Plaice in pond	Negligible	Nil	Larvae small and probably premature
				Lobster pond			
1934	May 26–Oct. 22	July 3–Aug. 26	July 9, 17°·7	*p*H 8·3–8·5	July 11–Aug. 12 2080 per gal.	1,770	Pond covered mid-May to end of August
1935	(June)–Oct. 10	June 22–Aug. 26	July 6, 16°·7	*p*H 8·6–8·8	July, 217 per gal. Aug. 3, 40 per gal.	Nil	Pond covered for 1 week only
1936	May 10–Oct. 26	June 23–July 12: Aug. 10–Sept. 7	July 27, 16°·6	..	..	..	A few larvae used for a culture-house experiment
				East pond			
1938	(May)–(Oct.)	June 18–Aug. 27	Aug. 13, 18°·8	*p*H 8·65–8·8	Negligible	Nil	Larvae small, premature

* A date in brackets is estimated by extrapolation.

filter method. Qualitative records were kept at Port Erin. From 1935 onwards, however, all analyses, quantitative and qualitative, have been made at Port Erin. After some preliminary experiments a satisfactory method of sampling was adopted. 10 c.c. samples of sea water were centrifuged for 10 min. and 9 c.c. were removed. Sample drops of the remaining 1 c.c. were examined on a haemacytometer slide. Eight counts were made for each sample of water and the average value recorded. The first analyses were based on size alone and the plankton divided into groups of under and over $5\,\mu$. From 1937 onwards, however, much greater discrimination was exercised. Five groups of organisms were established and used as the basis of analysis:

(i) Organisms of 2μ or less.
(ii) Flagellate forms of 2–$5\,\mu$.
(iii) Non-motile forms of 2–$5\,\mu$.
(iv) Organisms of 5–$10\,\mu$.
(v) Organisms over 10μ.

The results of the analyses are recorded in Table II.

TABLE II. MICROPLANKTON COUNTS AND ANALYSES OF POND WATERS

			Monthly averages—No. per mm.^{3}				Maximum peak	
Pond	Year	Month	Total count	No. of organisms over $5\,\mu$ in size	No. of organisms less than $5\,\mu$ in size	Flagellates $5\,\mu$ or less in size	Date	No. of organisms per mm.^{3}
Lobster pond	1934	Aug.	25	..	..	..	..	..
	1935	July	110	55	55	..	July 9	150
		Aug.	89	43	46	..		
	1936	Aug.	71	28	43	31	Aug. 10	92
West pond	1934	July	91	..	..	..	Aug. 2	213
		Aug.	119	..	..	..		
	1935	July	121	58	63	..	Aug. 21	175*
		Aug.	100	45	55	..		
	1936	June	35	10	25	22	Aug. 26	78†
		July	50	17	33	32		
		Aug.	68	37	31	31		
		Sept.	56	21	35	20		
	1937	June	110	27	83	61	July 12	220
		July	164	63	101	84		
		Aug.	130	21	109	80		
	1938	June	635	32	603	16	July 6	1093‡
		July	939	47	892	118		
		Aug.	546	49	497	65		
East pond	1938	June	151	14	137	60	July 27	211
		July	176	19	157	70		
		Aug.	187	28	159	47		

* At the 2 ft. level maximum count of 244 per mm.^{3} on August 21.
† Lower counts due to frequent additions of fresh sea water.
‡ Very high counts due to presence of fish (plaice) in pond.

SPAWNING STOCK KEPT IN TANKS AND SMALL VESSELS

In each of the five seasons under review, an increasing number of the spawning stock was kept indoors in small tanks and trays. In contrast to the results experienced in the "ponds" a reasonably consistent output of larvae was maintained in indoor vessels. In some years the whole experimental programme was concerned with larvae liberated under these conditions. This method brought several advantages. When the oysters were few in number in each tray, an individual emitting larvae could be readily detected and the larvae collected. The latter were all of one age, in marked contrast to the condition of those in the ponds, and when used in experiment gave opportunity for more trustworthy comparisons. In maintaining oysters in small vessels, running sea water or twice-daily changes effected with minimum temperature change is a factor in success. Sea water from the storage tanks of the Station was used. Since this water is unfiltered even a brief period of storage affects its planktonic content, and compared with freshly pumped sea water, certain flagellates sometimes appear in greatly augmented numbers. There is thus a probability that sufficient food was always present in the water supplied to the spawning oysters. Nevertheless, on a few occasions, deliberate additions of food organisms were made to the vessels, but no enrichment with nutrient materials intended artificially to raise the plankton content was attempted, nor were the vessels placed under lighting conditions suitable for algal development.

In general no attempt was made to control temperature, but in 1937 and 1938 a certain number of oysters were kept at a raised temperature in the culture-house for a period of time before and during actual liberation. It must be recorded that in the "Hatchery" trays larvae of high viability, yielding a high percentage of spat-fall, have been produced at temperatures (12°–13°·5 C.) well below the level hitherto regarded as minimum for such production, i.e. about 15°·5 C.

It would appear as if a slight but sudden rise of temperature were essential to initiate the act of liberation, but the extent of such rise and the actual temperature are dependent upon the temperature level at which, up to that stage, development has proceeded.

EXPERIMENTS ON A LABORATORY SCALE

During the four years 1934–7 understanding of the various factors involved in larval culture accumulated slowly, but the experience gained formed a foundation for the 1938 experiments in which significant results were obtained and which demand full description. The work of 1934–7 forms, therefore, a historical background to that of 1938 and only brief reference to it need be given. Each of the earlier years contributed its share of information upon which experimental methods were revised and control gained over the numerous factors affecting the larvae. By the end of 1937, from the point of view of experimental technique, the most convenient layout and procedure was reached. All technical improvements were incorporated in the organization of the culture-house of which a description follows.

THE CULTURE-HOUSE

After one season of purely exploratory work, using a variety of vessels under such conditions as could be maintained in the existing laboratories at the Biological Station, it was realized that a properly equipped "culture-house" with facilities for temperature control and a variety of sources of water supply was essential. Plans were drawn and a building erected (see Fig. 1).

The building is of lean-to form, 15 ft. × 8 ft. It is 7 ft. high at the front and 11 ft. high at the back and is glazed on the roof and on the sides above a 3 ft. timbered skirting. Within it are two benches to accommodate culture vessels. Two heaters of common horticultural pattern are fitted under the back and front benches respectively. Together they maintain a temperature level of 20°–22° C.

Exposure to light is not uniform over the whole structure. To mitigate the possible ill-effects of too strong overhead lighting a roof-screen, made of hessian, was in use. The effect of this screen was to reduce the mean light intensity to 38 % of its full value as roughly determined in five directions by a photo-electric exposure meter. Even with this screen constantly in use there was inequality of illumination over the benches. For a variety of local reasons less light is received by the middle of the front than by the ends of the building. Sunlight falls predominantly on the southern end of the culture-house in the forenoon and on the northern end late in the afternoon. The distribution of mean daily light intensity, so far as it was incident on the exposed surfaces of the culture vessels, was determined by electric photometer for front and back benches. The results which were purely relative indicate that the average illumination falling on the front and back benches respectively, calculated on a whole day's readings with a wide range of overclouding, stood in the ratio of 100 : 76·5. The inequality between the ends and middles of the benches varied greatly with the altitude of the sun; on the daily mean (front and back benches) the illumination at the south end exceeded that in the middle of the benches in the ratio of 100 to 70. To attempt to rectify this inequality of illumination the glass of the south side was covered by coarse muslin. These arrangements were intended to secure as nearly as possible uniform illumination to all jars so that comparisons exclusive of the light factor could be made, but despite the precautions taken, the differences in illumination could not be completely eliminated and the "end" positions of the benches have frequently yielded results different in character from those of experiments occupying positions nearer the middle of the bench.

It was realized that the light intensity even if it were made uniform was not necessarily at its optimum value. The central two-light sash in the middle of the front bench was glazed with "vita-glass", but in view of the diffused character of the internal lighting, it is not felt that this fact is of special significance.

Experimental Equipment

The principal equipment consists of experimental vessels in the form of seventeen glass bell-jars, of 20 l. capacity, arranged along the front and back benches as shown on the plan. Three additional vessels not forming part of the main series can also be accommodated along the south side. The volume of sea water used in these vessels is 16 l., and when continuously changing water is called for, this is effected by a drip-feed from a distributing system of glass tubes with screw-clipped jets which is carried round the culture-house at a level slightly above the top of the bell-jars. Batteries of carboys containing different kinds of sea water are linked to the distributing system in such a way that any vessel can be fed from either or both of two sources. To prevent loss of larvae the outflow tubes are screened with bolting silk (Wydler's No. 12). Arrangements are made for cleaning this filtering surface when necessary. The reservoirs of water are filled from cans of 6 or 8 gal. capacity in which the water is brought in from the sea. The cans are fitted with a removable lid which can be clamped down on to a soft rubber gasket which forms an effective seal. A hose connexion is then made between the carboy and a tube passing through the lid to the bottom of the can and, on air being pumped into the can by means of a hand-operated motor-tyre inflator, the water is forced up into the carboy, whence an initial act of suction serves to fill the distributing tubes and jets.

Stirring and aeration is provided for by glass plunger plates, suspended from a light braced framework of timber, hinged to the roof as shown in the figure, and maintained in slow oscillation by a mechanism based on the Scott-Dannevig Tipping Bucket. (Fig. 1.)

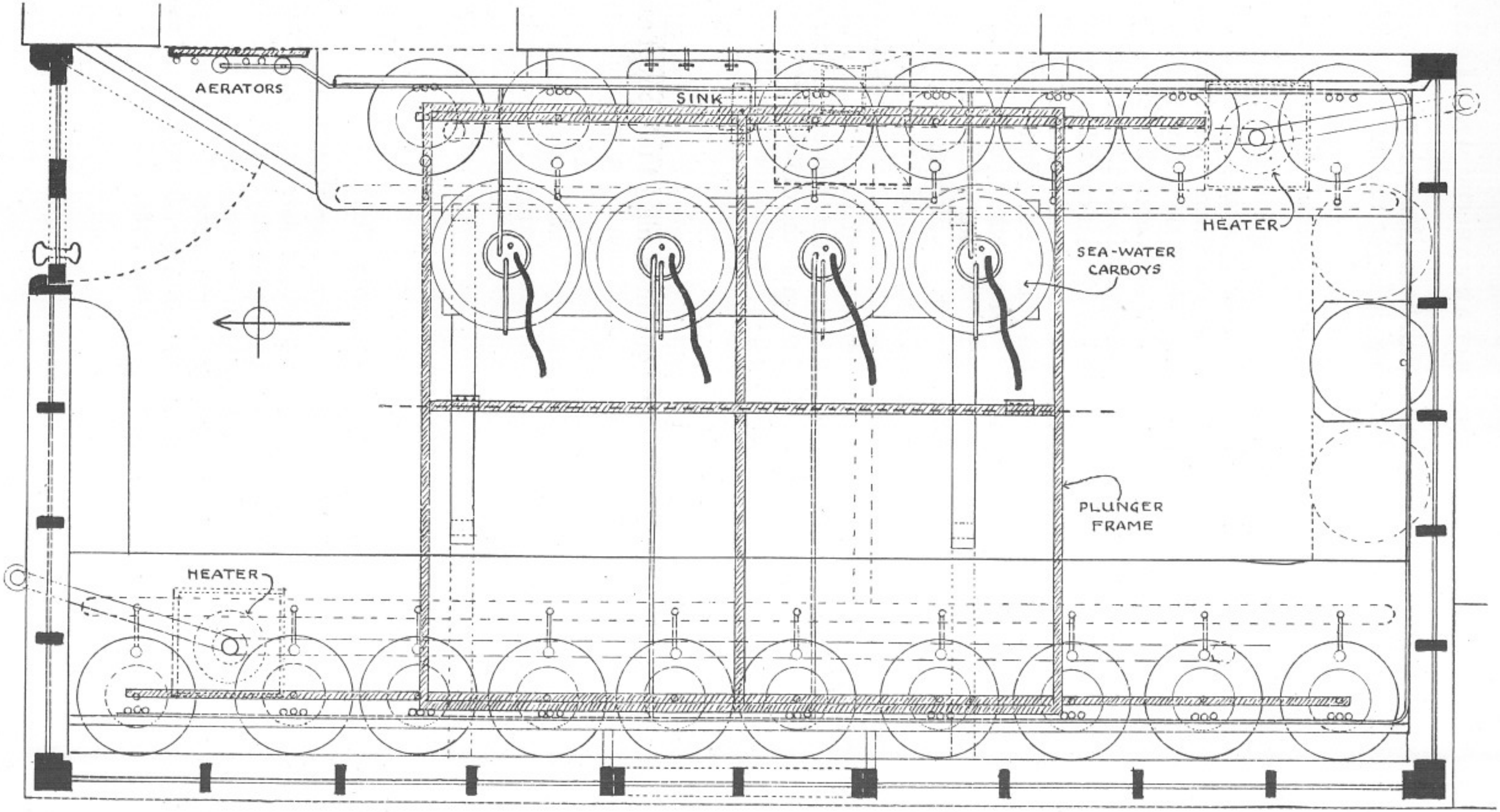
Aeration by actual bubbling has been made use of in all experiments in substitution for or along with plunger stirring. For this purpose two large Gemmill aerators, connected in parallel are fitted as shown in Fig. 1. Compressed air from these is led by glass tubing round the culture-house and thence by capillary jets to each vessel.

BIOLOGICAL DATA

The experience of previous workers supports the assumption that oyster larvae feed on a diet consisting largely of plant organisms. The object of the present enquiry was to determine the identity and nature of those organisms which give most successful results in rearing larvae.

The utilization or otherwise by the larvae of a given algal organism is obviously determined, in the first instance, by the size of the organism in relation to the feeding mechanism of the larvae. A diameter of 10 μ is generally

PLAN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PLUNGER FRAME
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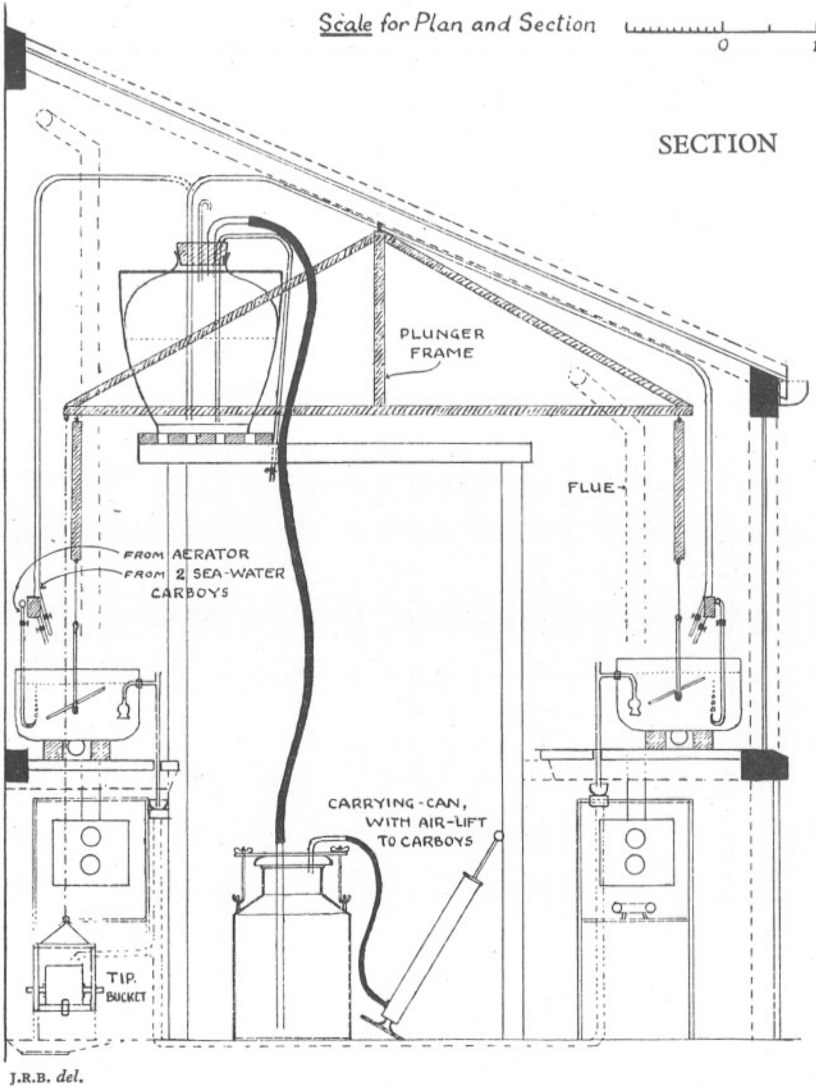

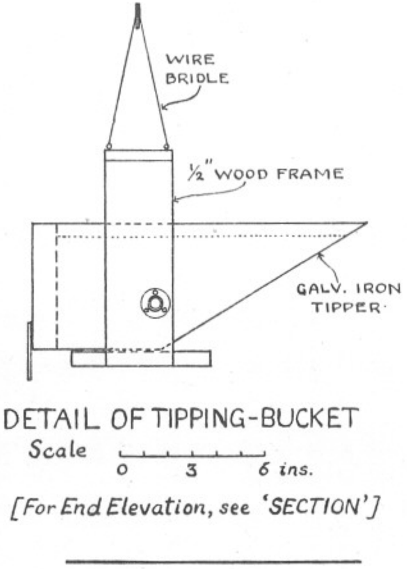

J.R.B. *del.*

Fig. 1. Experimental culture-house for work on oyster larvae, at the Marine Biological Station, Port Erin, Isle of Man.

accepted as the limit of size above which a particle cannot be ingested by a newly liberated larva, and in consequence, the possible variety of plant cells available is somewhat restricted.

Many of the reproductive zooids of larger algae, which might conceivably equally well serve the same purpose as unicellular microphyta, lie within the 10 μ limit. Both these types of organisms were used in the experiments, but after a little experience, it was found that the unicellular microphyta were more successful, and latterly were exclusively used.

EXPERIMENTS WITH ALGAL ZOOIDS

The difficulties arising from the use of zooids of larger algae were several. Primarily, the irregularity of release and the uncertainty of securing an adequate daily supply made precise experiment difficult. Further, the zooids were sensitive to changes in media and were liable to lose motility rapidly when added to the experimental vessels. This fact was important as it is necessary that food material should be evenly distributed.

Zooids of *Enteromorpha compressa* Grev., *E. Linza* J. Ag. var. *lanceolata* (Kütz.), and *Chorda filum* Stackh. were tried and discarded. Eggs of *Fucus* mashed into particles small enough to be ingested with their included glycogen and also spermatozooids were tried. But when it was found that the larvae in the ponds, feeding upon the natural plankton, were developing more rapidly than those in the experimental vessels, it was decided to concentrate on the use of microplankton as the source of food supply.

EXPERIMENTS WITH MICROPLANKTON

Naturally the microplankton of the "ponds" suggested itself for the first trial, but attention was later directed to the use of sea water from the open sea.* At a later stage still the natural planktonic content was augmented in the culture jars, but finally, as a result of the experience so gained, the method was adopted of adding pure cultures of organisms to sea water whose natural plant population had been previously removed by filtration through a Berkefeld filter. Though this method is now accepted as likely to lead to good results, something of value emerged from the earlier methods used and the results may be briefly summarized as follows:

(*a*) *Using Sea Water without addition of Microplankton*

(i) "*Pond*" *Water*.

Larvae from the pond, in the pre-settlement stage were brought into the laboratory and induced to settle in small glass vessels under controlled conditions. During this phase the development of the rudimentary foot of

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* Referred to subsequently as "outside" sea water.

the larva into a long tongue-like process could be readily observed. In 1936 as many as 60 % of such larvae settled as spat in culture vessels at a higher temperature than that of the "pond" in which less than 1 % of settlement occurred. Experiments with larvae at an earlier stage of development also gave some measure of success. A small percentage reached the settlement stage.

(ii) "*Outside*" *Sea Water*.

Better results were obtained when "outside" sea water with its naturally included plankton was used as a culture medium for larvae which had been liberated into a dish in the Hatchery. In this experiment 4·5 % of the larvae achieved settlement. Further experiments on the same lines confirmed the results obtained and emphasized the need for close scrutiny of the nature of the naturally occurring plankton. Special attention was paid to the types and sizes of the micro-organisms present in the sea water supplied to the larvae. Small flagellate forms were cultured for use as additions to sea water.

(*b*) *Sea Water with Augmented Plankton*

One of the first flagellate organisms made use of in this way was *Gymnodinium simplex* (Lohmann). Indications had been given in earlier experiments that the larvae were taking in this organism from the "pond" water. It was therefore isolated, developed in pure culture and added to unfiltered (and later to filtered) sea water, though without any great success. The explanation of its failure lies possibly in the fact that it increases in size in culture and the naturally occurring small stages which might have been useful as food for larvae were absent.

(*c*) *Filtered Sea Water with added Pure Cultures of Flagellates*

The use of unfiltered sea water, though it gave certain promise of success, involved the considerable labour of determining its planktonic content before adding a culture of organisms. It also constituted an uncontrollable factor. Clearly, for experimental purposes, the use of sea water from which the natural plankton had been filtered provided better opportunity of comparing relative values of added organisms, but unfiltered sea water continued to be used when comparison between pure and mixed diet was desired.

As early as 1935 experiments in which *Coccomyxa* (a non-motile green unicell, 3–4 μ) was added to filtered sea water, gave promise of success. Some growth of the larvae was obtained; a few reached the "eyed" stage though no settlement occurred.

Gymnodinium simplex was also tried in filtered sea water but without success. It served a useful purpose, however, in directing attention to the use of flagellates as alternative to non-motile organisms in feeding experiments.

Belief that the former might serve a useful purpose was strengthened when analysis of the microplankton of "outside" sea water and "pond" water revealed the presence, in both, of flagellate as well as non-motile forms in the size-groups of under 5 μ as well as over 5 μ. Several of the smaller flagellates were therefore isolated and developed in pure culture. They proved to be more stable in size than *Gymnodinium*. Their use served as the basis for experiment in 1937 and was extended and developed in 1938. In pure culture they have been added to filtered sea water and their usefulness tested against controls in which unfiltered sea water, with and without the addition of flagellates, has been used.

These minute organisms used in culture have been referred to their appropriate algal group but they have not yet been precisely identified. The literature relating to minute algal flagellates in sea water is scanty and a considerable field of research is open to exploration.

In all, six flagellates, temporarily labelled "B", "C", "D", "F", "H" and "I" have been isolated and made the basis of experiment. The size-range, colour of the culture and tentative classification (according to Fritsch) of each species are tabulated below:

"B"	4–5 μ (golden brown)	Chrysophyceae, Chrysomonadales
"C"	6–7 μ (golden brown)	Chrysophyceae, Chrysomonadales
"D"	4–7 μ (red)	Cryptophyceae, Cryptomonadales
"F"	1·5–2 μ (greenish yellow)	Unclassifiable
"H"	5–6 μ (yellowish green)	Chlorophyceae, Polyblepharidaceae
"I"	3–5 μ (golden brown)	Chrysophyceae, Chrysomonadales

Some of these species were isolated by one of the authors (M. W. P.) but assistance in this matter was also received from Dr F. Gross while working at the Plymouth Laboratory. Those isolated at Port Erin were taken from the water of the "ponds" or from sea water collected outside Port Erin Bay, and all are maintained in "Erdschreiber"* culture solution. Two stock cultures of each species are always kept, in volumes of 1000 and 100 c.c. respectively, each in a wide-necked conical flask capable of holding twice the volume. All flasks are illuminated by north light only and the contents are subcultured monthly. The seasons 1937 and 1938 were devoted to this aspect of the work. In 1937 very little experimental work could be done owing to the failure of the stock oysters to produce viable larvae, either in the pond or in indoor trays. Only two apparently normal broods of larvae were liberated. These were used in experiment but after a few days, the larvae sank to the bottom of the culture vessels, showing signs of degeneration of the velum; in many cases the larger velar cilia had been cast off. The data here recorded are therefore largely drawn from the experiments of 1938.

In the following account the number given to a bell-jar refers to the

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* "Erdschreiber" culture solution: $NaNO_3$, 0·1 g.; Na_2HPO_4, 0·02 g.; soil extract, 50 c.c.; sea water, 1000 c.c.

positions in the culture-house, numbered 1–20 in Fig. 2, below. Since the incidence of light varied according to the position of the jar and also the mechanical limitations of the culture-house prevented the inclusion of jars 17, 18, 19 and 20 in the plunger-stirring system and of 18, 19 and 20 in the drip-feed supply mechanism, the numbers given to the jars define their position and are of some significance.

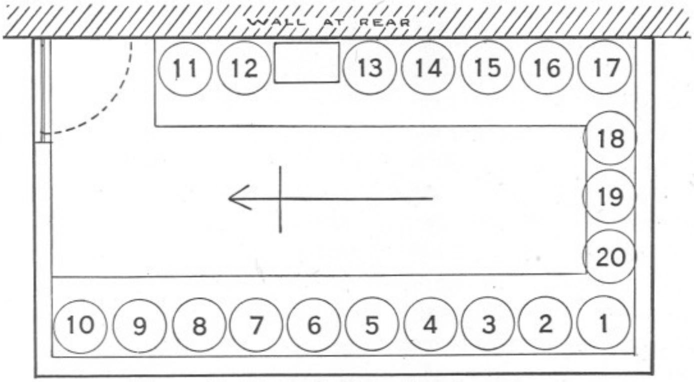

Fig. 2. Position of bell-jars in culture-house.

THE EXPERIMENTS OF 1938

The experiments of 1938 differ from earlier ones in that they were carried out with newly emitted larvae of uniform age. All the experiments are therefore comparable one with another except for the fact that larvae liberated by different oysters may show differences in size and viability. The larvae were liberated either in the culture-house tanks, or in the Hatchery trays. The water supplying these tanks and trays had a *p*H value approximately equal to that of the sea water outside Port Erin Bay, which was used exclusively in all the 1938 experiments. Readings of the *p*H value of the sea water in the culture vessels were recorded at the beginning of an experiment and periodically while it was in progress. Temperature readings, recorded twice daily, at 10 a.m. and 6 p.m. were, in practice, taken more frequently, since changes in the weather had to be counteracted by the opening and closing of the culture-house windows in order to maintain the water in the bell-jars at a steady temperature between 20° and 22° C.

Qualitative observations on the microplanktonic organisms either occurring naturally in the sea water or added to it in the course of experiment, were made periodically and the number of organisms per cubic millimetre of sea water recorded. When unfiltered "outside" sea water was used, analyses were carried out using the same grouping of organisms as that adopted in the estimation of the pond microplankton (p. 342). In experiments in which pure cultures of flagellates were tried as the sole supply of food for the larvae, a quantity of a rich culture was added every other day, the volume being proportioned to the count of organisms present, a count of approximately 50 per mm.^{3} being accepted as standard.

In all experiments in which filtered sea water was used, the larvae, before being added to the culture vessels, were washed very thoroughly in changes of filtered sea water to remove extraneous organisms. The number of larvae put into each jar was only roughly estimated but at the close of the experiment exact counts of all spat, surviving larvae and empty shells were made, so that the actual initial number of larvae added could be known and the true percentage of settlement calculated. To facilitate the measurement of growth, larvae were divided into size groups differing by 15 μ and in any sample the percentage of larvae in each group was recorded. Comparison of analyses of samples at various times in the course of an experiment and at the end gave data upon which the rate of growth could be calculated. The ages of the larvae were recorded as days after liberation from the parent.

As soon as spat-fall occurred the numbers of spat were counted at frequent intervals with a view to obtaining a curve representing the rate of spat-fall. In order to avoid the recounting of thousands of spat at frequent intervals, shells were replaced by fresh ones as soon as approximately a hundred spat had settled on them. Valves of *Pecten maximus* were used mainly as spat-collectors, but oyster, mussel and limpet shells were occasionally substituted. Comparison of spat-fall on upper and lower surfaces and on individual shells in different positions in the culture vessels showed inequality of settlement, but the factors controlling this distribution are not yet apparent.

Serial Record of the Experiments

The laboratory experiments carried out in 1938 fell into twelve consecutive groups; ten were devoted to the main problem of investigating the feeding and growth of the larvae, and the remaining two were short-period experiments intended to solve subsidiary problems.

Group I (Table III) was set up to test the efficiency of Berkefeld-filtered "outside" sea water plus added organisms as contrasted with "outside" unfiltered sea water. It was found that the larvae failed to develop with filtered "outside" sea water. This must have been due either to the filtering of the sea water or to the unsuitable nature of the organism, flagellate "D", which had been added. To test this point, groups II and III (Tables IV and V) were set up, with different broods of larvae respectively. In these groups the following were contrasted as media for larval culture:

(*a*) Filtered sea water.
(*b*) Filtered sea water plus flagellate, "F".
(*c*) Filtered sea water plus flagellate, "I".
(*d*) Unfiltered sea water.
(*e*) Unfiltered sea water plus flagellate, "I".
(*f*) Filtered sea water gradually replaced by unfiltered water.

At the end of these experiments it was found that the greatest success had been obtained in culture vessels to which flagellate "I" had been added irrespective of whether filtered or unfiltered sea water had been used. This appeared to indicate that the successful settlement was connected with the presence of flagellate "I". The same type of result was obtained in both groups II and III.

In group V (Table VII) relative values of filtered and unfiltered sea water plus flagellate "I" and unfiltered sea water without addition were tested. The results of these experiments confirmed the view that the addition of flagellate "I" was a significant factor, for excellent settlement results were obtained with filtered sea water plus flagellate "I" (99%) and unfiltered sea water plus flagellate "I" (84%), while no settlement occurred in unfiltered sea water alone. Similar experiments with flagellate "I" were repeated later in the season in groups VIII, XI and XII (Tables X, XIII and XIV) but gave less uniform results.

Groups VI, VII and IX (Tables VIII, IX and XI) were directed towards ascertaining the relative values of "B", "C", "D", "H" and "I" as food material. Of these "H" and "I" were superior to the rest.

The other groups of experiments were intended to solve subsidiary problems. Group IV (Table VI) was set up to test the effect of the addition of culture solution ("Erdschreiber") *per se* on the larvae. It was found to be negligible.

The experiments in group X (Table XII) demonstrated the extent to which the larvae removed the organisms from the sea water in the culture vessels. A series of counts were made and checked against a control. It was found, by comparison, that in the vessel provided with the larvae, food organisms disappeared from the fluid at an average rate of 24,000 per larva per day.

An experiment was brought to an end when it was judged that no further growth or settlement was likely to take place. The usual signs indicating that such a time had been reached were the loss of active motility on the part of the larvae and their congregation in heaps on the bottom of the jar. Examination of such larvae showed that many were obviously deteriorating and that numbers of the shells were empty. When observations on successive days showed that such deterioration was progressive and that most of the larvae had become affected the experiment was brought to an end.

A detailed synopsis in tabular form (Table XV) of each group of experiments and a summary table embodying the results of all the groups (except IV and X) follow. In compiling the serial records the following abbreviations are used:

C.H., culture-house;
A., air-stirred;
P., plunger-stirred;
D.–F., drip-fed;
U.O.S., unfiltered "outside" sea water;
F.O.S., filtered "outside" sea water.

Table III. Group I. June 23–July 27 1938. To compare the Survival of Larvae in Culture-house in Unfiltered Sea Water and Filtered Sea Water with added Flagellate "D"

Conditions of Experiment. Jars were A., P. and D.-F. Larvae liberated in culture-house from "Yealm" oyster, June 23 and "Lochryan" oyster, June 25.

	U.O.S., D.-F. with U.O.S.		F.O.S. with Flagellate "D", D.-F. with F.O.S.	
Position of jar in C.H.	1	3	2	4
No. of larvae in jar	11,000	8721	8000	11,000
Source of parent	Lochryan	Yealm	Yealm	Lochryan
Food supply	Micro-organisms present in U.O.S.	Micro-organisms present in U.O.S.	Flagellate "D"	Flagellate "D"
No. of micro-organisms per mm.^{3}	June 25 18	18	100	50
	28 20	21	140	74
	July 5 36	36	151	90
	14 61	38	..	..
	21 26	19	..	..
Analysis of organisms	Flagellate, 55% (under 2μ common) Non-mobile, 45% 5μ or less, 85% Over 5μ, 15%	Flagellate, 53% (under 2μ rare) Non-mobile, 47% 5μ or less, 89% Over 5μ, 11%	Flagellate "D" only	Flagellate "D" only
pH of water	8·07–8·22	8·07–8·20	8·08–8·25	8·07–8·20
Development of larvae	Age in days 1 165–180μ, 4% 180–195μ, 96% 11 210–260μ 13 Umbonate stages 16 210–225μ, 16% 225–240μ, 54% 240–255μ, 30% 18 "Eyed" stages present 20 1 spat 26 318 spat 32 745 spat	Age in days 1 180–195μ, 32% 195–210μ, 68% 13 210–270μ 15 Young "eyed" stages 18 210–225μ, 14% 225–240μ, 27% 240–255μ, 18% 255–270μ, 18% 270–285μ, 23% "Eyed stages" present 20 5 spat 22 129 spat 28 1883 spat 34 3121 spat	Age in days 1 180–195μ, 32% 195–210μ, 68% 7 180–210μ 13 Degenerating 15 Degenerating or dead	Age in days 1 165–180μ, 4% 180–195μ, 96% 5 180–195μ 11 Degenerating 13 Degenerating or dead
Final condition of larvae	180–225μ, 32·0% 225–255μ, 41·2% "Eyed" stages, 20·0% Settled as spat, 6·8%	195–225μ, 14·1% 225–255μ, 38·1% "Eyed" stages, 12·0% Settled as spat, 35·8%	(No growth) 180–210μ Settled as spat, Nil	(No growth) 180–195μ Settled at spat, Nil

TABLE IV. GROUP II. JULY 2–AUGUST 8 1938. TO COMPARE THE SURVIVAL OF LARVAE IN THE CULTURE-HOUSE IN U.O.S. AND F.O.S. WITH AND WITHOUT THE ADDITION OF FLAGELLATES "I" AND "F"

Conditions of Experiment. Larvae liberated on July 2 in culture-house by a "Yealm" oyster. Sizes of larvae, 180–195 μ, 96 %; 195–210 μ, 4 %. Jars were A., P. and D.-F.

		F.O.S.				U.O.S.	
		Drip-fed with F.O.S.			Drip-fed with U.O.S.	Drip-fed with U.O.S.	
Position of jar in C.H.		5	6	9	8	7	10
No. of larvae in jar		17,000	17,000	17,000	17,000	17,600	19,389
Food supply		Nil	Flagellate "F"	Flagellate "I"	Micro-organisms in U.O.S. alone	Micro-organisms in U.O.S. alone	Micro-organisms in U.O.S. plus Flagellate "I"
No. of micro-organisms per mm.^{3}	July 8	Nil	41	22	41	51	35
	15		34	20	28	23	31
	22		..	17	19	31	17
	29		..	37	..	60	111
	Aug. 4		..	72	..	..	..
Analysis of organisms		Nil	Flagellate "F" only	Flagellate "I" only	Flagellate, 70 % (under 2 μ common) Non-motile, 30 % 5 μ or less, 95 % Over 5 μ, 5 %	Flagellate, 48 % (under 2 μ common) Non-motile, 52 % 5 μ or less, 92 % Over 5 μ, 8 %	Flagellate, 63 % (35 % "I") Non-motile, 37 % 5 μ or less, 82 % Over 5 μ, 18 % (*Phaeocystis Poucheti* abundant July 29)
*p*H of water		8·06–8·20	8·05–8·19	8·08–8·24	8·07–8·20	8·08–8·22	8·05–8·38
Development of larvae		Age in days 5 180–195 μ 9 180–210 μ 18 180–210 μ 23 Degenerating	Age in days 5 180–210 μ 9 180–225 μ 18 180–240 μ 23 Degenerating	Age in days 5 180–220 μ 9 180–240 μ 18 180–260 μ 20 Young "eyed" stages present 23 "Eyed" stages present 24 65 spat 27 535 spat 33 901 spat	Age in days 5 180–210 μ 9 180–210 μ 18 180–225 μ 23 Degenerating	Age in days 5 180–210 μ 9 180–240 μ 18 180–260 μ 24 "Eyed" stages present 27 2 spat 33 6 spat	Age in days 5 180–215 μ 9 180–270 μ 13 Young "eyed" stages present 16 "Eyed" stages present 17 400 spat 18 1597 spat (50 % "eyed" larvae) 23 11,335 spat 31 15,689 spat
Final condition of larvae		(No growth) 180–210 μ Settled as spat, Nil	180–210 μ, 44 % 210–225 μ, 48 % 225–240 μ, 8 % Settled as spat, Nil	180–225 μ, 49·7 % 225–255 μ, 34·0 % "Eyed" larvae, 11·0 % Settled as spat, 5·3 %	180–195 μ, 26 % 195–210 μ, 30 % 210–225 μ, 44 % Settled as spat, Nil	180–225 μ, 47·07 % 225–255 μ, 40·00 % "Eyed" stages, 12·00 % Settled as spat, 0·03 %	180–225 μ, 6 % 225–255 μ 5 % "Eyed" stages, 8 % Settled as spat, 81 %

TABLE V. GROUP III. JULY 4–AUGUST 9 1938. DUPLICATE OF GROUP II, USING LARVAE FROM ANOTHER PARENT

Conditions of Experiment. Larvae liberated on July 3 into Hatchery tray by "Port Erin" oyster (2 years old). Size of larvae, 150–165 μ, 4 %; 165–180 μ, 38 %; 180–195 μ, 54 %; 195–210 μ, 4 %. Jars were A., P. and D.-F.

		F.O.S.				U.O.S.	
		Drip-fed with F.O.S.			Drip-fed with U.O.S.	Drip-fed with U.O.S.	
Position of jar in C.H.		11	12	15	14	13	16
No. of larvae in jar		2000	3300	3498	2296	3306	1824
Food supply		Nil	Flagellate "F"	Flagellate "I"	Micro-organisms in U.O.S. alone	Micro-organisms in U.O.S. alone	Micro-organisms in U.O.S. plus Flagellate "I"
No. of micro-organisms per mm.³	July 13	Nil	72	59	47	83	68
	21		37	24	41	20	31
	Aug. 3		35	..	..	17	..
	5		..	41	22	..	27
Analysis of organisms		..	July 13 and 21 Flagellate "F" only Aug. 3 Flagellate "F", 75 % Green Flagellate 25 % (15 μ)	Flagellate "I" only	Flagellates, 53 % (under 2 μ common) Non-motile, 47 % 5 μ or less, 89 % Over 5 μ, 11 %	Flagellates, 60 % (under 2 μ very common) Non-motile, 40 % 5 μ or less, 89 % Over 5 μ, 11 %	Flagellates, 60 % (40 % "I") Non-motile, 40 % 5 μ or less, 90 % Over 5 μ, 10 %
*p*H of water		8·13–8·22	8·12–8·20	8·12–8·23	8·12–8·20	8·12–8·20	8·12–8·22
Development of larvae		Age in days 10 180–195 μ, 33 % 195–210 μ, 67 % 23 Majority dead	Age in days 10 180–195 μ, 25 % 195–210 μ, 70 % 210–225 μ, 5 % 27 195–275 μ 32 "Eyed" larvae present 37 47 spat	Age in days 10 210–225 μ, 35 % 225–240 μ, 40 % 240–255 μ, 25 % 19 "Eyed" larvae present 23 371 spat 27 1980 spat 32 2766 spat 36 3178 spat	Age in days 10 195–210 μ, 15 % 210–225 μ, 75 % 225–240 μ, 10 % 19 "Eyed" larvae present 23 4 spat 27 67 spat 32 191 spat 37 296 spat	Age in days 10 195–210 μ, 25 % 210–225 μ, 75 % 27 195–270 μ 32 "Eyed" larvae present 37 6 spat	Age in days 10 210–225 μ, 35 % 225–240 μ, 40 % 240–255 μ, 20 % 255–270 μ, 5 % 19 "Eyed" larvae present 23 142 spat 27 818 spat 32 1463 spat 36 1587 spat
Final condition of larvae		(No growth) 180–210 μ Settled as spat, Nil	195–225 μ, 27·0 % 225–255 μ, 59·5 % "Eyed" stages, 12·0 % Settled as spat, 1·5 %	195–225 μ, 2 % 225–255 μ, 1 % "Eyed" stages, 6 % Settled as spat, 91 %	195–225 μ, 32 % 225–255 μ, 43 % "Eyed" stages, 12 % Settled as spat, 13 %	195–225 μ, 50·0 % 225–255 μ, 49·8 % Settled as spat, 0·2 %	195–225 μ, 2·5 % 225–255 μ, 8·74 % "Eyed" stages, 1·75 % Settled as spat, 87·01 %

TABLE VI. GROUP IV. JULY 6–16 1938. TO ASCERTAIN THE EFFECT OF CULTURE SOLUTION ("ERDSCHREIBER") *PER SE* ON DEVELOPING LARVAE

Conditions of Experiment. Larvae liberated in Hatchery tray on July 6 from "Yealm" oyster. Size of larvae, 165–180 μ, 8 %; 180–195 μ, 88 %; 195–210 μ, 4 %. Jars A. and P. (except 17), D.-F. 10,000 larvae in each jar.

	F.O.S., D.-F. with F.O.S.	U.O.S., D.-F. with U.O.S.	
Position of jar in C.H.	2	4	17
Food supply	Nil, 150 c.c. "Erdschreiber" added daily	Micro-organisms in U.O.S.; 150 c.c. "Erdschreiber" added daily	Micro-organisms in U.O.S.; 150 c.c. "Erdschreiber" added daily plus Flagellate "F"
*p*H of jars	8·12–8·20	8·13–8·24	8·11–8·23
No. of micro-organisms per mm.^{3} July 15	Nil	28	82
Analysis of organisms	..	Flagellate, 72 % (under 2 μ very common) Non-motile, 28 % 5 μ or less, 97 % Over 5 μ, 3 %	Flagellate, 60 % (mostly under 2 μ) Non-motile, 40 % 5 μ or less, 85 % Over 5 μ, 15 %
Final condition of larvae	Growth nil, still alive, normal in appearance, pale in colour	Some growth; normal in shape and colour	Some growth; normal in shape and colour

Table VII. Group V. July 12–August 3 1938. To estimate the Value of Flagellate "I" as Food for Developing Larvae

Conditions of Experiment. Larvae liberated July 12 into Hatchery tray by "Port Erin" oyster (3 years old). Size of larvae: 180–195 μ, 64 %; 195–210 μ, 36 %. Jars air-stirred and water changed by siphon.

	F.O.S.	U.O.S.	
Position of jar in C.H.	19	18	20
No. of larvae in jar	12,240	9853	10,000
Food supply	Flagellate "I"	Micro-organisms in U.O.S. plus Flagellate "I"	Micro-organisms in U.O.S.
No. of micro-organisms per mm.^{3}	July 19 60 28 34	54 65	21 21
Analysis of organisms	Flagellate "I" only	Flagellate, 70 % ("I", 60 %) Non-motile, 30 % 5 μ or less, 95 % Over 5 μ, 5 %	Flagellate, 51 % (under 2 μ abundant) Non-motile, 49 % 5 μ or less, 98 % Over 5 μ, 2 %
*p*H of water	8·19–8·30	8·18–8·26	8·18–8·25
Development of larvae	Age in days 6 240–260 μ 8 "Eyed" larvae present 9 1 spat 10 22 spat 13 10,667 spat 15 11,316 spat 17 11,778 spat 21 12,104 spat	Age in days 6 240–255 μ 8 "Eyed" larvae present 9 1 spat 10 31 spat 13 4415 spat 15 5287 spat 17 6148 spat 22 8302 spat	Age in days 6 180–210 μ 13 180–225 μ 15 180–270 μ 17 "Eyed" larvae present 22 Larvae degenerating
Final condition of larvae	180–225 μ, 0·1 % 225–255 μ, 0·1 % "Eyed" stages, 0·8 % Settled as spat, 99·0 %	240–255 μ, 5·7 % "Eyed" stages, 10·0 % Settled as spat, 84·3 %	180–195 μ, 5 % 195–225 μ, 93 % "Eyed" stages, 2 % Settled as spat, Nil

TABLE VIII. GROUP VI. JULY 27–SEPTEMBER 9 1938. TO ASCERTAIN THE RELATIVE VALUES OF FLAGELLATES "B", "C", "H" AND "I" AS FOOD FOR DEVELOPING LARVAE

Conditions of Experiment. Larvae liberated in Hatchery tray on July 27 from "Yealm" oyster. Size of larvae: 165–180 μ, 8 %; 180–195 μ, 64 %; 195–210 μ, 28 %. All jars filled with F.O.S.; and A., P. and D.-F. with F.O.S.

Position in C.H.	2	5	6	3	11
No. of larvae in jar	15,389	10,079	17,107 (but 11,704 transferred to jar 3 on Aug. 24)	11,704 (transferred from jar 6 on Aug. 24)	11,105
Food supply	Flagellate "B"	Flagellate "I"	Flagellate "H"	Flagellates "H" + "I"	Flagellate "C"
No. of micro-organisms per mm.^{3}	Aug. 1 19 12 37 22 44	19 24 31	30 30 42	(Aug. 28) 47	14 33 45
Analysis of organisms	Flagellate "B" only	Flagellate "I" only	Flagellate "H" only	Flagellate "H", 34 % Flagellate "I" 66 %	Flagellate "C" only
*p*H of water	8·20–8·25	8·18–8·25	8·13–8·24	8·20–8·22	8·18–8·22
Development of larvae	Age in days 7 210–255 μ 9 210–270 μ 12 "Eyed" larvae present, 285 μ 14 "Eyed" larvae present, 300 μ 16 2 spat 20 972 spat 24 2391 spat 28 4683 spat 30 5023 spat 33 7529 spat	Age in days 7 195–255 μ 9 195–270 μ 12 195–270 μ 14 "Eyed" larvae present, 285 μ 17 3 spat 20 159 spat 24 384 spat 27 392 spat	Age in days 7 195–240 μ 9 195–255 μ 17 195–270 μ 23 "Eyed" larvae present, 285 μ 28 Two-thirds of larvae removed to jar 3 30 60 spat 35 1157 spat 40 4103 spat	Age in days (Transferred from jar 6) 28 225–285 μ (mostly "eyed") 30 No spat 31 151 spat 34 5025 spat 35 5085 spat 38 7124 spat 45 11,151 spat	Age in days 7 210–255 μ 12 210–270 μ 17 "Eyed" larvae present, 285 μ 20 60 spat 24 941 spat 26 990 spat 27 994 spat
Final condition of larvae	210–225 μ, 2 % 225–255 μ, 15 % "Eyed" stages, 34 % Settled as spat, 49 %	195–225 μ, 37 % 225–255 μ, 23 % "Eyed" stages, 34 % Settled as spat 6 %	195–225 μ, 1 % 225–255 μ, 6 % "Eyed" stages, 17 % Settled as spat, 76 %	225–255 μ, 1·5 % "Eyed" stages, 3·2 % Settled as spat, 95·3 %	210–225, 10·5 % 225–255 μ, 25·0 % "Eyed" stages, 53·5 % Settled as spat, 11·0 %

TABLE IX. GROUP VII. AUGUST 1–SEPTEMBER 6 1938. TO ASCERTAIN THE RELATIVE VALUES OF DIFFERENTLY COLOURED FLAGELLATES AS FOOD FOR DEVELOPING LARVAE

Conditions of Experiment. Larvae liberated in Hatchery tray, July 30 from "Lochryan" oyster. Size of larvae: 180–195 μ, 76 %; 195–210 μ, 24 %. All jars filled with F.O.S.; A., P. and D.-F. with F.O.S.

Position of jar in C.H.	1	3	4
No. of larvae in jar	11,107	11,000	11,000
Food supply	Flagellate "D"	Flagellate "I"	Flagellate "H"
*p*H of water	8·20–8·24	8·18–8·24	8·14–8·22
Development of larvae	Age in days 4 180–210 μ 14 195–240 μ 20 195–255 μ (many dead) 32 Few "eyed" larvae present 38 7 spat	Age in days 4 180–210 μ 14 195–245 μ (many dead) 17 Degenerating 20 Degenerating or dead	Age in days 4 180–210 μ 14 195–240 μ 20 195–270 μ (many dead) 24 Few "eyed" larvae present 28 Degenerating or dead
Final condition of larvae*	195–225 μ, 39·94 % 225–255 μ, 32·00 % "Eyed" stages, 28·00 % Settled as spat, 0·06 %	200–245 μ, 100 % Settled as spat, Nil	195–225 μ, 48 % 225–255 μ, 40 % "Eyed" stages, 12 % Settled as spat, Nil

* Lack of success almost certainly due to sub-normal larvae; majority showed little activity and died off at early stage.

Table X. Group VIII. August 4–September 6 1938. To confirm Results of Group V

Conditions of Experiment. Larvae liberated in Hatchery tray on August 4, from "Yealm" oyster. Size of larvae: 165–180 μ, 8 %; 180–195 μ, 77%; 195–210 μ, 15 %. Jars air-stirred and water changed by siphon.

	U.O.S.	F.O.S.	
Position in C.H.	19	18	20
No. of larvae in jar	13,500	13,500	13,578
Food supply	Micro-organisms in U.O.S. plus Flagellate "I"	Flagellate "I"	Flagellate "I"
No. of micro-organisms per mm.^{3} on Aug. 18	52	23	41
Analysis of organisms	Flagellate, 80 % (62 % "I") Non-motile, 20 % 5 μ or less, 98 % Over 5 μ, 2 %	Flagellate "I" only	Flagellate "I" only
*p*H of water	8·23–8·25	8·22–8·26	8·22–8·24
Development of larvae*	Age in days 6 195–220 μ (abnormal) 14 Deformed 18 Majority dead	Age in days 6 210–225 μ (abnormal) 11 "Eyed" larvae present, 225 μ With foot, 232 μ 14 20 spat 18 215 spat 22 341 spat 27 485 spat 33 698 spat	Age in days 6 195–225 μ (abnormal) 11 "Eyed" larvae present, 225 μ 15 7 spat 18 117 spat 22 690 spat 27 801 spat
Final condition of larvae	195–225 μ, 96 % 225–240 μ, 4 % Settled as spat, Nil	195–225 μ, 64 % "Eyed" stages, 31 % Settled as spat, 5 %	195–225 μ, 71 % "Eyed" stages, 18 % Settled as spat, 11 %

* After a few days larvae showed signs of shell irregularity. The edge of the shell appeared to have grown inwards, constricting and deforming the velum. The "eyed" stage was recorded at 225–250 μ.

TABLE XI. GROUP IX. AUGUST 8–29 1938. TO ASCERTAIN THE RELATIVE VALUES OF FLAGELLATES "B" AND "I" AS FOOD FOR DEVELOPING LARVAE

Conditions of Experiment. Larvae liberated in Hatchery tray on August 6, from "Port Erin" oyster (3 years old). Size of larvae: 180–195 μ, 53%; 195–210 μ, 47%, and from "Yealm" oyster August 7. Size of larvae: 180–195 μ, 44%; 195–210 μ, 56%. All jars filled with F.O.S. A. and P., D.-F. with F.O.S.

Position in C.H.	7	8	9	10
No. of larvae in jar	9000	9000	11,877	8699
Source of parent	Port Erin	Yealm	Port Erin	Yealm
Food supply	Flagellate "B"	Flagellate "B"	Flagellate "I"	Flagellate "I"
No. of micro-organisms per mm.^{3}	Aug. 16 59 22 29	45 31	22 31	111 61
Analysis of organisms	Flagellate "B" only	Flagellate "B" only	Flagellate "I" only	Flagellate "I" only
*p*H of water	8·18–8·21	8·18–8·21	8·16–8·21	8·22–8·24
Development of larvae	Age in days 4 195–210 μ 9 195–240 μ 11 195–260 μ 13 195–270 μ 17 Degenerating 23 Majority dead	Age in days 3 195–210 μ 8 195–230 μ 10 195–270 μ 12 195–270 μ 17 Degenerating 22 Majority dead	Age in days 4 195–210 μ 9 225–255 μ 11 "Eyed" larvae present, 285 μ 13 9 spat 15 3458 spat 16 6495 spat 17 8418 spat 18 9621 spat 21 10,536 spat 23 11,051 spat	Age in days 3 195–210 μ 8 195–255 μ 10 "Eyed" larvae present, 300 μ 11 6 spat 12 120 spat 14 558 spat 17 859 spat
Final condition of larvae	195–225 μ, 52% 225–255 μ, 44% 255–270 μ, 4% Settled as spat, Nil	195–225 μ, 36% 225–255 μ, 44% 255–270 μ, 20% Settled as spat, Nil	225–255 μ, 2·32% "Eyed" stages, 4·64% Settled as spat, 93·04%	210–225 μ, 10% 225–255 μ, 40% "Eyed" stages, 40% Settled as spat, 10%

TABLE XII. GROUP X. AUGUST 8–12 1938. TO DEMONSTRATE THE RATE OF INGESTION OF FLAGELLATES BY DEVELOPING LARVAE

Conditions of Experiment. Larvae liberated in Hatchery tray, August 7, by "Yealm" oyster. Size of larvae: 180–195 μ, 44%; 195–210 μ, 56%. Jars filled with F.O.S. A., P. No change of water.

Position of jar		15	16
No. of larvae in jar		Nil	10,000
Food supply		Flagellate "I" added to give 78 per mm.^{3} at beginning of experiment	Flagellate "I" added to give 76 per mm.^{3} at beginning of experiment
No. of micro-organisms per mm.^{3}	Aug. 8	78	76 (larvae added)
	9	75	56
	10	76	52
	11	65	32
	12	72	15
*p*H of water		8·20 (constant)	8·20–8·23

Comment. Jars 15 and 16 received equal illumination as measured by photometer. The decrease of Flagellates in 16 amounts to 24,000 organisms per larva per day.

TABLE XIII. GROUP XI. AUGUST 9–19 1938. TO REPEAT PREVIOUS GROUPS USING FLAGELLATE "I"

Conditions of Experiment. Larvae used were liberated on August 9 into Hatchery tray by Port Erin oyster (4 years old). Size of larvae: 180–195 μ, 96%; 195–210 μ, 4%. Number of larvae per jar, 10,000. All jars were supplied with F.O.S., A., P. and D.-F. with F.O.S.

Position of jar	12	13	14
*p*H of water	8·19–8·22	8·21–8·22	8·21–8·22
Food supply	Nil	Flagellate "I"	Flagellate "I"
No of micro-organisms per mm.^{3} on Aug. 17	Nil	27	20
Development of larvae Age in days			
6	180–210 μ	195–225 μ	195–225 μ
8	180–210 μ	Majority degenerating	Majority degenerating
10	Degenerating	Velum abnormal	Velum abnormal
*Final condition of larvae	180–210 μ, 100% Settled as spat, Nil	195–225 μ, 100% Settled as spat, Nil	195–225 μ, 100% Settled as spat, Nil

* Lack of success almost certainly due to sub-normal larvae.

TABLE XIV. GROUP XII. AUGUST 29–SEPTEMBER 26 1938. TO REPEAT GROUP XI WITH LARVAE LIBERATED LATE IN THE SEASON

Conditions of Experiment. Larvae liberated in Hatchery tray, August 27, by "Blackwater" oyster. Size of larvae: 165–180 μ, 4%; 180–195 μ, 92 %; 195–210 μ, 4 %. Jars filled with F.O.S. A., P., D.-F. with F.O.S. Supplied with Flagellate "I".

Position of jar	7	9	10
No. of larvae in jar	13,400	24,000	3400
No. of micro-organisms per $mm.^3$	Sept. 5 35 11 31 15 28	30 21 15	40 45 41
Analysis of organisms	Flagellate "I" only	Flagellate "I" only	Flagellate "I" only
*p*H of water	8·10–8·25	8·10–8·25	8·20–8·25
Development of larvae	Age in days 12 180–225 μ 16 180–230 μ 18 180–255 μ 23 "Eyed" larvae present 24 A few spat 30 522 spat	Age in days 12 180–225 μ 16 180–260 μ 18 180–270 μ "Eyed" larvae, 260 μ With foot, 270 μ 21 A few spat 23 Over 100 spat 24 277 spat 30 1192 spat	Age in days 12 180–225 μ 16 180–240 μ 23 "Eyed" larvae present, 24 A few spat 30 484 spat
Final condition of larvae	180–225 μ, 35 % 225–255 μ, 23 % "Eyed" stages, 38 % Settled as spat, 4 %	180–225 μ, 46 % 225–255 μ, 38 % "Eyed" stages, 11 % Settled as spat, 5 %	180–225 μ, 20·9 % 225–255 μ, 56·8 % "Eyed" stages, 8·0 % Settled as spat, 14·3 %

TABLE XV. SYNOPTIC TABLE OF LABORATORY EXPERIMENTS (EXCLUDING GROUPS IV AND X) 1938

Group and date	Position of jar	Source of parent	Date of liberation	Size range of larvae	Water supply*	Food supply	Growth of larvae	Settlement %
I June 25–July 27	1	Lochryan	June 25	165–195 μ	U.O.S.	Micro-organisms in sea water	Fair	6·8
	2	Yealm	23	180–210 μ	F.O.S.	Flagellate "D"	None	Nil
	3	Yealm	23	180–210 μ	U.O.S.	Micro-organisms in sea water	Fairly good	35·8
	4	Lochryan	25	165–195 μ	F.O.S.	Flagellate "D"	None	Nil
II July 2–Aug. 5	5	Yealm	July 2	180–210 μ	F.O.S.	Nil (control)	None	Nil
	6	Yealm	2	180–210 μ	F.O.S.	Flagellate "F"	Slight	Nil
	7	Yealm	2	180–210 μ	U.O.S.	Micro-organisms in sea water	Fair	0·03
	8	Yealm	2	180–210 μ	F.O.S. to U.O.S.	Micro-organisms in sea water	Slight	Nil
	9	Yealm	2	180–210 μ	F.O.S.	Flagellate "I"	Fair	5·3
	10	Yealm	2	180–210 μ	U.O.S.	Micro-organisms in sea water plus "I"	Very good	81·0
III July 4–Aug. 9	11	P.E. (2 yr. old)	July 3	150–210 μ	F.O.S.	Nil (control)	None	Nil
	12	P.E. (2 yr. old)	3	150–210 μ	F.O.S.	Flagellate "F"	Fair	1·5
	13	P.E. (2 yr. old)	3	150–210 μ	U.O.S.	Micro-organisms in sea water	Slight	0·2
	14	P.E. (2 yr. old)	3	150–210 μ	F.O.S. to U.O.S.	Micro-organisms in sea water	Fairly good	13·0
	15	P.E. (2 yr. old)	3	150–210 μ	F.O.S.	Flagellate "I"	Excellent	91·0
	16	P.E. (2 yr. old)	3	150–210 μ	U.O.S.	Micro-organisms in sea water plus "I"	Very good	87·01
V July 12–Aug. 3	18	P.E. (3 yr. old)	July 12	180–210 μ	U.O.S.	Micro-organisms in sea water plus "I"	Very good	84·3
	19	P.E. (3 yr. old)	12	180–210 μ	F.O.S.	Flagellate "I"	Excellent	99·0
	20	P.E. (3 yr. old)	12	180–210 μ	U.O.S.	Micro-organisms in sea water	Slight	Nil
VI July 27–Sept. 10	2	Yealm	July 27	165–210 μ	F.O.S.	Flagellate "B"	Good	49·0
	5	Yealm	27	165–210 μ	F.O.S.	Flagellate "I"	Fairly good	6·0
	6	Yealm	27	165–210 μ	F.O.S.	Flagellate "H"	Very good	76·0
	3	Yealm	27	225–285 μ	F.O.S.	Flagellates "H" and "I"	Excellent	95·3
	11	Yealm	27	165–210 μ	F.O.S.	Flagellate "C"	Very good	11·0
VII Aug. 1–Sept. 6	1	Lochryan	July 30	180–210 μ	F.O.S.	Flagellate "D"	Fair	0·06
	3	Lochryan	30	180–210 μ	F.O.S.	Flagellate "I"	Slight	Nil
	4	Lochryan	30	180–210 μ	F.O.S.	Flagellate "H"	Fair	Nil
VIII Aug. 4–Sept. 6	18	Yealm	Aug. 4	165–210 μ	F.O.S.	Flagellate "I"	Shell deformed	5·0
	19	Yealm	4	165–210 μ	U.O.S.	Micro-organisms in sea water plus "I"	Shell deformed	Nil
	20	Yealm	4	165–210 μ	F.O.S.	Flagellate "I"	Shell deformed	11·0
IX Aug. 8–Aug. 29	7	P.E. (3 yr. old)	Aug. 6	180–210 μ	F.O.S.	Flagellate "B"	Fair	Nil
	8	Yealm	7	180–210 μ	F.O.S.	Flagellate "B"	Fair	Nil
	9	P.E. (3 yr. old)	6	180–210 μ	F.O.S.	Flagellate "I"	Excellent	93·04
	10	Yealm	7	180–210 μ	F.O.S.	Flagellate "I"	Good	10·0
XI Aug. 9–Aug. 19	12	P.E. (4 yr. old)	Aug. 9	180–210 μ	F.O.S.	Nil (control)	None	Nil
	13	P.E. (4 yr. old)	9	180–210 μ	F.O.S.	Flagellate "I"	Very slight	Nil
	14	P.E. (4 yr. old)	9	180–210 μ	F.O.S.	Flagellate "I"	Very slight	Nil
XII Aug. 29–Sept. 26	7	Blackwater	Aug. 27	165–210 μ	F.O.S.	Flagellate "I"	Fairly good	4·0
	9	Blackwater	27	165–210 μ	F.O.S.	Flagellate "I"	Fair	5·0
	10	Blackwater	27	165–210 μ	F.O.S.	Flagellate "I"	Fair	14·3

Groups I and II carried out with larvae liberated in culture-house.
Groups III to XII carried out with larvae liberated in Hatchery trays.
Groups VII, VIII and XI, on account of abnormality of larvae, are disregarded in subsequent discussion.

* U.O.S. Unfiltered "outside" sea water; F.O.S. Filtered "outside" sea water.

REVIEW OF RESULTS

In the groups of experiments dealing with the growth of larvae, forty individual experiments were carried out; in nine of these, belonging to groups VII, VIII and XI, the larvae were found to be non-viable, or showed abnormalities at an early stage of the experiment. Since no reliable deductions could be made from the use of such larvae, these nine experiments have been excluded from general discussion.

Thirty-one experiments therefore come under review. Of these, two were controls in filtered sea water without added food. In twenty-two of the remaining twenty-nine, settlement of larvae was obtained, the average settlement being 39·5 %.

As the main object of these experiments was to test the food value of certain small flagellates, the greater number of culture vessels were supplied with filtered sea water to which flagellate cultures were added. Some of the experiments, however, were carried out with the use of unfiltered "outside" sea water with and without the addition of flagellates. Two experiments were also set up with filtered sea water which was subsequently changed to unfiltered sea water. A summary of results grouped according to water and food supply is given in Tables XVI and XVII.

TABLE XVI. DETAILS OF SETTLEMENT WITH VARIOUS TYPES OF FOOD SUPPLY IN BERKEFELD-FILTERED AND IN UNFILTERED "OUTSIDE" SEA WATER

Sea water ...	Filtered								Unfiltered	
	Flagellates							Unfiltered "outside" sea water added		
Food supply ...	"I"	"H"	"H" and "I"	"B"	"C"	"F"	"D"		None added	Flagel-late "I"
Percentage settlement	99·0	76·0	95·3	49·0	11·0	1·5	0·0	13·0	35·8	87·01
	93·04	..	..	0·0	..	0·0	0·0	0·0	6·8	84·3
	91·0	..	..	0·0	..	..	..	..	0·2	81·0
	14·0	..	..	..	..	..	..	..	0·03	..
	10·0	..	..	..	..	..	..	..	0·0	..
	6·0	..	..	..	..	..	..	..	..	..
	5·3	..	..	..	..	..	..	..	..	..
	5·0	..	..	..	..	..	..	..	..	..
	4·0	..	..	..	..	..	..	..	..	..

From the results obtained, the food value of the different flagellates can be roughly assessed as follows:

(i) Good to very good, "I" and "H".
(ii) Fair, "B" and "C".

The highest figures for percentage settlement (99 %, 91 %) were reached in experiments in which flagellates were added to filtered sea water, but the figures for parallel and comparable experiments in which flagellates were added to unfiltered sea water were not far behind (84 %, 87%). The number of such comparable pairs of experiments is probably too small to give valuable data, but, taking the average of their results, the percentage settlement is found to be 84 % in unfiltered and 65 % in filtered sea water, in each case with the addition of flagellate "I". The further fact emerges that both gave vastly superior results to comparable experiments in which "outside" unfiltered sea water, *without addition*, was used (0·03 %, 0·2 %).

TABLE XVII. COMPARISON OF SETTLEMENTS WITH VARIOUS TYPES OF FOOD SUPPLY

Sea water	Added food	No. of jars and result: Total	Settlement	No settlement	Average settlement in all jars %
F.O.S.	Nil	2	0	2	0
	"B"	3	1	2	16·3
	"C"	1	1	0	11·0
	"D"	2	0	2	0
	"F"	2	1	1	0·75
	"H"	1	1	0	76·0
	"I"	9	9	0	36·4
	"H" and "I"	1	1	0	95·3
	"Outside" sea water	2	1	1	6·5
U.O.S.	Nil	5	4	1	8·6
	"I"	3	3	0	84·1

One experiment was tried in 1938 using a mixed diet of flagellates "H" and "I" as food for the larvae, "I" being added when the larvae were well advanced. The 95·3 % settlement obtained suggests that the suitability of "mixed" as opposed to "pure" diet should be the subject of further investigation. It has been observed that in the majority of the experiments in which flagellate "I" has been used, settlement has proceeded almost to completion within twenty days, whereas in the two experiments in which flagellate "H" was used a comparable settlement occurred only after the lapse of thirty-five days.

Scrutiny of Table XVII shows inconsistency of result that demands consideration. After eliminating such differences of percentage settlement as may be associated with the factors of food materials and character of water supply, there still remains a number of discrepant results which cannot be satisfactorily explained by either of these factors.

Divergent results are seen in comparable experiments in which the only variable factor is that associated with the origin of the larvae. Broods of larvae differ in quality one from another and their viability is undoubtedly a factor of importance in experiment. It is not, however, always possible to assess the physiological state of the larvae by inspection at the liberation stage, although as soon as signs of deterioration make their appearance, an experiment can be discarded.

In other experiments variation in result appears to be associated with the position, in relation to illumination, of the bell-jars in the culture-house (see p. 351). Reviewing the entire experimental series, jars which gave settlements of over 80 % were those situated in the comparatively well-lighted positions at the ends of the benches, whereas a low average settlement coincided in the main with the positions of lower light intensity. Much remains to be done to disentangle so many coincident factors, but of the reality of the effect of these factors in larval culture there is now little doubt.

In 1938, as in earlier years, considerable variation was noted in the time-relations of larval settlement under which heading may be included not only the duration of larval life prior to settlement, but also the rate of settlement in its vigorous initial phase, and the total period over which spat-fall may be extended. These points are illustrated by Fig. 3, in which are embodied data from four representative experiments, all of which yielded a spat-fall exceeding 90% of the initial larval count.

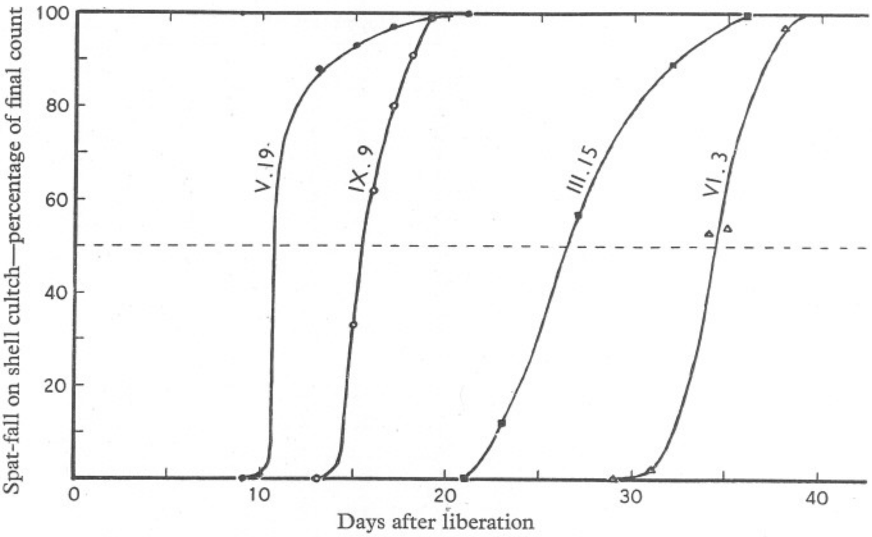

Fig. 3. Variations in the time-relations of larval settlement in four representative experiments. (Numbers on curves indicate group and position.)

In the figure, the progress of spat-fall (expressed as a growing percentage of the final spat-fall realized) is plotted against time, in "days after liberation". The four curves shown are similar in general form, and indicate that spat-fall has an initial phase of greater or less rapidity, followed by a "tailing-off", as maximum spat-fall (whatever its absolute value) is approached. Apart, however, from general similarity of type, the spat-fall curves show a wide range of variation. It will be seen that (*a*) the onset of substantial settlement (say 10 % of the final settlement realized) may occur at any time within

11–33 days after liberation, and (*b*) the rate of settlement, as indicated by the slope of the curve, over the first 50%, may vary as 1 to 3.

Settlements exceeding 95% were realized at either end of the time-scale, and since all experiments were carried out at a temperature of 20°–22° C., the factor of temperature cannot, in this instance, be directly associated with the length of larval life before settlement.

As to the actual duration of larval life under the conditions of experiment in the culture-house, a minimum duration was observed in group V (jars 18 and 19), in which two larvae were found to have settled after 9 days, and the vast majority after 11–14 days. In other experiments 20–25 days elapsed before the greater part of the settlement was achieved, while in certain experiments of group VI, there was no considerable settlement until the 32nd day, and some larvae were still unmetamorphosed after 40 days. This appears to be an exceptional figure and due to special causes.

Of the total spat-fall in the experiments, 85% was on shells (chiefly *Pecten maximus*), 13% on glass surfaces (jars, plunger plates and aerator tubes), and 2% of the spat had metamorphosed without attachment. Out of the spat-fall occurring on shells, irrespective of whether the convex or concave surface of the valves was uppermost, 47% were found to be on the upper, i.e. the illuminated surface, and 53% on the lower shaded surface.

DISCUSSION

In order to understand fully the significance of the data provided by the series of investigations recorded above, it may be of advantage to compare some of the results obtained with the findings of other investigators who have made observation on the behaviour and growth of oyster larvae in relatively small volumes of water.

Kändler (1930), working in Heligoland, obtained a small settlement of spat in large vessels supplied with a continuous flow of sea water. It is assumed that small organisms present in the inflowing sea water served as food for the larvae. Erdmann (1933), using a technique devised by Hagmeier in 1932 in which minute organisms present in sea water were developed in pure culture by the Schreiber method and used as food by the larvae, reports successful settlement experiments. He speaks of 15,000 spat obtained in twelve vessels (Tongefässe). This work was carried out in a specially built culture-house.

It is also known that samples of *Ostrea edulis* sent over to America there produced larvae, a very large proportion of which developed and later settled as spat. The rich planktonic content of the natural sea water clearly supplied sufficient food material for the larvae.

Two lines of enquiry were thus indicated. The first relates to the maintenance of oyster larvae in sea water in which the natural plankton supplied the food material; and the second is concerned with experiments in which addition of cultures of organisms suitable as food material for larvae, is made to the sea water.

Despite the comparative paucity of settlement obtained in the earlier experiments cited, the fact that settlement occurred at all, showed that the conditions obtaining in vessels of small size are not wholly inimical to the culture of larvae. With refinement of technique, it has now been proved possible to conduct critical experiments on a laboratory scale, and so to control or vary the conditions as to afford a close analysis of the separate factors governing larval life.

The high rate of mortality among developing larvae, which has been the experience of many workers in the field, may be considered to be attributable to two sets of factors which are inseparably associated with the fact of isolation of any small body of water. These factor-groups may be described as "biological" and "biophysical"—the one concerns the presence or absence of the appropriate food material, and the conditions leading to the further production of that material; the other involves the delicate physical balance, or dissociation-equilibrium, upon which the continued usefulness of sea water as a medium for growth and development so greatly depends. Experimentally, it is relatively easy to control the grosser physical conditions such as temperature and illumination, and even to observe their effects, and a considerable body of knowledge has been accumulated by ourselves, and by other workers in the field, upon which we were able to draw when making plans for the culture-house in 1935. This culture-house provided, as nearly as resources would permit, an optimal environment for that more intimate enquiry into food requirements and the character of water supply which we have indicated.

Taking first the latter problem, the obvious approach to the question lies in avoiding, so far as possible, any procedure, such as storage, undue illumination, or chemical addition, which is likely to promote or increase disturbance of internal equilibrium. To a certain extent this has been achieved by the use of sea water collected well outside the limits of littoral influence, transporting it as rapidly as possible to the culture-house, and using it (by way of a drip-feed system) in such a way as to minimize the period of its sojourn in any experimental vessel. Experiments on these lines (other factors, of course, being suitable) have yielded a high degree of success, but the authors do not on that account claim that "outside" sea water is the only appropriate medium for larval cultivation. Continued growth and settlement of larvae has been realized at Port Erin, Conway and elsewhere, under conditions far removed from those associated with open waters. In such experiments, it is our belief that the large volumes of the enclosures concerned, or special experimental safeguards if on the laboratory scale, have contributed to the maintenance of the essential biotic and physical equilibrium, and we are still convinced that, as a factor in the success of *experiments on the laboratory scale*, the use of natural water from the open sea, untreated otherwise than by filtration, is of paramount importance.

Turning to the biological aspect of the problem, from which it would appear that failure to settle might be due to insufficiency or unsuitability of food material, the line of experiment indicated was simply to add cultures of organisms to the sea water used in experiment. Using growth and percentage settlement as criteria of success, it could then be determined which organisms in culture, alone or in conjunction with others, provided the best food material for the larvae.

Perusal of the records of 1938 shows that the percentage settlement therein recorded for experiments in which certain flagellates have been used as food for the larvae, so greatly exceeds any previous record for similar experiments, that the conclusion is inescapable, that for these particular experiments the demand for suitable food supplies and a reasonably normal biophysical environment have been adequately satisfied. In this connexion, attention may be drawn to the results of an experiment recorded in Table VII in which 12,104 spat were obtained from 12,240 larvae originally introduced into one bell-jar.

The feasibility of rearing oyster larvae by artificial feeding has now been definitely established and this field of enquiry is open to further exploration. Up to the present, six separate flagellate organisms have been tested as food material for larvae. One of the most interesting facts that has emerged most clearly from the results already obtained, is that the six organisms differ markedly in their usefulness. The settlement-ratio is from 0·06 to 99 %. The six organisms may be grouped in pairs, giving respectively good, medium and poor results, but with all of them some settlement was obtained.

The question naturally offering itself for solution is the reason why, other factors being equal or as nearly equal as experimental conditions permit, the values of these flagellates as food for larvae should differ so markedly one from another.

In actual experiment, not one of the organisms, even those classed as good, gave uniform results, but the inconsistency shown is possibly due, in part at least, to the supervention of factors outside experimental control. One of the chief sources of trouble lies in the fact that larvae from different oysters are not equally viable (see groups V, VIII and XI, Tables VII, X and XIII). At the present stage of experiment there is no evidence that the length of larval life is affected by the point in time within the spawning period at which they are liberated.

Leaving aside, however, these imposed and uncontrollable factors, differences between the flagellates themselves were detectable and almost certainly played a discriminating part in their service as food for larvae. Among these differences size is undoubtedly important. All the flagellates used in the experiments lie below the limit of size at which ingestion is possible, but the six organisms cover a range of 1·5–7 μ and the question arises, which size of organism provides the best source of food material for the larvae. Equal numbers of organisms of different size do not constitute equivalent bulk, and, on general principles the larger organisms, provided they can be ingested, should supply the better food material for the larvae; but the matter is not quite so simple as that, since the flagellates differ from one another in motility. Under the microscope, they are distinguishable from one another by character as well as by rate of movement, and the ease with which they can be taken in by the larvae depends upon the effective sweeping action of the ciliary feeding mechanism relative to the bulk and movement of the food organism. It is probable, but this is a point for future investigation, that the organisms which are most readily taken in are not those of maximum ingestible size.

The greatest difference which these organisms show among themselves is that of colour. From the point of view of the larvae this is probably of major importance. Flagellates "B", "C" and "I" are golden brown, but "I" is clearly distinguishable from the other two by a quality which is hard to define. Not necessarily deeper in tint, it has a "shining" quality that the others lack. "D" is very definitely pinkish red; its colour is very deep and unmistakable in cultures of advanced development, but it forms a somewhat turbid fluid giving the appearance of a "shot" effect of grey and red. "H" is a green with a strong yellow cast, and "F" is yellow with a tinge of green.

Amongst algae in general a correlation between the colouring matter of the chromoplast and the nature of the food material stored has been clearly established. Among smaller forms both characters play their part in the problem of classification. It appears probable that the varying usefulness exhibited by these differently coloured organisms, depends directly upon the degree to which the included algal food reserves, glycogen, oil, etc. serve the immediate needs of the developing larvae. In support of this view it may be mentioned that certain preliminary histological enquiry into food reserves of the larvae themselves, demonstrated the presence of oil globules in all stages of normal larvae from the white-sick stage to the well-developed "eyed" stage. The globules were confined mainly to the epithelial cells of the alimentary tract but they do also occur in other tissues. Similar tests for glycogen gave negative results. The desirability of further research in this field is clearly indicated.

SUMMARY

The work described in this paper is a contribution to the general problems of rearing the larvae, and growing the spat of the European flat oyster, *Ostrea edulis* L.

The specific aspect of the problem dealt with in detail is the place taken by minute motile organisms (naked dinoflagellates and other unicellular algae) in the food requirements of the developing veliger larvae.

Six such flagellate organisms, ranging in size from $1\cdot5$ to $7\,\mu$ in diameter, have been isolated from sea water, and are maintained in pure culture, under conditions described. Pending specific identification, these are denoted by

letter-labels only. These organisms have been used, over a period of years, in feeding experiments with oyster larvae.

The experimental work has taken place on a laboratory scale, on which scale pure culture technique and rigorous control of conditions are alone possible.

An essential preliminary to valid feeding experiments has been the stabilization of the biophysical environment (including water conditions) at an optimum level. This has involved the construction of a culture-house, with full experimental control, the details of which are described. The use of uncontaminated sea water, collected well off-shore, is strongly advocated for small-scale experiments of this character. A temperature range of 20°–22° C., an avoidance of considerable or sudden *p*H change, screening from direct sunlight, plunger stirring and/or aeration by bubbling and slow water change, are all contributory factors on the physical side.

Given good environmental conditions, much yet depends on the inherent viability of the liberated larvae. Larvae liberated in small vessels at temperatures as low as 13°–15° C., have proved to be quite as viable as those produced at 20°–21° C., in large or semi-natural enclosures at Port Erin and elsewhere.

Feeding experiments, extending in all over five seasons, have demonstrated the special suitability of several of the flagellates, held in pure culture, and given either separately or mixed, to serve as food capable of maintaining the growth of larval oysters from liberation stage up to and including settlement. The most successful of these (denoted "H" and "I") are of a greenish yellow or golden brown colour, and measure 3–6 μ in diameter.

In the most successful experiments, the number of larvae carried through from liberation to settlement, under appropriate physical conditions, and with a diet of the organisms "H" and "I", or both together, exceeds 90 %, in one case 99 %, of the number introduced into the experimental vessel, and indicates the measure of success on the experimental scale.

An appreciation of the major physical factors, and of the feeding problems associated with larval development on the laboratory scale has now been attained. The inherent quality of "viability" and certain responses as yet obscure still demand investigation. When this is done, a sound experimental basis should be available for an attack on the ultimate problem of the consistent production of oyster larvae and spat on a commercial scale.

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THE DEVELOPMENT OF ISOLATED RESTING SPORES INTO AUXOSPORES IN *DITYLUM BRIGHTWELLI* (WEST.)

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(Text-figs. 1–2)

The resting spores of *Ditylum* are formed as a result of a peculiar kind of plasmolysis of the protoplast (Gross, 1939); they are small spherical bodies lying inside the old cell wall. Since one-half of the cell wall is only slipped over the other half it is likely that in the sea they might become separated and the resting spore proper would drop out of the shell. In a previous paper (Gross, 1937) it was stated that in old cultures a considerable number of resting spores could be found outside the parental shells, and when transferred into fresh culture medium they only expanded in volume. Since then more attention has been paid to such isolated resting spores and the formation of new cell walls has been frequently observed.

In order to obtain sufficient material resting spores formed in crowded cultures under laboratory conditions were removed from the shells. This was done under a low-power binocular with the aid of micro-glass needles, the points of which were bent at 90 degrees. The bent end of the glass needle was pressed against the shell perpendicularly to the long axis a short distance from the centre. One-half of the shell usually gave way and fell aside and the resting spore, if situated in the centre of the cell, dropped out. If it was lying excentrically it could be "squeezed out" by slight pressure with the needle or by slight agitation with a pipette.

When placed in fresh culture medium the isolated resting spore (Fig. 1*a*) started germinating. The process is essentially the same as that occurring inside the shell, but, owing to its absence, the germinating resting spore has a very unusual appearance. At first a varying number of very fine protoplasmic processes are sent out in all directions (Fig. 1*b*) lending the spore a superficial resemblance to a Heliozoan. These processes when formed inside the parental shell connect the resting spore with the cell walls. This stage was reached by most cells in about 1–3 hr. Then the cell flattened down and the protoplasmic processes became more conspicuous. Chromatophores passed along these processes and the protoplast gradually expanded (Fig. 1*c*). New "pseudopodia" and branches of the old ones were formed and others absorbed, the cells showing a striking resemblance to certain amoebae. In the course of one to two days the cell body became bigger and the "pseudopodia" correspondingly shorter until the cell assumed a spherical shape again (Fig. 1*d*). Of several hundreds of resting spores kept under close observation not a single one developed into the bigger spherical body by simple expansion; all passed through the "amoeboid" stage.

As regards their structure these spherical bodies resembled auxospores (Gross, 1937) in every respect. But they very often adhered to the bottom of the watch glass and in most instances only developed when they were gently detached from the glass. (This was done by directing a current of water from a pipette towards them.) Once they were freed they developed in the same way as auxospores. The cell elongated and became more cylindrical and in about 24 hr. one valve was formed (Fig. 1*e*) and in another day the second. After that the cell started dividing (Fig. 1*f*).

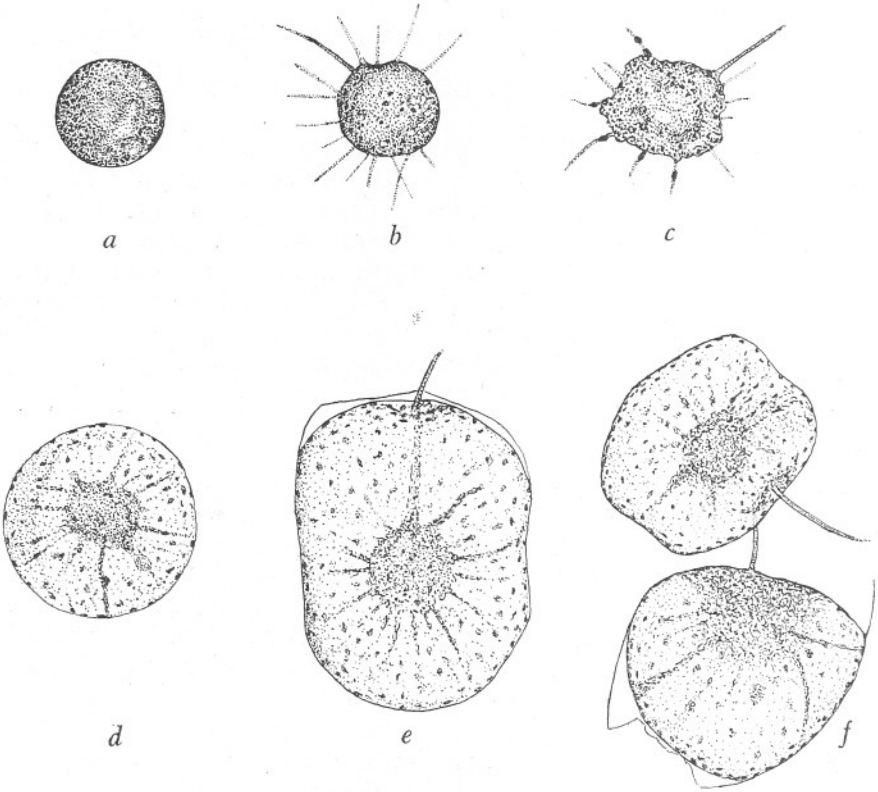

Fig. 1. *a–f* were traced from photographs; *a*, resting spore separated from the shell on May 3, 12.45 p.m., photographed at 2.45 p.m.; *b–f*, stages of germination of the same resting spore; *b*, photographed at 6 p.m.; *c*, on May 6; *d*, on May 7; *e*, on May 10; *f*, on May 11.

The result of this kind of development is that the cell derived from the isolated resting spore and its progeny always possess a very large diameter.

An isolated resting spore regularly passes through the auxospore stage during development. Whatever the diameter of the cells may be that have formed the resting spores, these always develop into very broad cells of a diameter of 80–100μ. In one instance the average diameter of twenty-five cells that had undergone resting spore formation (*a*) was 41·3μ. One resting spore from this sample was isolated and the average diameter of twenty-five cells developed from it was 103·4μ (*b*); that of twenty-five cells developed from auxospores in the same culture 85·0μ (*c*). The cells of *a* varied in diameter from 39·5 to 44μ; those of *b* from 88·5 to 109μ. Both *a* and *b* originated from one cell each. The twenty-five (*c*) cells were taken from a colony of broad cells produced in the same culture as *a*. The colony had probably originated from several auxospores, and the cells showed a wider variation in diameter, viz. from 70 to 127·5μ.

In this experiment the diameter of the cells which originated from the isolated resting spore was more than twice that of the parental cell. When resting spores of narrower cells were isolated the difference was larger still.

"Artificial" resting spores (Gross, 1939) induced by the action of 3·3% sodium chloride solution developed in a very similar manner when isolated from the shell and placed in culture medium. Fig. 2*a* shows one such resting spore inside the shell and Fig. 2*b–f* are typical stages of its development after isolation. This particular cell was slightly injured when being removed from the cavity slide after the drawing of Fig. 2*e*. The second valve did not develop for some days and the subsequent division was abnormal. In other experiments most of the cells developed quite normally and gave rise to large cell colonies. Like the natural resting spores the isolated "artificial" resting spores tended to adhere to the glass in the auxospore stage, and the "auxospores" had to be detached before further development could take place.

In one instance twelve "artificial" resting spores were isolated from the cell walls. The parental cells measured from 30 to 42μ in diameter. Nine of them developed into auxospores and then into broad cells which gave rise to an actively growing culture After 20 days twenty-five cells were measured; their diameter varied from 70 to 95μ with an average of 80·1μ.

Vegetative cells gradually plasmolyse in the absence of light and the resulting resting spores only recover, or germinate, when exposed to light. It has been found previously that "artificial" resting spores, even when placed in the dark, are capable of a temporary partial recovery (Gross, 1939). Isolated "artificial" resting spores when kept dark may develop as far as the auxospore stage.

In one experiment a sample of *Ditylum* was transferred into a solution of 0·6M NaCl, to 100 ml. of which 5 ml. of $M/5$ Na_2HPO_4 was added and twenty of the resulting resting spores were isolated from the shells and placed in culture medium in a dark box. After 19 hr. one cell was amoeboid; the others had formed auxospores by then. However, most of them were remarkably small. All auxospores were gently detached from the glass. During the

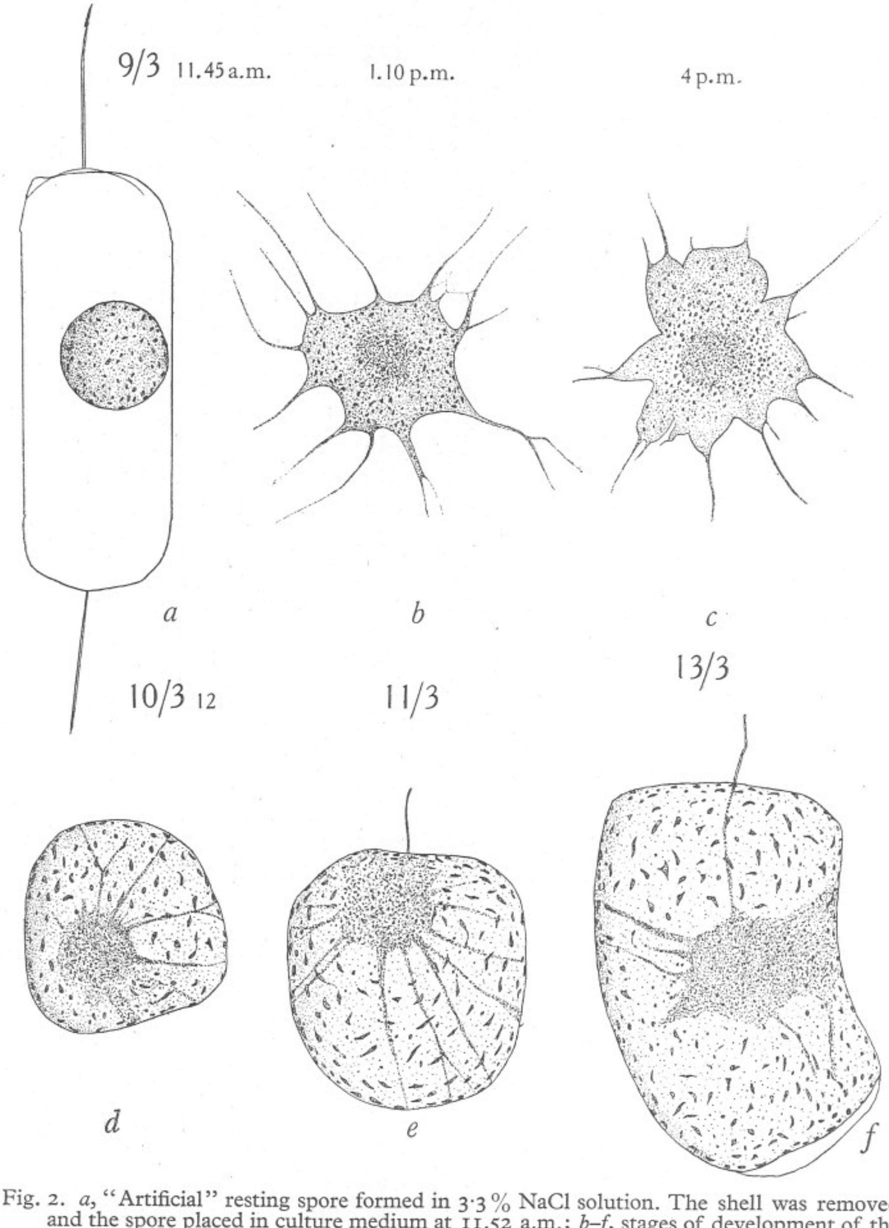

Fig. 2. *a*, "Artificial" resting spore formed in 3·3 % NaCl solution. The shell was removed and the spore placed in culture medium at 11.52 a.m.; *b–f*, stages of development of the same resting spore. × 400.

following 24 hr. no further development took place except that the one amoeboid cell had by then also formed an auxospore. The day after only one fair-sized and three small auxospores were present while all the others had become amoeboid again. Seven days later the amoeboid cells had only very short "pseudopodia" and there was only one auxospore left, which had the protoplast contracted inside the auxosporal membrane. The dish was then placed on the window bench in light. After five days there were six groups of six, thirteen, four, five, eight and twenty-one broad cells respectively. Thus at least six cells had recovered and started multiplying again.

This experiment shows that isolated "artificial" resting spores kept in the dark, behave similarly to those inside the parental shells. The small auxospores correspond to the short protoplasts forming a secondary valve (Gross, 1939). Complete recovery, involving the formation by the auxospore in the dark of a new shell, was never observed. That the majority of resting spores only developed into small auxospores is probably due to the necessity of expending energy for the maintenance of the cell turgor.

The gradual decrease in the cell diameter of a diatom population is normally counteracted by the formation of auxospores. This also takes place in *Ditylum* cultures whenever the cell diameter has decreased beyond a certain size (Gross, 1937). The above observations show that the formation of auxospores by the extrusion of the protoplast from narrow vegetative cells is not necessarily the only mode whereby the size of the diatom may be regulated. It seems very likely that in nature too a considerable proportion of resting spores become separated from the shells when sinking down to greater depths. Their subsequent germination would also lead to the formation of broad cells. The fact that isolated resting spores always develop first into auxospores and then into cells of about maximum diameter indicates that the size of a centric diatom is imposed upon the cell by the structure of its cell wall and the resulting peculiar mode of cell division. The protoplast as such is always capable of growing out into a broad specimen once it is liberated from its enclosing siliceous armour.

In the sea the period from one auxospore generation to another may last one year or, in some species, even two to five years (see Fritsch, 1935, p. 617). In cultures auxospore formation has been repeatedly found to take place only in diatoms whose diameter has decreased to a certain size. In *Ditylum* cultures auxospores only occur in populations of less than 45μ diameter. However, resting spores formed by cells of $50-70\mu$ diameter when liberated from their shells developed into cells of $90-110\mu$ diameter. Therefore, in studies concerned with changes in the size of diatoms from plankton samples of certain areas (Wimpenny, 1936; Garstang, 1937) the possibility will have to be taken into account that the appearance of broad cells may also be due to the germination of isolated resting spores.

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THE OSMOTIC RELATIONS OF THE PLANKTON DIATOM *DITYLUM BRIGHTWELLI* (WEST.)

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(Text-figs. 1–22)

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INTRODUCTION

The structure of *Ditylum Brightwelli* differs in several respects from that of ordinary plant cells. Most plant cells consist of a protoplasmic layer which surrounds a central vacuole containing the cell sap. Externally the protoplasm is enclosed by the cellulose cell wall. It is generally assumed that the protoplasmic layer is separated from the cell wall on one side and the vacuole on the other by plasma membranes. *Ditylum* is usually prism-shaped or cylindrical and, like all diatoms, possesses a siliceous wall consisting of two overlapping halves. Inside the cell wall lies the plasma membrane and in it are embedded numerous small spindle-, rod- or ellipsoid-shaped chromatophores. The protoplasm does not form a layer, but is concentrated around the nucleus in the centre of the cell and connected with the plasma membrane by a number of protoplasmic strands (Fig. 1*a*). The rest of the cell, i.e. the whole space between the central protoplasmic mass and the cell surface, except for the protoplasmic strands, is filled with cell sap.

That a very large proportion of the cell volume is made up by the cell sap can be demonstrated by the following experiment. If gentle pressure is applied to *Ditylum* by means of a bent micro-needle the protoplast shrinks rapidly inside the shell assuming a somewhat irregular spherical or tube or dumbbell shape. During and after the application of pressure and the ensuing reduction in the volume of the protoplast no trace of any structural element of the protoplasm could be detected outside the protoplast, provided the cells were compressed gently and not torn to bits. It appears that only a clear liquid, the cell sap, is expressed while the whole of the protoplasm is retained.

In a previous paper (Gross, 1937*b*) the formation of resting spores in cultures of *Ditylum* has been described. When a resting spore is being formed the plasma membrane retracts from the cell wall and the protoplast shrinks gradually, the protoplasm and the chromatophores becoming concentrated to a compact spherical body. At first it remains connected with the shell by means of a number of protoplasmic filaments which become resorbed in the course of shrinkage.

The germination of resting spores is an almost exactly reversed process. Fine protoplasmic processes are sent out and connect the spore with the old shell. The spore elongates and the "pseudopodia" become more conspicuous. Gradually the expansion of the protoplast is completed and the cell gains its normal appearance. Resting spores isolated from the shells are also capable of germination and formation of new cells (Gross, 1939).

The resting spore has a much smaller volume than the original cell. It has lost the cell sap and consists only of the more solid components of the cell, i.e. protoplasm, nucleus and chromatophores.

It may be pointed out that the protoplasm as such does not appear to change its consistency or its volume when passing into the resting spore condition. The main body of liquid lost by the cell is the cell sap and not water previously held imbibed by the protoplasm. On the other hand, the volume of the chromatophores decreases and they become very small spherical- or rod-shaped bodies of a very dense structure. It is possible that the liquid lost by them had been held by imbibition. However, the amount of water lost by the chromatophore appears insignificant compared with the loss due to the passing out of the cell sap.

The ratio resting spore volume to cell volume varies with the diameter and length of the cells. In very narrow cells (diameter 16μ) the "solid" material cannot be compressed into a sphere. The resting spore assumes an elongated shape and, in long cells, measures about a quarter of the cell volume. In cells of medium width (40–50μ) the resting spore measures one-third of the volume of a daughter cell immediately after division. The cell grows to about four times its volume before the next division takes place, while the ratio resting spore volume to cell volume decreases to 1 : 6. With the increase of the cell diameter the proportion of the "solid" material decreases. In prism-shaped cells of 65–75μ diameter the volume of a resting spore in a young daughter cell is only about 1/10 of the cell volume; that of a resting spore formed by a cell of maximum length 1/20 of the cell volume.

From the first attempts to analyse the conditions under which resting spores were formed (Gross, 1937*b*) it appeared that three factors were responsible for their formation: (1) crowding of the cultures,—unless there were about 1000 cells per ml. of culture medium no resting spores were formed; (2) low light intensity (winter daylight in the room); and (3) low temperature (below 12° C.). None of these factors could alone induce resting spore formation; only the interaction of all three seemed to be effective.

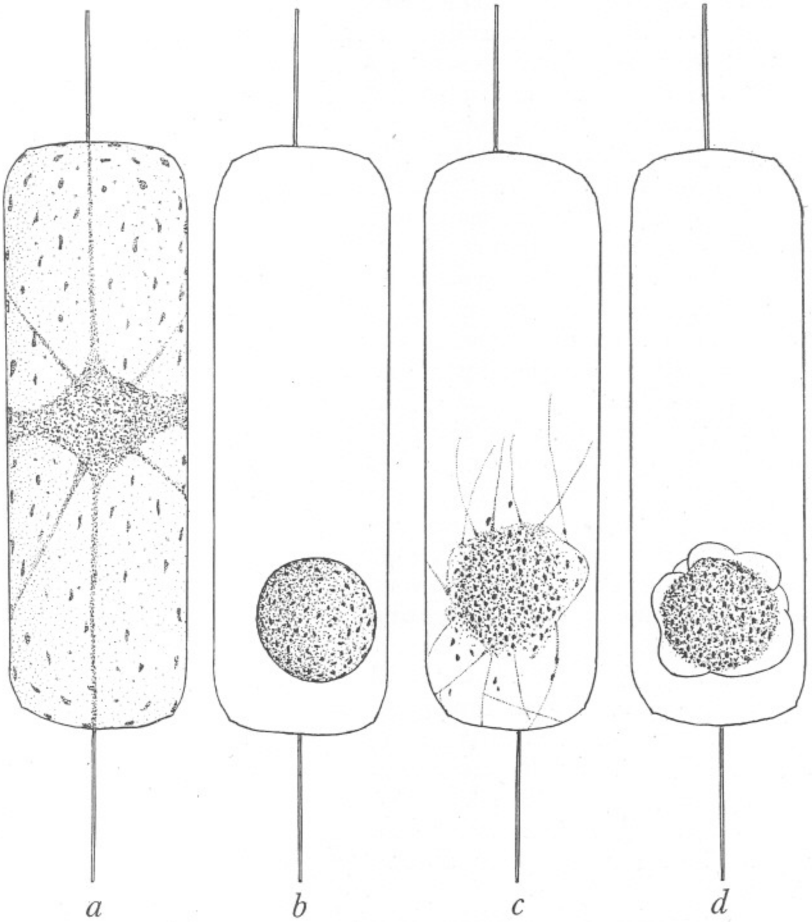

Fig. 1. *a*, normal vegetative *Ditylum Brightwelli*; *b*, the same cell drawn 5 min. after transference into 3·5 % NaCl solution; *c*, the same after 3 hr.; *d*, the same after 24 hr. × 450.

Subsequent experiments showed that the formation and germination of resting spores is based upon a very peculiar osmotic behaviour.

THE EFFECT OF SODIUM CHLORIDE SOLUTIONS

When placed in 3·5% NaCl solution the *Ditylum* cells showed an extremely rapid shrinkage. In a few seconds the protoplasts of almost all cells were reduced to small spherical bodies which resembled resting spores in every respect (Fig. 1*b*). After an interval of 3–4 hr., during which the "resting spores" remained unchanged, they assumed a slightly irregular shape and several, in some cells many, very fine protoplasmic processes were formed radiating from the "resting spore" in all directions (Fig. 1*c*). For several hours no further change took place, and after that the processes were gradually resorbed. The protoplasm and the chromatophores were concentrated to a small body as in the resting spore while, in many cells, the plasma membrane had expanded to form in some cells a clear spherical or spheroidal vesicle around it (similar to Figs. 5*b*, *c*). In other cells the membrane formed a bunch of two to five small vesicles around the condensed protoplasm or an irregularly shaped vesicle as in Fig. 1*d*, while a number of cells were again of the same structure as resting spores. No further change took place.

Most cells remained intact in the NaCl solution for 24 hr. and some for 48 hr.; after that they disintegrated. On replacing them in sea water during the first 2 days they completely recovered in 6–8 hr. The process of recovery was the same as the germination of resting spores already described.

A 3·5% NaCl solution might have been slightly hypertonic, thus causing plasmolysis. However, the result was the same in a 3·4 and 3·3% solution, where shrinkage also occurred almost instantaneously.*

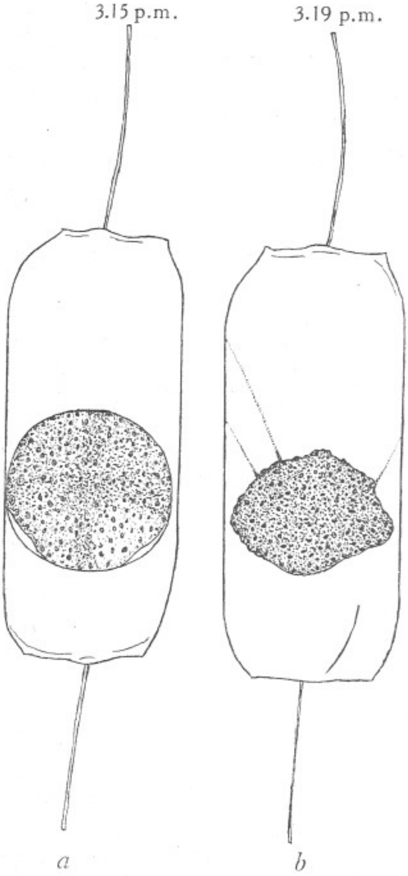

Fig. 2. *a*, the effect of 0·85% NaCl; *b*, the same cell 4 min. after transference into culture medium. Note further contraction and beginning of recovery. ×450.

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* If the cells are transferred very gently the reaction may be delayed for a few minutes in some cells. During that time they remain surrounded by the drop of sea water with which they were transferred. When they are removed to another place in the watch glass the reaction occurs at once.

The cells showed a very similar reaction in 1·7% NaCl which corresponds in salinity to about half that of sea water. It was not always as rapid as in the higher concentrations. In some experiments a few seconds elapsed before the cell membrane became distinctly detached from the cell walls. After 4–5 min. the majority of cells contained small spherical bodies of a similar structure to resting spores, but a number of cells showed either spherical or spheroid protoplasts larger than resting spores. In some cells their structure was uniform but less dense than that of resting spores; in others protoplasm and chromatophores were condensed at two poles, leaving the equatorial area structureless and transparent.

Fig. 2*a* shows a cell which had been placed in a 0·85% NaCl solution.

When transferred into a 0·5% NaCl solution some cells shrank quite considerably and formed spheroid or spherical bodies similar to Fig. 2*a*. None of the protoplasts showed such a strong reduction in volume as in higher concentrations. The majority of cells showed retraction of the membrane only at the poles with the protoplasm and chromatophores aggregated at one pole, or at one pole and at the side of the cell (Fig. 3), or at the two poles. The rest of the cells only reacted with a displacement of the chromatophores which formed irregular patches at the surface. These cells died without previous shrinkage.

When brought back from these hypotonic solutions into sea water or "Erdschreiber"—the culture medium used for *Ditylum* (Gross, 1937*a*)—the cells invariably reacted with an immediate further shrinkage, and after that they slowly recovered (Figs. 2*b*; 3*b*, *c*).

When left in 1·7% NaCl most cells disintegrated after 24 hr., in 0·8 and 0·5% after 2–6 hr. When recovered after transference into culture medium the cells usually divided the following day or the day after and showed no signs of injury whatever.

THE EFFECT OF NON-ELECTROLYTES

A dextrose solution of molar strength is approximately isotonic to sea water (McCutcheon & Lucke, 1928). The effect of such a solution on *Ditylum* was again quite unusual. The great majority of cells showed retraction of their membranes in the course of 3 min. No normal cell was found after 15 min., when the protoplasts of some cells had the shape and structure of resting spores, while many were spherical but slightly bigger (similar to Fig. 2*a*) and the rest spheroid in shape. 18 hr. later a number of cells were disintegrated; the rest showed maximum decrease of volume to that of resting spores.

In one experiment 140 cells were dead and fifty-two intact after 24 hr. After 45 hr. only three cells were alive. When transferred into culture medium during the first 24 hr. many cells completely recovered in about a day, the rest disintegrated.

The effect of a 0·8 *M* dextrose solution was similar in every respect. In

0·5 M solution the initial reaction was slightly less strong, but even here the majority of cells showed considerable shrinkage after a few minutes, and after 3 hr. the great majority of cells contained "resting spores" and somewhat bigger bodies (of the type of Fig. 2*a*). Most of the cells that remained in the solution disintegrated during the first 24 hr. When removed into culture medium during that period some cells recovered completely.

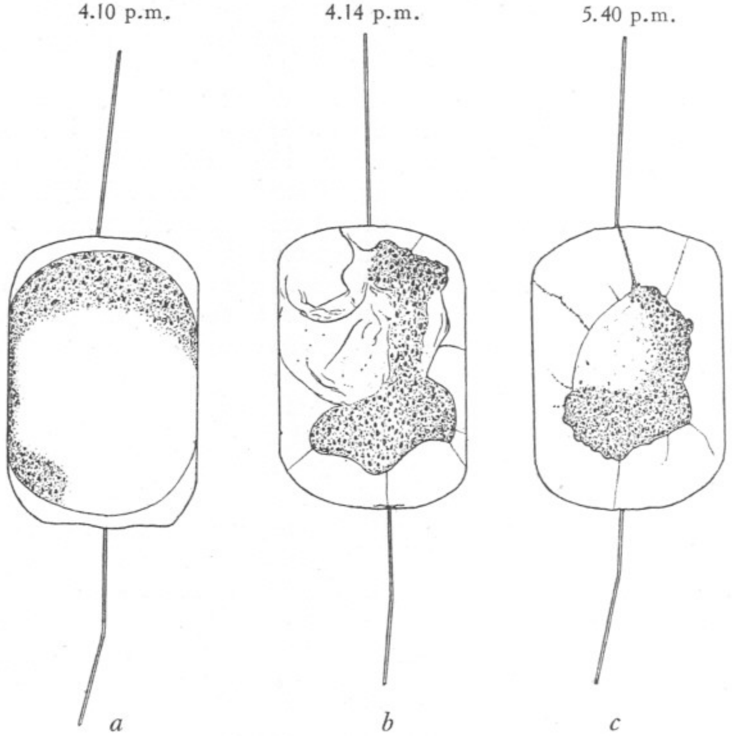

Fig. 3. *a*, cell in 0·5% NaCl solution; *b*, the same cell after 4 min. in half-diluted culture medium; *c*, the same, beginning of recovery in culture medium. Note the creases in the cell membrane in *b*. ×450.

Similar results were obtained with isotonic and hypotonic sucrose solutions. In most experiments shrinkage began in the majority of cells after 2–3 min. in 1 M solutions as well as in 0·6 and 0·4 M. In the molar solution some cells did not shrink at all, but their chromatophores became gradually extraordinarily pale and small. In the hypotonic solutions most cells after about an hour contained either "resting spores" or, as in the dextrose solutions, bigger spherical or spheroid-shaped protoplasts. They proved capable of recovery and subsequent division (Fig. 4, note further shrinkage on transference into culture medium prior to recovery).

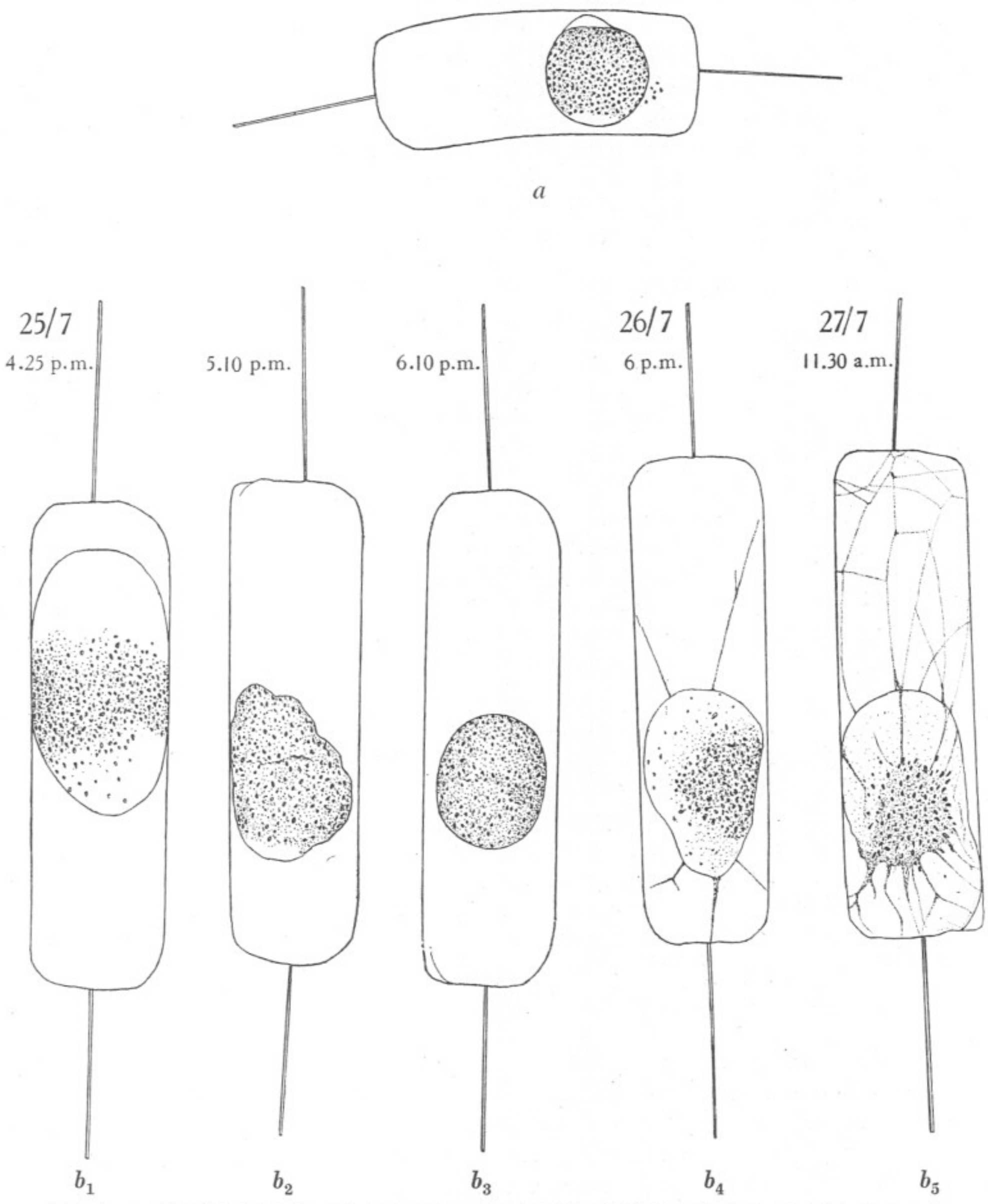

Fig. 4. *a*, cell after 1 hr. in 0·4 *M* sucrose solution; b_1, another cell after 20 min. in 0·4 *M* sucrose; b_2, the same cell transferred into culture medium; b_3, showing further contraction; b_4 and b_5, stages of recovery. ×450.

The cells survived in sucrose solutions for about the same periods as in dextrose.

The shrinkage of the cells described above has a striking similarity to the phenomenon occurring in plant cells when they are placed in hypertonic media, i.e. to plasmolysis. It is, in fact, similar to what occurs when *Ditylum* is placed in hypertonic sea water (see p. 402). *Ditylum* is, however, remarkable for the fact that "exosmosis" not only occurs in hypertonic media but also in various isotonic, and even in strongly hypotonic, media.

THE EFFECT OF UNBUFFERED SALT SOLUTIONS

In a mixture of NaCl and $CaCl_2$* plasmolysis occurred in all cells but not so rapidly as in NaCl alone. It was only after 5–30 min. that the cell membranes showed slight retraction from the shell. After 1–3 hr. the majority of cells contained bag or tube-shaped protoplasts (similar to Figs. 6*b* and 8, IV*a*). Continuous shrinkage led in some cells to the formations of spindle-shaped bodies (of the type shown in Fig. 8, V*a*) with a few protoplasmic filaments connecting them with the shells. Other cells were like Fig. 5*a*. This cell was drawn $5\frac{1}{2}$ hr. after its transference into the salt solution, and it shows that the aggregation of the protoplasm and the chromatophores at the centre took place faster than the contraction of the plasma membrane. A later stage of plasmolysis of such cells is shown in Fig. 5*b*.

Finally, after 3–8 hr. the great majority of cells contained either "resting spores" or structures of the type shown in Fig. 5*c*, d_1. "Resting spores" resulted from a further shrinkage of the spindle-shaped protoplasts, while the cells with a clear area around the compact body containing protoplasm, nucleus and chromatophores (Figs. 5*c*, *d*) were the final stage of "plasmolysis" of cells such as shown in Fig. 5*a*, *b*.

All cells survived in $NaCl + CaCl_2$ for 24 hr. and more than 50 % for another day. After 3 days all were dead. As long as they showed no sign of disintegration they readily recovered in 6–12 hr. when transferred into culture medium (Fig. 5d_1, d_2) and subsequently multiplied. It may be noted that on transference into sea water no further shrinkage occurred such as was repeatedly observed when cells that had not completely plasmolysed in hypotonic NaCl or dextrose solutions were placed back in sea water.

What is the effect of $CaCl_2$ alone? In a 0·6 *M* $CaCl_2$ solution (equimolecular to a 3·5 % NaCl solution) the cells were rapidly driven to the surface by diffusion currents. Almost all protoplasts shrank rapidly, but before they had formed a spherical body their content disintegrated. Only very few "resting spores" were formed among several hundreds of cells.

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* At first the solution was made up by dissolving 3·38 g. NaCl and 0·12 g. $CaCl_2$ in 100 ml. glass-distilled water. In later experiments 48 ml. *M* NaCl and 1·09 ml. *M* $CaCl_2$ were made up to 100 ml. with distilled water, the proportion being the same as used by Allen (1914) for artificial sea water. There was no difference in the results obtained with either of the solutions.

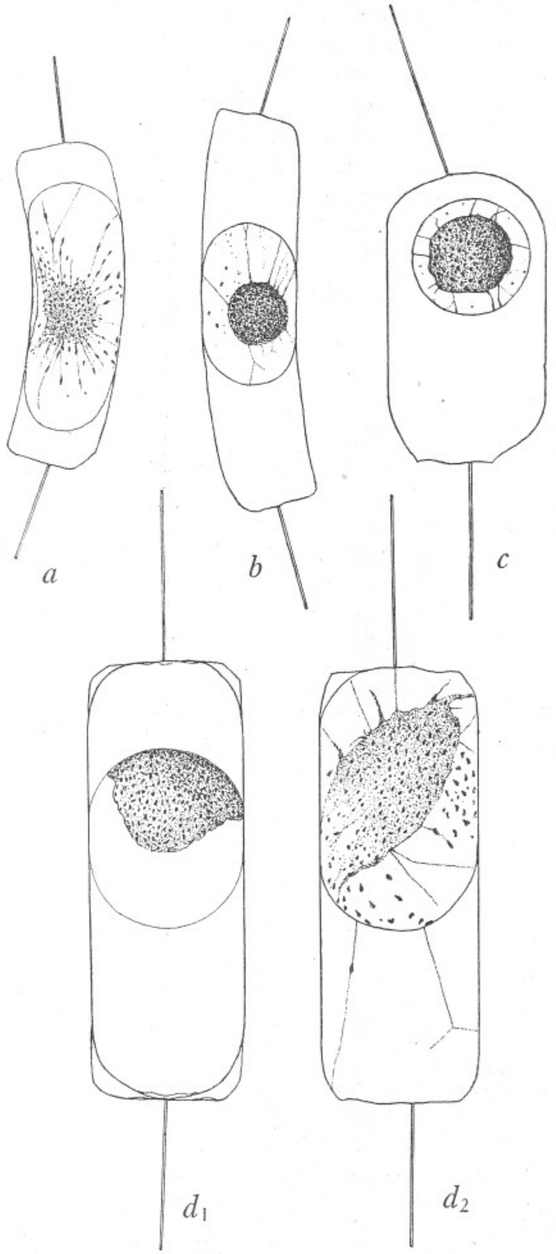

Fig. 5. The effect of $NaCl + CaCl_2$. *a*, a cell after $5\frac{1}{2}$ hr. in $NaCl + CaCl_2$; *b*, another cell drawn after $20\frac{1}{2}$ hr.; *c*, after 24 hr.; d_1, drawn after 24 hr. and then placed in culture medium; d_2, the same cell $3\frac{1}{2}$ hr. later. *a*, *b*, ×200; *c*–d_2, ×400.

In a 0·3 *M* $CaCl_2$ solution the reaction was far less violent. The cells remained suspended in the solution and the great majority of them formed "resting spores" in 1–3 sec. The rest plasmolysed more slowly and only after several minutes formed either "resting spores" or spherical bodies of the same diameter as the shell. Some cells showed plasmolysed protoplasts similar to Fig. 5 *c*, *d*. Most cells died after 24 hr. in $CaCl_2$; the remaining cells recovered when transferred into culture medium.

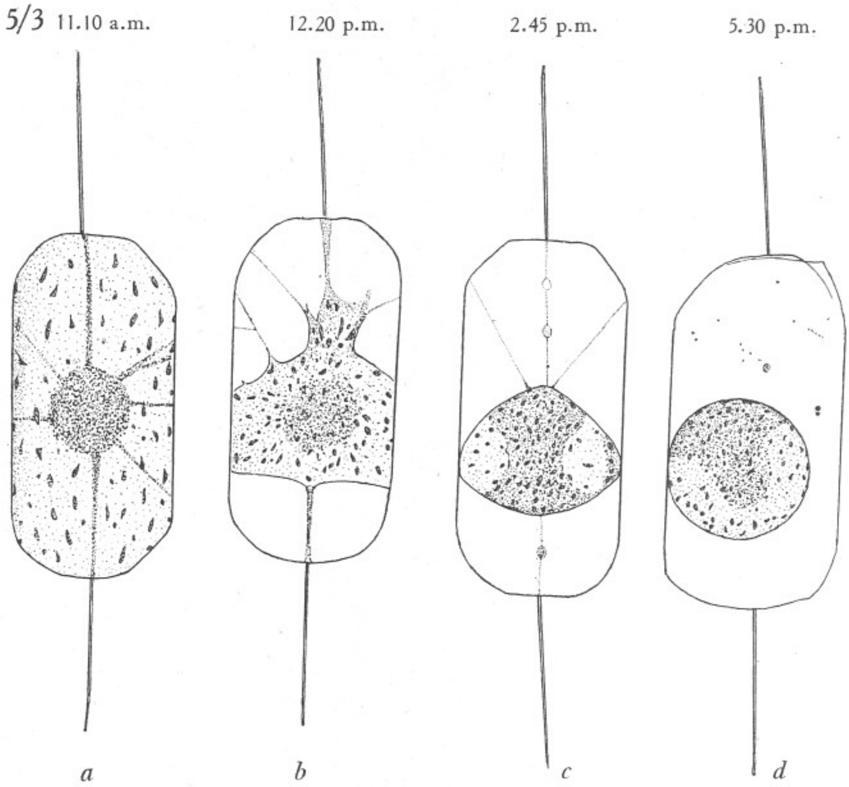

Fig. 6. *a–d*, plasmolysis of a cell in unbuffered artificial sea water. × 450.

Thus in $CaCl_2$ alone the cells reacted very much as in NaCl alone. Only in the presence of both is there a marked delay in the plasmolysis of the cells.

In a mixture of NaCl, $MgCl_2$ and $MgSO_4$ in similar proportions to that in sea water the cells behaved exactly as they did in NaCl alone.

In a solution containing the chief constituents of sea water, i.e. NaCl, KCl, $CaCl_2$, $MgCl_2$ and $MgSO_4$ in the proportions used for artificial sea water (Allen, 1914), the shrinkage of the protoplast proceeded at about the same rate as in $NaCl + CaCl_2$ and in a similar manner (Fig. 6). In many cells the shrinkage of the membrane proceeded simultaneously with that of the rest of the protoplast, resulting, after 6–8 hr., in the formation of bodies similar to resting spores (Fig. 6). In other cells the initial connexions with the shells were absorbed at an early stage and the protoplasm and chromatophores became more quickly aggregated near the centre, leaving the poles of the vesicle more or less clear.

In this salt solution most cells remained alive for 2 days and some as long as 5 days. When transferred into culture medium they all recovered.

In all experiments care had to be taken to remove the diatoms from the culture with as little medium as possible. As a rule a sample of cells was "washed" once or twice, i.e. transferred from one watch glass containing the salt solution into a fresh one.

THE EFFECT OF THE HYDROGEN-ION CONCENTRATION

The next step to improve the artificial sea water was the adjustment of the *p*H to that of natural sea water which varied between 8·0 and 8·1. This was done either by the addition of $NaHCO_3$ or of $NaOH + Na_2HPO_4$*.

In an artificial sea water of *p*H 7·8–8·0 the great majority of cells remained quite unchanged. Some cells showed rapid partial plasmolysis but they soon recovered in the same medium.

When left in the artificial sea water a number of cells divided once, but never more than once. After several days the cells became slightly abnormal in appearance, strongly refractive and the chromatophores grew very small. In the course of 8–10 days an increasing number of cells showed shrunken protoplasts, and even a small number of proper "resting spores" were formed. These did not recover any more, unless they were transferred into natural sea water or culture medium. In some experiments the majority of cells did not plasmolyse at all, but showed a displacement of the chromatophores towards the poles and the equator. After 10–12 days all cells died.

Cells which had formed "resting spores" in NaCl solutions or in artificial sea water without bicarbonate completely recovered when placed in buffered artificial sea water (Fig. 7; on the fourth day the cell had perfectly normal structure, and only afterwards the chromatophores became small and strongly refractive).

Since cells remain normal in an artificial sea water of *p*H8 while they completely plasmolyse in the course of a few hours in the same solution without the adjustment of the *p*H, it is obvious that a certain hydrogen-ion concentration is very important for the maintenance of the cell turgor, i.e. the normal shape and water content of the vegetative *Ditylum* cell.

The following experiments were made to investigate the influence of *p*H on some of those electrolyte and non-electrolyte solutions, the plasmolysing effect of which was previously described. 3% NaCl solutions of *p*H 8·9, 7·8, 6·9, 5·9, 4·8, 4 and 3·2 were prepared by the addition of $NaHCO_3$ and HCl

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* I am indebted to Dr L. H. N. Cooper and Dr H. W. Harvey for their kind help in questions relating to the *p*H and its determination.

respectively, and samples of *Ditylum* placed in them. In the solutions of *p*H 4·0–8·9 the reaction was quite the same as described for the neutral NaCl solution (p. 384); the cells plasmolysed completely in a few seconds to form "resting spores" or slightly larger spherical bodies (stages VI and VII of Fig. 8) and made an attempt towards recovery in the formation of fine protoplasmic processes and slight expansion of the cell membrane after several hours, only to return to the spheroid or spherical stage (Fig. 8, V *b*, VI *b*, VII) the next day. At *p*H 3·2 some cells reacted in the same manner while the rest died immediately or after slight plasmolysis.

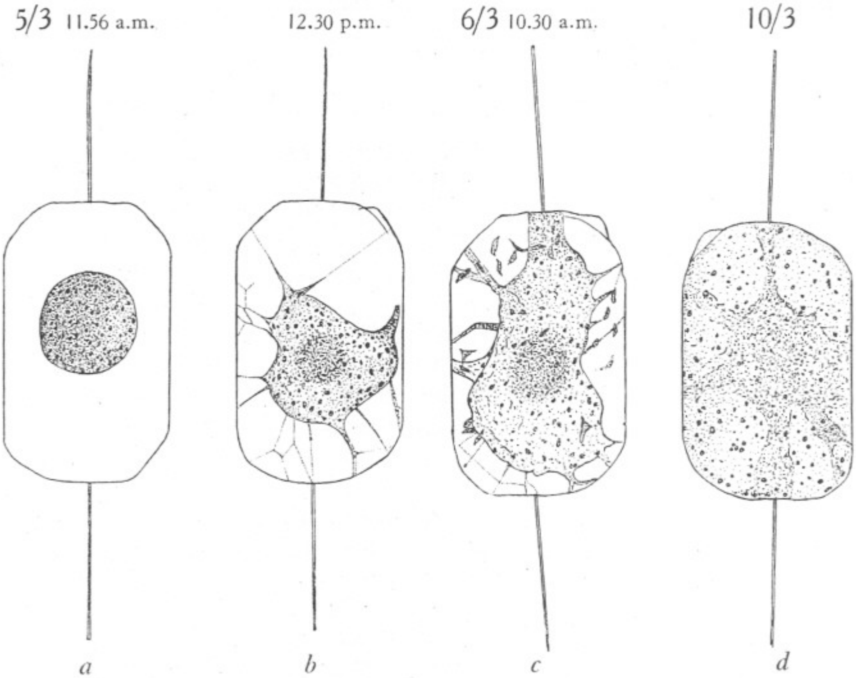

Fig. 7. *a*, a cell plasmolysed in 3·3 % NaCl; *b–d*, the same cell recovering in buffered artificial sea water. ×450.

While there was no difference in the reaction of the cells in the NaCl solutions of different *p*H, cells plasmolysed in the solutions of higher *p*H remained intact for a longer time than those in lower *p*H. Thus in one experiment in which thirty cells were placed in each of the solutions there were alive, and capable of complete recovery, after 43 hr.:

17 cells in *p*H 8·9
8 cells in *p*H 7·8
6 cells in *p*H 6·9
3 cells in *p*H 5·9
0 cells in *p*H 4·8–3·2

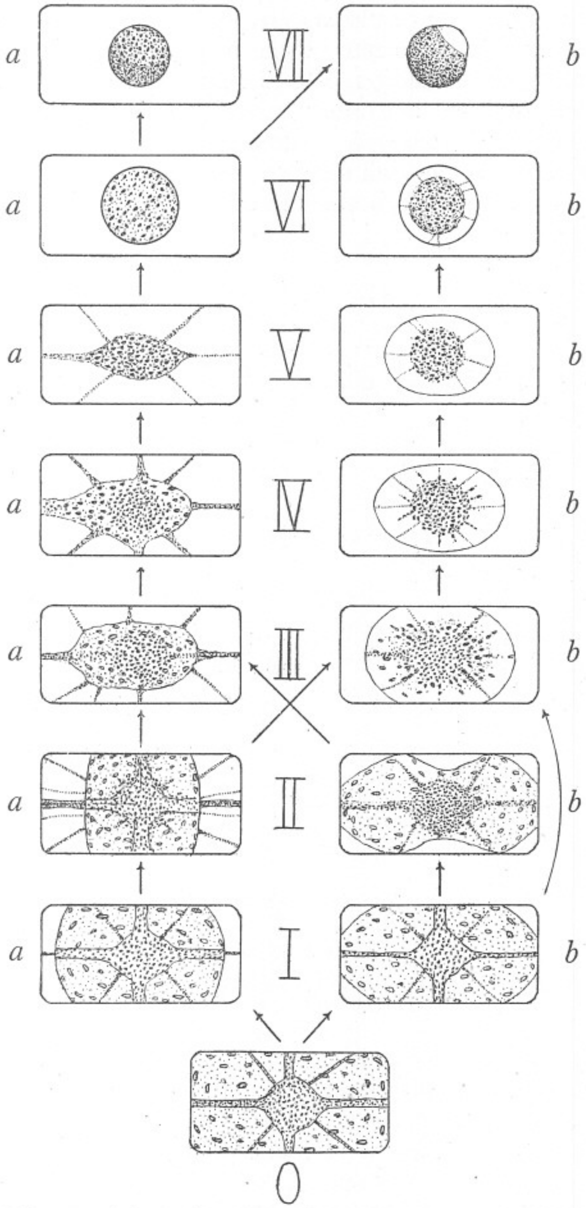

Fig. 8. Diagram of the various successive stages of plasmolysis in *Ditylum*.

In molar solutions of dextrose of different *p*H there was a distinct, if only slight, increase in the rate of plasmolysis with the increase of hydrogen-ion concentration. In Fig. 9 the rate of plasmolysis is represented for the two extreme *p*H values, i.e. 8·1 and 3·1. The curves for the other values investigated, i.e. *p*H 7·2, 6·6, 6·3, 5·3, and 4·2, would lie between those drawn. Stage O–VII of plasmolysis correspond to those drawn diagrammatically in Fig. 8.

It is noteworthy that no such attempt towards recovery, consisting in the formation of fine pseudopods, occurred in dextrose solutions as was observed in NaCl solutions.

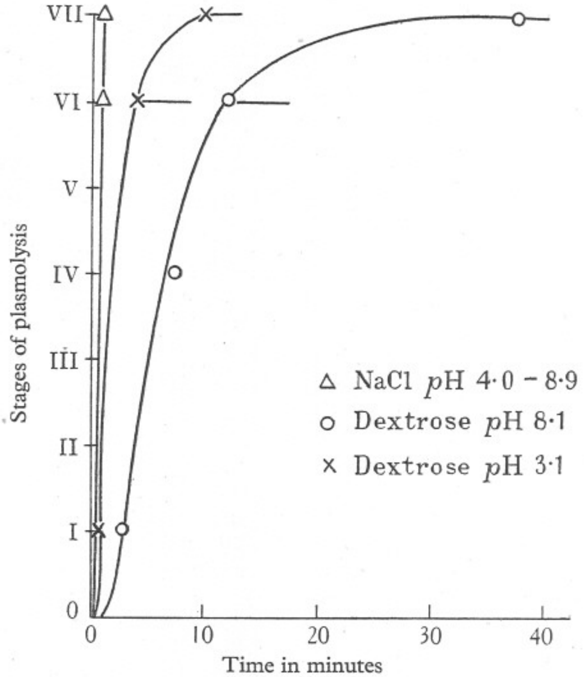

Fig. 9. Rate of plasmolysis in NaCl and dextrose solutions of different *p*H. Stages I–VII refer to Fig. 8.

The behaviour of the cells in isotonic NaCl + $CaCl_2$ solutions (in the same proportions as on p. 388) of different *p*H is represented in Fig. 10 for the *p*H values 3·1–6·9, and Fig. 11 for *p*H values of 6·9–9·0. The experiments on which these curves are based were made on subsequent days, and on the second day the temperature was several degrees higher than on the first. This may perhaps explain the greater rate of plasmolysis of cells in *p*H 6·9 on one day (Fig. 11), compared with that of cells in the same medium on the previous day (Fig. 10). In both experiments the increase of the hydrogen-ion concentration entailed a very strong increase in the rate of plasmolysis. In the neutral

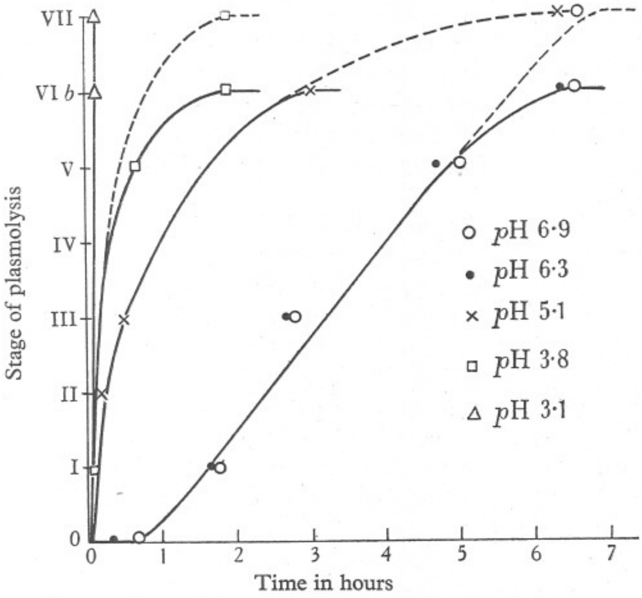

Fig. 10. Rate of plasmolysis in NaCl + $CaCl_2$ solutions of *p*H 3·1–6·9. Stages I–VII as in Fig. 8.

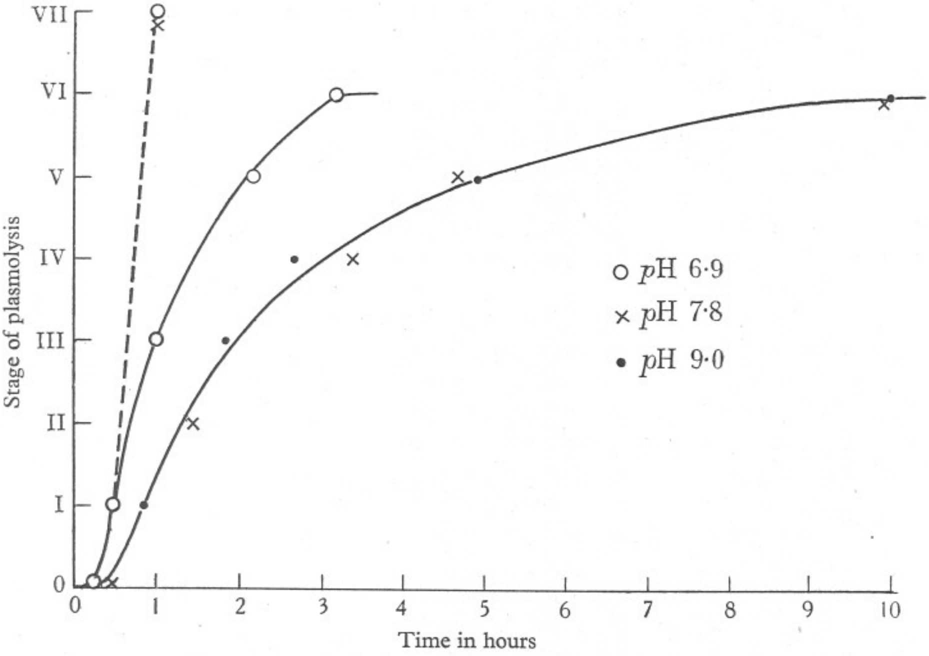

Fig. 11. Rate of plasmolysis in NaCl + $CaCl_2$ solutions of *p*H 6·9–9·0. Stages I–VII as in Fig. 8.

salt solution (*p*H 6·9, Fig. 10) the protoplasts were shrunk to small spherical bodies (stage VI and a few VII; Fig. 8) after 6 hr., while at *p*H 3·1 about half the cells formed resting spores in 5 min., and the rest after about 10 min. In the other experiment there was no difference in the behaviour of cells in *p*H 7·8 and 9·0. In both solutions all cells had passed into stage VI after about 10 hr., whereas the cells in the neutral salt solution had reached that stage after 3 hr.

There were, however, some cells both in *p*H 7·8 and 6·9 (six and eight respectively out of thirty-five cells) which formed proper "resting spores" after only 1 hr. (see interrupted curve in Fig. 11). These "resting spores" behaved in a similar manner to those in NaCl alone, sending out fine processes after 3 hr. and resorbing them again after some time, the resting spores assuming a somewhat irregular shape.

As in NaCl alone considerably more "resting spores" were intact after 48 hr. in solutions of high *p*H values than in those of low *p*H.

In nature *Ditylum* never meets conditions involving the absence of, or even a strong reduction in, the concentration of either sodium chloride or calcium chloride. However, the fact that the *p*H is of great importance for the maintenance of the cell turgor brought the curious phenomena of plasmolysis more into line with the formation of resting spores under normal culture conditions. It appeared that the "crowding factor" (p. 383) might perhaps be resolved into fluctuations of the hydrogen-ion concentration due to the presence of a large diatom population. Experiments showed in fact that the *p*H of the sea water or the culture medium has a pronounced effect upon *Ditylum*.

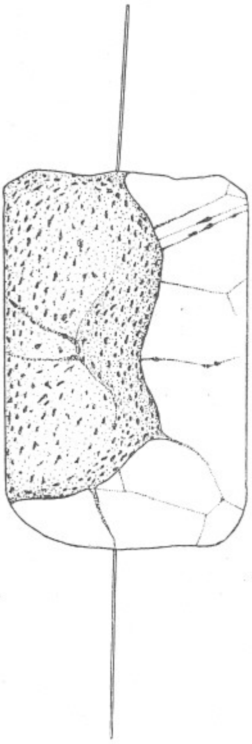
Fig. 12. Cell plasmolysed in culture medium of *p*H 6·9, drawn after 20 min. ×450.

In preliminary experiments sea water was made more acid by blowing expired air through it. Most experiments were made with media of a *p*H of about 7·0. The cells were kept in solid watch glasses and a glass lid was sealed on with vaseline, so as to prevent, or at least to delay, the gas exchange with the atmospheric air. Samples of the acidified media without any cells were similarly kept and after some time the *p*H tested, at first colorimetrically and in later experiments with the aid of the Beckman *p*H meter. It was found that after 24 hr. the *p*H had never risen to more than 7·5.

The reaction was quite strong when cells from rich cultures were transferred into a medium of *p*H 7. From 30 to 90 % of them—the number varying in different experiments—showed strong "plasmolysis"; some of them immediately after transference, the rest in the course of 30 min. The contraction was restricted to the poles (as in Fig. 8, II *a*, *b*) or proceeded further and resulted in tube or amoeboid-shaped protoplasts similar to Fig. 6*b* (see also Fig. 12).

After 24–48 hr. the cells had recovered and the *p*H of the medium had become normal again. Resting spores were on the whole very rarely formed. When samples of cells were taken from young cultures only few of them showed plasmolysis.

Solutions of a wider range of *p*H were prepared by the addition of HCl to the culture medium, and the results are shown in Fig. 13. Cells placed in *p*H 7·3 (the *p*H increased to 7·6 by the next day) remained normal. In culture medium of *p*H 6·0 the majority of cells showed distinct signs of plasmolysis after an hour. After about 10 hr. all protoplasts were amoeboid or spheroid-shaped (Fig. 8, III *a*, *b*), but after 21 hr. all cells were normal again, the *p*H having risen to 7·4.

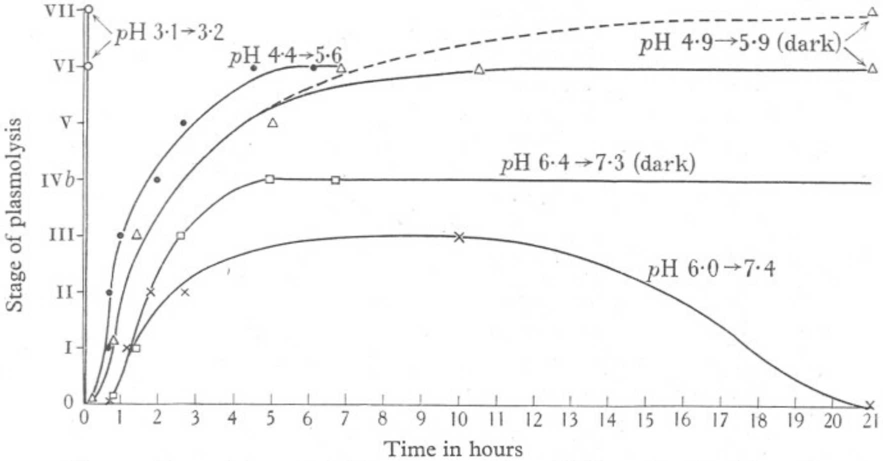

Fig. 13. Rate of plasmolysis in culture medium of *p*H 3·1–6·0. At *p*H 7·3 the cells remained unaffected. Stages I–VII as in Fig. 8.

At *p*H 6·4, when the cells were kept in the dark, they plasmolysed to stage III (Fig. 8) after $2\frac{1}{2}$ hr. and to stage IV after 5 hr. and remained in this stage until the next day when the *p*H had increased to 7·3. Afterwards the cells continued plasmolysis at the same rate as in normal medium in the absence of light (see p. 404).

The effect of *p*H 4·4 (rising to 5·6 in the course of a day), and of *p*H 4·9 (rising to 5·9) when kept in the dark, is shown in Fig. 13. The rate at which the cells passed through the various stages of plasmolysis increased considerably with the decrease of *p*H. At *p*H 4·9 in the dark some cells formed regular resting spores, while the rest proceeded to stage VI.

The reaction in the culture medium of *p*H 3·1 was very striking. Some cells plasmolysed after 1 min., the majority after $2\frac{1}{2}$ min., and in 5 min. the majority had formed resting spores and the rest slightly larger bodies. After 24 hr. most of them were disintegrated. As long as they remained alive they readily recovered when transferred into culture medium of normal *p*H.

Thus the effect of NaCl solutions remains the same at all *p*H values tested. In dextrose solutions there is a slight, in $NaCl + CaCl_2$ solutions and sea water a marked, increase in the rate of plasmolysis with increasing hydrogen-ion concentration. Except in sea water of higher *p*H values the equilibrium volume of the protoplast was the same in all solutions, varying between stage VI and the final stage of plasmolysis VII (Fig. 8) irrespective of the *p*H. In sea water of *p*H 6–7 the cells only plasmolysed to stage I–IV. However, this cannot be regarded as an equilibrium volume, since when exposed to light they recovered, probably owing to increased cellular activity (p. 409), while in the dark they continued plasmolysis at a reduced speed.

In the upper layers of the sea the variations of *p*H are very small (Atkins, 1922, 1923). It seems, however, that under certain circumstances a small change of hydrogen-ion concentration is sufficient to affect *Ditylum*. It was frequently noticed that some of the cells transferred from dense cultures into fresh culture medium showed strong contraction of their protoplasts after a few seconds. Cells like Fig. 12 were often noticed and sometimes even a few "resting spores". Subsequently all those cells recovered and had perfectly normal structure after 4–6 hr. When cells were transferred from young cultures into fresh culture medium plasmolysis never occurred. It seems very likely that the *p*H of the medium around the actively photosynthesizing colonies was higher than that of the fresh medium and that the change of *p*H had caused the shrinkage of the protoplasts. This is supported by the fact that when cells from dense colonies were gently pipetted away to another part of the Petri dish which was free of *Ditylum*, some cells also contracted quite considerably.

THE EFFECT OF THE MOLECULAR CONCENTRATION OF THE MEDIUM

(*a*) *Isotonic media*

The effect of some isotonic solutions has been described before. One more illustration may be given for the fact that isotony of the medium, i.e. isotony with sea water, is not sufficient for the maintenance of the cell turgor in *Ditylum*. It concerns the effect of mixtures of sea water and 3·3% NaCl solution in various proportions.

In a mixture of 1 vol. 3·3% NaCl and 1 vol. sea water there was no immediate reaction but about 50% of the cells showed the beginning of the retraction of the cell membrane after 1–5 hr. After further 15 hr. the number of normal cells was negligible; the rest showed amoeboid or spindle-shaped protoplasts or small spherical bodies (stage VI*b*, Fig. 8). Next day the great majority showed such spherical protoplasts, while a few had died. During the following 4 days all cells disintegrated.

In a mixture of 4 vol. 3·3 % NaCl and 1 vol. sea water cells plasmolysed immediately on transference, the rest did so in the course of 20 min. when more than half of the cells had formed "resting spores". The rest were spheroidal or amoeboid or spindle-shaped. However, in an hour or so most of the "resting spores" began to recover, so that 3 hr. after the start of the experiment there was no "resting spore" to be seen. In 10–12 hr. the "germination" proceeded to stages similar to III and IV*a* in Fig. 8 but no cell ever became entirely normal. On the contrary, the protoplasts began to contract again, and by the following day the cells had shrunk again to stages VI*a* and VII (Fig. 8).

The effect of a mixture of 10 vol. 3·3 % NaCl and 1 vol. sea water was very similar.

The decisive factors bringing about plasmolysis of the cells in the above experiments may have been (1) reduction in the amount of calcium present, and (2) increase of the hydrogen-ion concentration. As in some experiments previously described (pp. 391, 397, 398), the cells were capable of adaptation to the new medium, i.e. after strong initial contraction their protoplasts recovered. However, in mixtures of NaCl solution and sea-water recovery was never complete. It is noteworthy that not even a partial and temporary recovery has taken place in the mixture 1 : 1, although this contained more of the natural medium than the mixtures subsequently used. Correlated with this behaviour is probably the fact that in the mixture 1 : 1 plasmolysis proceeded almost as slowly as in darkness, while in stronger dilutions of sea water with the NaCl solution it took place very rapidly (see pp. 408, 411).

(*b*) *Hypotonic media*

The peculiarity of the osmotic relations of *Ditylum* is also demonstrated by experiments with diluted sea water. When transferred into half-diluted sea water a number of cells showed shrinkage, and after 3 hr. the majority were in stage II–VI of plasmolysis (Fig. 8), while some cells formed almost completely regular "resting spores". By the next day all cells had recovered and some had even divided. Since April 1937 a culture of *Ditylum* was kept in half-diluted culture medium, and it was still flourishing in February 1939 when it was abandoned.

Cells which remained normal and those which had recovered in half-diluted sea water invariably contracted to at least the stage II (Fig. 8) when transferred into sea water. Then again they recovered.

In 25 % sea water (1 vol. culture medium and 3 vol. distilled water) many cells plasmolysed at once, others more slowly, most of them becoming spheroidal in about an hour. A few resting spores were also formed. Only a few cells became bent, the two halves of the shell forming an angle, as in auxospore formation (Gross 1937*b*), and the protoplast bulging out through the slit. The next day the cells appeared unchanged, but on the following day the majority of them disintegrated while the rest completely recovered. A culture was started with these cells and it could be maintained for 18 months in culture medium of 25% the normal salinity.

In sea water diluted with 5 vol. of distilled water the reaction was very similar. A few cells did not shrink but showed a displacement of the chromatophores towards the poles in the course of 10 min. As in 25% sea water only a few cells showed the phenomenon which one would have expected to observe in all hypotonic media, i.e. swelling of the protoplast and the separation of the two halves of the shell, with the protoplast bulging out between them as a big spherical body. Most cells died in about 30 min.

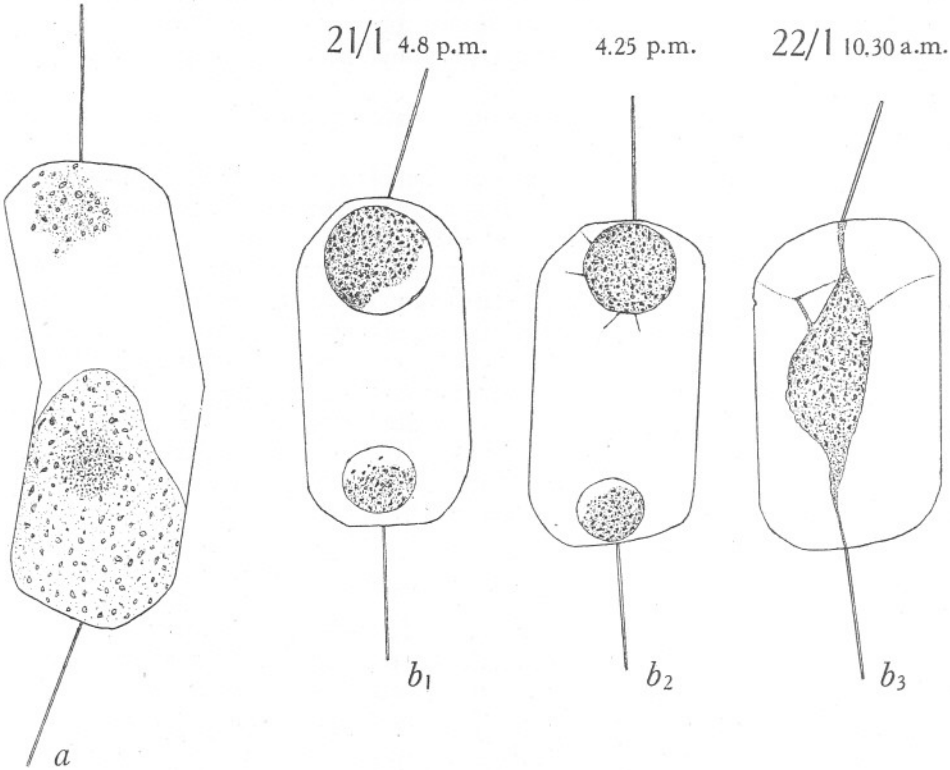

Fig. 14. The effect of a fresh water medium ("Volvox" solution). *a*, a cell which was placed in "Volvox solution" at 3.26 p.m., drawn at 3.28; b_1, cell which was put in the "Volvox solution" at 3.54 p.m. and transferred into diluted culture medium after one minute; b_1–b_3, stages of recovery of the same cell. × 400.

In 10% sea water most cells, immediately on transference, showed strongly shrunk protoplasts, either spheroidal or of irregular shape. All cells disintegrated after about 5 min. When transferred into sea water after 1 min. some of them recovered completely.

Considering these unusual reactions of cells to hypotonic media one has to keep in mind that the dilution of sea water entails not only a decrease in the salt concentration but also an increase in the hydrogen-ion concentration. The *p*H of half-diluted sea water was found to be 7·8, of 25 % sea water about 7·2, and of 10 % sea water approximately 7.

In order to study the effect of a fresh-water solution the cells were placed in Mainx's so-called "Volvox solution"* which has been used in culturing *Volvox*, *Daphnia* and other fresh-water organisms. Even here the majority of cells plasmolysed rapidly. In a number of cells the protoplast was torn into two portions contracting at the opposite poles (Fig. 14). The plasmolysed cells were capable of complete recovery when brought back into sea water, or better in diluted sea water first, within 5–10 min. from the beginning of the experiment. Cells of the type shown in Fig. 14*a* also recovered on transference to culture medium (Fig. 14b_1–b_3).

In most experiments a considerable number of cells did not plasmolyse but only showed displacement of the chromatophores and the protoplasm towards the two poles without contraction of the cell membrane. Not a single cell showed the bending of the shell and subsequent extrusion of the protoplast such as was observed in some cells in sea water diluted with 3 and 5 vol. of distilled water.

The results obtained with (glass-) distilled water varied in different experiments. In one instance an immediate displacement of the protoplasm and the chromatophores took place, either towards the centre (Fig. 15) or the side of the shell, and a few seconds later the chromatophores changed colour and the protoplast disintegrated.

In another experiment no change took place for about 30 sec. after transference into distilled water, and then some cells plasmolysed, their protoplasts becoming spheroidal in shape, while in others the chromatophores appeared concentrated at the poles and at the equator. Disintegration occurred after 3–4 min.

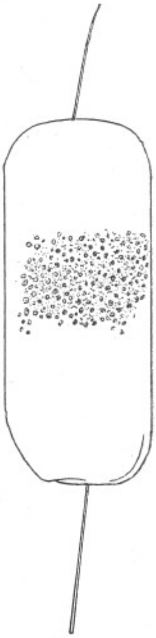

Fig. 15. The effect of distilled water. × 400.

In a sample from another culture, placed in distilled water, most cells remained unchanged except that their chromatophores became irregularly aggregated in patches at the surface. A few cells plasmolysed and their protoplasts assumed a regular spherical shape. In another experiment some cells shrank to less regularly shaped bodies as shown in Fig. 14*a*.

All the changes that occurred in distilled water appeared to be irreversible. None of the cells transferred back into culture medium recovered; all disintegrated at once.

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* Consisting of 1 vol. soil extract, made up with Plymouth tap water, and 6 vol. distilled water.

(*c*) *Hypertonic media*

In a medium of the total salt concentration of approx. 3·9% (100 ml. culture medium + 0·5 g. NaCl) the reaction of the cells, if any, was slow and weak. After 5 min., five out of about 100 cells showed stage I*b* of plasmolysis (Fig. 8). After 2½ hr. the majority of cells were slightly plasmolysed. The important fact was, however, that after 22 hr. only few had remained so, while the rest were perfectly normal again. Many divided the next day.

Cells of normal structure when transferred from hypertonic medium into pure sea water invariably plasmolysed after 1–10 min. to approximately the stage II (Fig. 8) and then recovered in a few hours.

In a concentration of about 4·4% (100 ml. culture medium + 1 g. NaCl) the cells plasmolysed slightly in the course of 5 min. An hour later the majority of cells had again quite normal appearance. No further change took place during the next 24 hr. and after that, in the course of about a week, most cells contracted again (to approximately stage III*b*, Fig. 8). The rest remained normal for 13 days but no cell divided.

When placed in culture medium of normal salinity 5 days after the beginning of the experiment, cells of normal appearance contracted and then recovered. But after that very few divided; most of them appeared to have been injured.

An interesting reaction could be observed in those cells which after initial plasmolysis in the hypertonic medium had recovered and then, after a few days, had plasmolysed again. When these cells were placed in culture medium of normal salt concentration the protoplasts which occupied only about two-thirds of the length of the shell expanded in about 30 sec. so as to fill out the shell completely. However, after 2–3 min. most of them plasmolysed again, some to a greater extent than they had before. Finally, they recovered as regards their external appearance but no division took place. The cells have apparently been injured during their long exposure to the hypertonic medium.

In a medium of 4·9% salinity (100 ml. culture medium + 1·5 g. NaCl) the cells plasmolysed and reached stages I*a*–II*a* (Fig. 8) in about an hour. In the course of further 3–4 hr. all double cells and short entire cells recovered, i.e. became normal in appearance.

After 5–24 hr. all cells plasmolysed again, many much more strongly than at the beginning of the experiment (similar to Figs. 3*a* and 17*a*). A few cells formed bodies resembling resting spores. After 4 days all cells disintegrated.

When transferred into normal culture medium the plasmolysed cells (Fig. 16*a*) showed the same phenomenon as described above. In ½–1 min. their protoplasts expanded (Fig. 16*b*) and in some cells filled out the entire shell, but after 5–10 min. they shrank again (Fig. 16*c*). None of these cells recovered completely and none was capable of division.

It must be pointed out that this phenomenon was only observed in cells which after the initial plasmolysis had recovered and then plasmolysed again, i.e. in cells which had been in the hypertonic solution over night. Cells which were put back into normal medium shortly after the initial plasmolysis to a stage like Fig. 17*a*, i.e. 5–6 hr. after the beginning of the experiment, did not swell. On the contrary, most of them responded with a further shrinkage. Most of these cells recovered completely and divided on the next day.

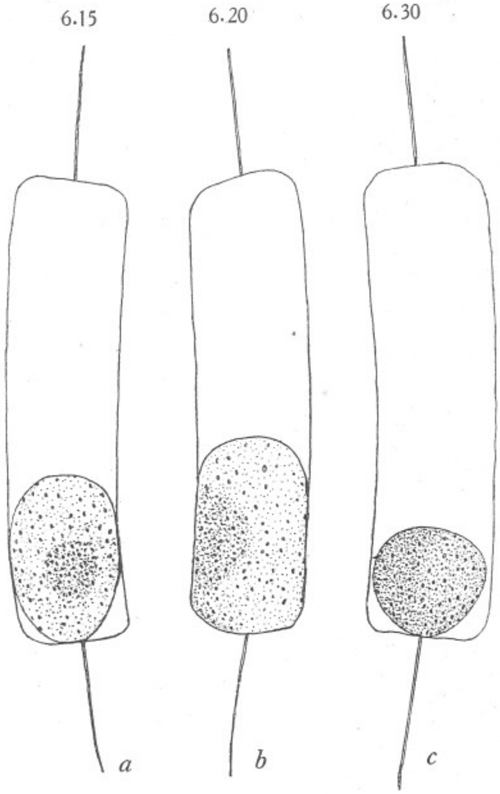

Fig. 16

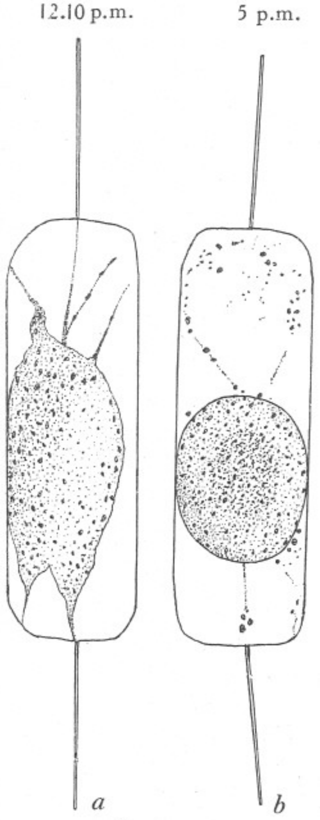

Fig. 17

Fig. 16. *a*, a cell after 75 hr. in sea water + 1·5 % NaCl; *b*, swelling on transference into normal culture medium; *c*, subsequent contraction. × 450.

Fig. 17. *a*, a cell 60 min. after transference into a strongly hypertonic medium (culture medium + 3 % NaCl); *b*, the same cell, left in the hypertonic medium, 5 hr. later. × 450.

In a medium of approximately 6·4 % salt (100 ml. culture medium + 3g. NaCl) all cells rapidly plasmolysed to about the same extent as shown in Fig. 17*a*. After 5–9 hr. they assumed at first a spheroidal (Fig. 17*b*) and later a spherical shape and a size somewhat larger than resting spores. They remained intact for less than 3 days. When brought back into normal medium 6 hr. after they had been placed in the hypertonic solution their protoplasts swell rapidly after 1 min., filling out the shell to slightly more than half its length. However, in an hour they were again strongly plasmolysed, a few of them showing small spherical protoplasts, others spheroidal or more irregularly shaped bodies. Next day the cells were quite normal, and all had divided. During the following days they rapidly multiplied.

At first sight it appears peculiar that cells plasmolysed in stronger hypertonic solutions should be more capable of recovery, when transferred into normal culture medium, than those plasmolysed in less hypertonic media. Stronger hypertonic solutions seemed to injure the cells less than solutions of lower salinity. The fact must be taken in account, however, that (1) in the 6·4% solution the maximum plasmolysis of the protoplast is attained in much shorter time than in solutions of lower salt concentrations, and (2) that recovery is not based on endosmosis (see p. 411); on the contrary, where rapid swelling owing to the intake of water did take place a further contraction eliminated the water taken in on transference into normal medium. Of the cells that showed rapid endosmosis and underwent such a secondary plasmolysis many, but not all, appeared permanently injured.

THE EFFECT OF THE ABSENCE OF LIGHT

In the first experiment (May 4) forty cells were transferred to a watch glass filled with culture medium, and this was placed in a large box lined with black paper. After 24 hr. all cells were distinctly plasmolysed, some only slightly and others to a considerable degree, showing "amoeboid"-shaped protoplasts. After 48 hr. they reached stage IV (Fig. 8). Several cells were taken out and left standing in daylight. Two hours later some of them had recovered and next day all had quite normal appearance. The cells which had remained in the dark box showed further shrinkage of their protoplasts in the next few days. From the 14th till the 30th no observations could be made, and by the 31st some cells were dead, while the rest contained small spherical protoplasts of the same structure as resting spores. On June 2 the watch glass was placed in light, and although the medium had not been changed the cells recovered completely and subsequently divided.

In another experiment twenty cells of a larger diameter were placed in the dark. Plasmolysis was distinct after 16 hr. (Fig. 18). 24 hr. later the protoplasts were "amoeboid". During the following days the "pseudopodia" were gradually resorbed, and the first "resting spores" were completed on the 10th day.

These experiments have been repeated many times, and the results of some of them are represented in Fig. 21. The first distinct sign of plasmolysis was observed after 15–22 hr. of absence of light. The "amoeboid" stage (II *a* and IV*a*, Fig. 8) was reached after 2–3 days. 4–6 days of darkness resulted in spindle-shaped protoplasts of the type shown in Fig. 19. After 7–12 days all cells showed maximum plasmolysis and contained spherical bodies of the same

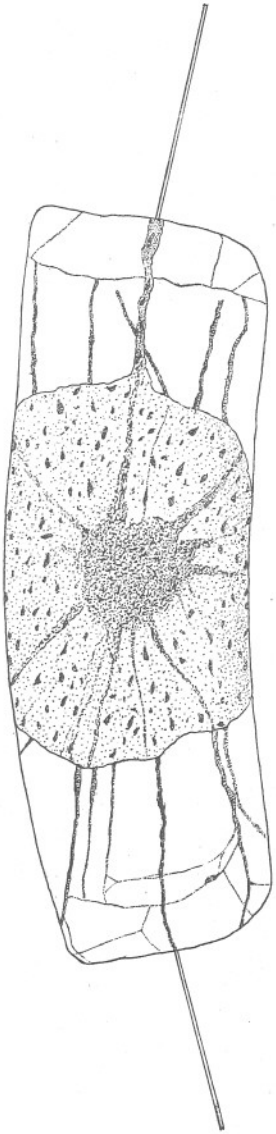

Fig. 18

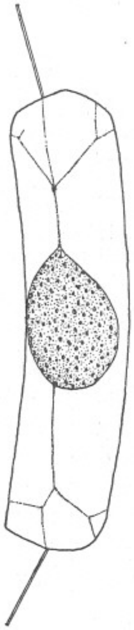

Fig. 19

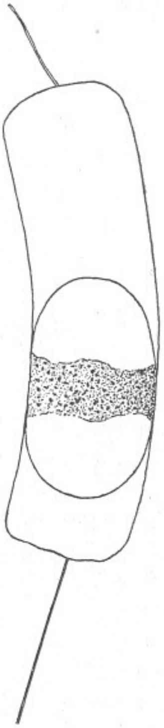

Fig. 20

Fig. 18. Plasmolysis of a cell kept in the dark for 16½ hr., in normal culture medium. ×450.

Fig. 19. Plasmolysis of a cell from a culture kept in half diluted culture medium after 6 days of darkness. ×450.

Fig. 20. Plasmolysis of a cell kept in normal culture medium after 6 days of darkness. ×450.

appearance as resting spores. Only a small number of cells had "resting spores" with a clear cap on one pole or structures like Fig. 20.

The effect of temperature has not been investigated in detail, but from experiments at different room temperatures and at varying low temperatures in an ice-box it appears that the rate of plasmolysis increases with rising temperature. Thus at temperatures varying from 19–22° C. (in June) spindle-shaped protoplasts were observed after 3–4 days, and the first resting spores after 7 days of darkness, while in May, at a temperature varying from 13 to 16° C., the "spindle" stage was only reached after 8–9 days and the first resting spores were formed on the 12th and 13th days.

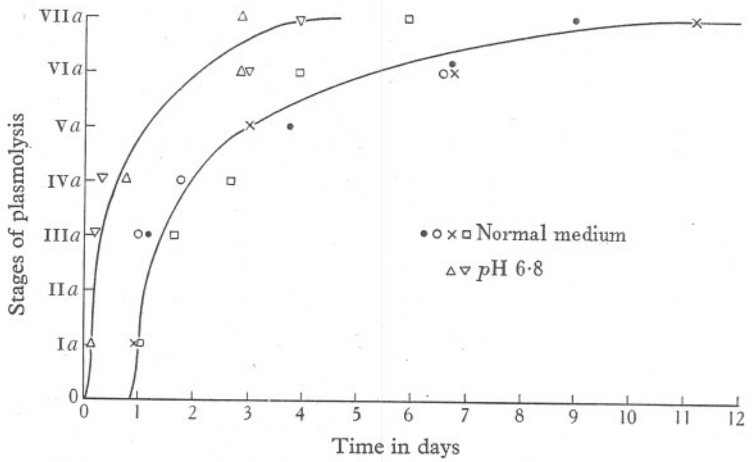

Fig. 21. Rate of plasmolysis in culture medium of normal pH, and at pH 6·8, in the absence of light.

In these experiments the only factor that could have been responsible for plasmolysis and the formation of resting spores was the absence of light and the inhibition of photosynthesis. Changes of the medium were of no importance. Plasmolysis occurred and resting spores were formed when single cells were kept in 2 ml. of culture medium and this was renewed daily.

After the formation of resting spores the cells were kept in the dark for another 3 weeks and more. When exposed to daylight they began at once to recover. In some cells the first "pseudopodia" were formed 15 min. after being placed in daylight and 5–7 hr. later the cells were quite normal. In others the beginning of recovery was delayed and the first protoplasmic processes formed only after 1–2 hr.

Ditylum kept in half-diluted culture medium responded to darkness in a very similar manner (Fig. 19).

It may be mentioned that whenever "double cells" were placed in the dark box the daughter cells always separated and grew to a considerable extent, and only then began to plasmolyse. On the other hand, long entire cells when placed in the dark often divided before they showed any sign of plasmolysis.

The fact that *Ditylum* invariably plasmolyses in the absence of light shows that light is essential for the maintenance of the cell turgor for periods longer than 15–22 hr. The explanation of this unusual phenomenon seems to be that the maintenance of the water content of the cells involves work and, consequently, the expenditure of energy, and that the reserve substances resulting from photosynthesis are, to a large extent, used up during 15–22 hr. of darkness. After that period the turgor cannot be fully maintained; the protoplast gradually loses the cell sap and collapses.

This suggestion is supported by the following experiments. Cells plasmolysed in 3·4% NaCl were transferred back into normal culture medium and the dishes were placed in a dark box. Without exception the cells began to recover. In one experiment the first "pseudopodia" formed by the resting spores could be seen under low power in less than 1 hr., and after 2½ hr. most of the thirty cells, used in this experiment, showed spindle-shaped protoplasts. After 21 hr. two long cells had formed a secondary valve and their protoplast filled only about one-third of the original length of the cell (Fig. 22) but had in all other respects the structure of the vegetative cell. A shorter cell was almost filled out by the protoplast; a few had narrow tube-shaped protoplasts and the rest contained "amoeboid"-shaped protoplasts. 24 hr. later there were four cells with secondary valves and correspondingly short protoplasts of normal structure; the other cells were not noticeably changed. During the following 2 days they did not recover any further, and the cells with the secondary valves plasmolysed again and assumed amoeboid shape. Gradually all cells returned to the stage of resting spores. After that when exposed to daylight they all recovered completely on the same or by the following day.

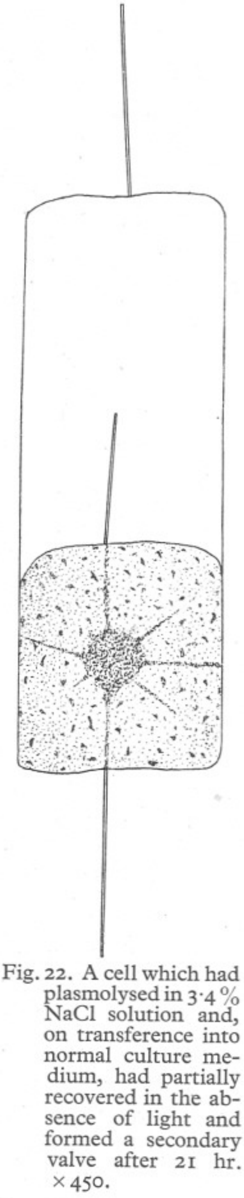

Fig. 22. A cell which had plasmolysed in 3·4% NaCl solution and, on transference into normal culture medium, had partially recovered in the absence of light and formed a secondary valve after 21 hr. ×450.

The experiments were repeated many times, some in an ice-box at a temperature of 6–8° C., and always with very similar results. All rapidly formed "resting spores" were capable of a partial recovery in the dark. Some short cells showed a temporary complete recovery and some long cells recovered to a certain extent and formed secondary valves. All of them, when remaining in the dark, plasmolysed and slowly returned to the resting stage.

It appears therefore that: (1) When cells kept in culture medium are placed in the dark their store of sources of energy is slowly exhausted and the actively maintained cell turgor gradually collapses. It can be built up again only in the presence of light. (2) When cells are rapidly plasmolysed in isotonic sodium chloride solution and then transferred back into culture medium and placed in the dark, the store of reserve substances is sufficient to provide energy for partial and temporary recovery of all cells, and the temporary complete recovery of short cells. During that recovery process the reserve substances become exhausted and therefore the protoplast gradually returns to the resting stage.

Both darkness and increased hydrogen-ion concentration (p. 397) have a plasmolysing effect on *Ditylum*. When the two factors are combined the effect is increased (Fig. 21). In some experiments resting spores were formed after 48 hr. at *p*H 6·8.

DISCUSSION

From the results of the experiments described in the preceding pages it seems that *Ditylum* does not fit into the normal concept of an osmotic system (see Lucke & McCutcheon, 1932). It does not obey the law of Avogadro-van't Hoff, since the protoplasts of the cells have quite different volumes in various electrolyte and non-electrolyte solutions isotonic with sea water. Moreover, their cell sap passes out of the protoplast and this diminishes in size when the cells are placed in solutions hypotonic to sea water.

The plasmatic membrane of *Ditylum* cannot be regarded as semi-permeable since the transfer of water between the cell and the medium is to a large extent independent of the difference in osmotic pressure between cell content and medium, and therefore does not follow the laws of osmosis and diffusion. For example, complete plasmolysis takes place in artificial sea water, while no plasmolysis occurs and the pressure exerted by the cell sap is maintained when the *p*H of the same solution is adjusted to that of natural sea water. The cells plasmolyse in half-diluted and 25% sea water, but may recover subsequently and continue growth and multiplication in these hypotonic media. They show only slight plasmolysis in sea water, the concentration of which has been raised to 4 and 5% salt, and here also complete recovery and, at 4%, growth can take place. Finally, complete plasmolysis is brought about by the absence of light, without a change in the concentration or any other change of the medium.

Since an osmotic system implies the presence of a semi-permeable membrane and an exchange of water between the cell and its environment subject to the laws of diffusion, the conclusion may be drawn that *Ditylum* does not behave as an osmotic system. The changes in the volume of *Ditylum* protoplasts which can be brought about by changes in the concentration and composition of the surrounding medium are not governed by the laws of osmotic equilibrium.

The factors which determine the exchange of water between *Ditylum* and its environment appear to be as follows:

(1) *Presence of sodium and calcium chloride.* In NaCl solutions the cell sap escapes and the plasma membrane retracts almost momentarily from the cell

wall, and in a few seconds the protoplast is reduced to a small resting spore. A similar reaction takes place in $CaCl_2$ alone. However, in a solution containing both NaCl and $CaCl_2$ plasmolysis is markedly delayed and resting spores are completed only after 4–8 hr. Thus in the presence of sodium and calcium chloride the rate at which water passes out of the cell is considerably reduced.

(2) *An appropriate hydrogen-ion concentration.* No water is lost by the cells in an artificial sea water of *p*H 8·0, while, in the absence of the buffer, the cells react similarly to those placed in a solution of NaCl and $CaCl_2$ alone. Cells plasmolysed in NaCl or in unbuffered artificial sea water recovered when transferred into buffered artificial sea water. Increase of the hydrogen-ion concentration of the normal culture medium leads to maximum plasmolysis at *p*H values below 6·0, and at *p*H 3 the rate of plasmolysis becomes as high as in NaCl solutions. The effect of *p*H is also very marked in solutions of $NaCl + CaCl_2$, but complete plasmolysis takes place at all *p*H values. In dextrose solutions there is a slight increase in the rate of plasmolysis with the increase of hydrogen-ion concentration, while the change of *p*H of NaCl solutions does not produce an appreciable change in their effect.

(3) *Metabolic activity of the cells.* The fact that the cells, when kept in the dark, are not capable of maintaining their full water content and turgor for longer than 15–22 hr. can, it seems, only be explained by the assumption that the cell constantly expends energy in work concerned with the maintenance of its turgor. The food stores resulting from a day's active photosynthesis are apparently greatly reduced during that short period, and the supply of energy becomes insufficient for the cellular activity necessary for the maintenance of the equilibrium between the water content of the cell and its environment. In 7–12 days the loss of water from the cell reaches its maximum and the protoplast its minimum volume.

It seems clear that we are not dealing here with true osmotic effects, and the question arises whether we may not be concerned with imbibitional phenomena. It was shown by Kotte (1915) and Walter (1923) that certain marine algae, on transference into strongly hypertonic salt solutions, exhibit marked swelling of the pectic membrane and comparatively little reduction in volume. Similarly, fertilized *Echinus* eggs, as found by Gray (1923–4), show only a slight reduction in total volume when placed in hypertonic sea water. The endoplasmic phase shrinks markedly, while the ectoplasm absorbs water and increases in bulk. The amount of water held by the ectoplasm seems to depend largely on the conditions which determine the uptake of water by imbibition, whereas the amount of water held by the endoplasm depends on the osmotic pressure of the external medium.

Comparable effects were observed by Wigglesworth (1933) in gill cells of mosquito larvae. If the intact larva is immersed in hypertonic NaCl, so that the inner membrane of the gills is still in contact with the haemolymph, the cells do not shrink but swell up enormously. "This is probably because the NaCl can diffuse into the cells through the outer membrane. The cells thereby become hypertonic to the haemolymph and absorb water from this by osmosis."

From a consideration of the cellular structure of *Ditylum* it appears that imbibitional effects do not account for the peculiar behaviour of this diatom in the various solutions. *Ditylum* does not possess a membrane comparable to the pectic membrane of the algae or the hyaline ectoplasm of the sea-urchin eggs, nor is it in contact with two different media as were the gill cells. The essential difference, however, seems to be that the protoplasm as such does not undergo any noticeable changes in volume during plasmolysis or recovery of *Ditylum*. When the cell passes into the stage of a resting spore the protoplasm, consisting of the central portion and several strands radiating from it, becomes concentrated to a spherical body without losing water to any noticeable extent. During recovery again only the distribution of the protoplasm is altered, it becomes decentralized, but only very slight swelling takes place, if at all; whereas considerable expansion of the protoplasm would result from the imbibition of large quantities of liquid. As mentioned before (p. 382), the chromatophores lose water during plasmolysis, but the amount of liquid held by them is insignificant compared with the cell sap which, in the vegetative cell, fills the large space not occupied by the protoplasm, and which is lost during plasmolysis.

The behaviour of the root tips of the eel grass, *Zostera marina* (Osterhout, 1913), shows a certain resemblance to that of *Ditylum*. The application of distilled water and fresh water causes in the cells of *Zostera* "false plasmolysis" i.e. a contraction of the protoplasm which often closely resembles the true plasmolysis produced by hypertonic sea water. These contractions are, however, as a rule irreversible, at least as soon as they have passed a certain stage. Osterhout saw the cause of these effects in an increase in the permeability of the semi-permeable plasma membrane, and of internal cell membranes, as the result of which some or all of the substances which maintain the osmotic pressure of the cell diffuse out; the protoplasm then shrinks as the result of loss of water from the vacuoles. This explanation, if correct for *Zostera*, would not apply to *Ditylum* which also plasmolyses in various isotonic salt solutions.

However, the most important fact which, to my knowledge, has no parallel among plant cells is the plasmolysis in the absence of light. As no change in the concentration of the medium occurred, and changes in the other qualities could be prevented by frequent renewing of the culture medium, it seems that the cell cannot be regarded as being in an osmotic equilibrium with sea water.*

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* It might be argued that carbohydrates dissolved in the cell sap normally help to maintain the osmotic pressure of *Ditylum* and that in the dark the carbohydrates are used up in respiration, with the result that the osmotic pressure is reduced and the cell plasmolyses. Against this may be said that if inorganic salts would contribute to the osmotic pressure, and the membrane were semi-permeable, the pressure should be reduced, and consequently plasmolysis should proceed, only to a certain extent, i.e. until an osmotic equilibrium is reached. However, plasmolysis in the absence of light is a continuous process leading to the maximum shrinkage of the protoplast, and we would have to conclude that the osmotic pressure is maintained exclusively by reserve carbohydrates dissolved in the sap. That this is not so is shown by the

The maintenance of the turgor is dependent on some metabolic activity which is reduced and finally stopped with the exhaustion of sources of energy, and the problem arises what kind of cellular activity is responsible for the maintenance of the turgor. It may be tentatively suggested that the cell sap of *Ditylum* is not isotonic but hypotonic to sea water. From this assumption it would necessarily follow that, unless the membrane is completely impermeable to water, the cell must possess a mechanism which prevents plasmolysis and maintains the low molecular concentration of the cell sap against the osmotic gradient. It is possible that the cellular activity involves the secretion of water inwards to make up for the loss of water outwards due to the permeability of the membrane to water; and that in the dark, owing to the exhaustion of reserve material, this secretion is gradually stopped.

In this connexion the fact may be considered that all cells plasmolysed in the various isotonic solutions recovered when placed in culture medium. Therefore the intake of water occurred either in the absence of an osmotic gradient or, if the cell sap is hypotonic to sea water, against the osmotic gradient. This would be explained by the assumption that the cell is actively secreting water from the outside inwards, perhaps in a similar way to the gut wall and the kidney which can effect a transference of water from a hypertonic solution to one which is more dilute. The possibility has been suggested that here the transfer is affected by an active metabolic process of secretion (see Gray, 1931).

This may also find support in the fact that the liquid present in the cells exposed to hypotonic media, or taken in rapidly on transference from hypertonic media into sea water, is never utilized in the process of expansion during recovery but is passed out prior to recovery (see pp. 385, 386, 403). Recovery is always a slow process (lasting at least 4–6 hr.) and involves the formation of fine pseudo pod-like protoplasmic processes, and gradual and uneven expansion of the protoplast along those processes (see also Gross, 1939).

The work required for the recovery of a resting spore is not linked up with the actual process of photosynthesis. Resting spores formed in crowded cultures will germinate in darkness at a temperature of 4–6° C. provided they are placed in fresh culture medium (Gross, 1937*b*). Artificial resting spores, formed in NaCl solutions, will also recover to a certain extent when placed in culture medium in the dark (p. 407). It is only when resting spores are formed in the dark in normal culture medium that recovery will not take place unless the resting spores are exposed to light. This shows that during the slow process of plasmolysis in the dark the available reserve substances become exhausted.

That the cellular activity concerned with the maintenance of the cell turgor is linked up with oxidative processes is indicated by preliminary experiments with cyanides which cause rapid plasmolysis of *Ditylum*.

behaviour of cells which have plasmolysed in a NaCl solution. When such "resting spores" are placed in culture medium in the dark they are capable of an almost complete, if only temporary, recovery (see p. 407). How, then, does the cell produce the necessary high concentration of carbohydrates in the absence of photosynthesis?

It may be noted that as regards the mechanism of diastole of the contractile vacuole it is also assumed (Kitching, 1938) that water is secreted into the contractile vacuole by the vacuolar membrane itself, while solutes are in general not able to enter the vacuole from the cytoplasm. The contractile vacuole is supposed to bale out water as fast as this comes in through the body surface, but to retain within the organism the cytoplasmic solutes. In *Ditylum* on the other hand, it appears that water is secreted into the cell as fast as it passes out through the body surface.

Evidence of perhaps a similar secretory work in plant cells was recently found by Bennet-Clark & Bexon (1939) who showed that the vacuolar sap of copper-beech leaves has an osmotic pressure of 8–11 atm., "that the hydrostatic pressure within the cells is about 25–35 atm., and that the difference is attributable to secretory work done by the living protoplasts".

The very rapid plasmolysis in NaCl and dextrose solutions suggests an increase in the permeability of the cell membrane to water in the direction inside-outside. McCutcheon & Lucke (1928), in experiments on *Arbacia* eggs, showed that small amounts of Ca and Mg were effective in slowing down osmosis in hypotonic dextrose solutions. A similar effect of Ca on the permeability of cells was found by Weil & Pantin (1931) in *Gunda ulvae*. It has also been found that the ectoplasm of *Echinus* eggs rapidly becomes unstable in the absence of calcium (Gray, 1923–4). In *Ditylum* there is apparently no antagonistic effect of sodium and calcium. Both together considerably delay plasmolysis, and this effect may be due to reduced permeability of the cells to water. The very rapid plasmolysis in respectively NaCl and $CaCl_2$ alone could then be regarded as loss of water caused by the membrane becoming unstable and highly permeable to water.

It is difficult to appreciate whether, and how, an increase of the hydrogen-ion concentration of the medium which has a strong plasmolysing effect on *Ditylum* also affects the permeability of the cell membrane to water. McCutcheon & Lucke (1928) suggest that increase in hydrogen-ion concentration of dextrose solutions tends to decrease permeability. Therefore, in order to reduce permeability in *Ditylum* the cell sap and not the surrounding medium should possess a high hydrogen-ion concentration. Preliminary experiments actually indicate that the cell sap in some other plankton diatoms, *Biddulphia sinensis* and *Coscinodiscus* sp., is acid in reaction. A *p*H of about 4·5 was found by placing, and in some instances crushing, those diatoms in an unbuffered fluid containing the indicator.

The effect of the decreased *p*H of the medium on *Ditylum* may perhaps be related to the effect of *p*H on the interfacial tension of the lipoid layer of the cell membrane. It was found that a solution of oleic acid which at *p*H 2 is not ionized at the interface and has an interfacial tension of 20 dynes, at *p*H 12 has a tension of about 1 dyne and is completely ionized at the interface (Harvey & Danielli, 1938).

There is little doubt that the formation and germination of resting spores is an important factor in the seasonal variation in the abundance of plankton diatoms in the sea. In *Ditylum* several conditions must be fulfilled to enable it to maintain the turgor of the vegetative cell. The absence of any of the three factors, detailed on p. 409, causes loss of water and the shrinkage of the cell membrane, in short the formation of resting spores.

The first condition, i.e. the presence of calcium and sodium, is always realized in the sea. It can only be of importance in the control of the penetration of the diatom into brackish water.

The second factor, i.e. an adequate *p*H of the medium, may be important in the control of the vertical and seasonal distribution. It has been suggested before (p. 398) that changes in the "local" *p*H around growing diatom populations might represent part at least of the "overcrowding" factor which has been recognized as one of the causes of resting spore formation.

The third factor, i.e. metabolic activity of the cells, is derived from the importance of photosynthesis for the maintenance of the cell turgor. Low light intensity combined with an increase in the CO_2 concentration of the water in which a large diatom population is suspended may cause plasmolysis and consequently the sinking of the diatoms in the sea. A large and actively respiring zooplankton population might have a similar effect.

SUMMARY

During resting spore formation *Ditylum* loses the cell sap and the volume of the resulting resting spore is one-third to one-twentieth of the cell volume.

Ditylum plasmolyses in 3·5–1.7 % NaCl solutions, and in a few seconds the protoplast is reduced to the size and structure of a resting spore. In 0·5 % NaCl there also occurs a considerable reduction in volume. The plasmolysed cells recover completely when removed into sea water. Rapid plasmolysis was also observed in isotonic and hypotonic dextrose and sucrose solutions and in solutions of $CaCl_2$.

In a solution of $NaCl + CaCl_2$ plasmolysis occurred in all cells, but it only began after 5–30 min. and was completed in most cells in 4–8 hr. In a mixture of NaCl, $MgCl_2$ and $MgSO_4$ the cells reacted as in NaCl alone; with KCl and $CaCl_2$ added to it (artificial sea water) the reaction was similar to that in $NaCl + CaCl_2$ only.

When the *p*H of the artificial sea water was adjusted to 8 all cells remained unchanged. Cells that had plasmolysed in NaCl or in unbuffered artificial sea water recovered on removal into artificial sea water of *p*H 8. The effect of NaCl solutions was the same at all *p*H values tested. In dextrose solutions there was a small, in $NaCl + CaCl_2$ and in sea water a very strong, increase in the rate of plasmolysis with increasing hydrogen-ion concentration.

The cells plasmolysed in hypotonic sea water, in a fresh-water medium and some even in distilled water. In hypertonic sea water of 3·9 to 4·9 % salt plasmolysis was slow and was followed by recovery in the hypertonic media.

In 6·4% salt the cells plasmolysed more rapidly and only recovered when brought back into normal culture medium.

Ditylum plasmolyses in the absence of light in normal culture medium. The retraction of the cell membrane began after 15–22 hr. and after 7–12 days the resting spores were completed. These could be kept for more than 3 weeks in the dark and when exposed to daylight they began to recover at once.

Cells which had rapidly plasmolysed in 3·4% NaCl solution and were brought back into culture medium and placed in the dark were capable of an almost complete but temporary recovery.

It is concluded that *Ditylum* does not behave as an osmotic system. The factors determining the exchange of water between *Ditylum* and its environment appear to be (1) presence of NaCl and $CaCl_2$, (2) a pH similar to that of sea water, and (3) a vital activity of the cells. It is suggested that the work involves the secretion of water.

The work reported above was started in 1936 at the Marine Laboratory in Plymouth where it was made possible by a grant from the Society for the Protection of Science and Learning, supplemented by the Jewish Scholarship of the Marine Biological Association, and later by a grant of the Development Commission. It was continued in the Department of Zoology of the Edinburgh University. The author would like to acknowledge his gratitude to all concerned with the allocation of those grants; and to Dr E. J. Allen, Dr Stanley Kemp and the staff of the Plymouth Laboratory as well as to Prof. J. Ritchie, his sincere thanks for their unfailing help, interest and encouragement. He is also indebted to Dr W. R. G. Atkins and Prof. J. Gray for valuable criticisms.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS PART V. NOTE ON THE GILLS OF *AMUSSIUM PLEURONECTES*

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 80, 1937–8, *pp.* 321–9

The gills of *Amussium pleuronectes* L., a species from shallow water, have been found to be plicate and heterorhabdic, thus differing in structure from those of the deep water species, *A. dalli*, *A. meridionale*, and *A. lucidum*, which Ridewood found to have flat and homorhabdic lamellae. The gills of *A. pleuronectes* closely agree with those of the Pectinidae also possessing plicate and heterorhabdic lamellae. It is concluded that Ridewood's classification of the Amussiidae with the Mytilacea cannot be upheld; the position of this family is with the Pectinacea as in Pelseneer's classifications of 1888, 1906, and 1911.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART VI. THE PATTERN OF THE LATERAL CILIATED CELLS OF THE GILL FILAMENTS OF THE LAMELLIBRANCHIA

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 80, 1937–8, *pp.* 331–44

The patterns of the lateral ciliated cells of the gill filaments have been examined in a number of lamellibranchs and figures given. In the Protobranchia the lateral ciliated cells, except for a row on the abfrontal side, have no definite shape or arrangement, the ends being pointed and interdigitating; in the higher lamellibranchs there is an orderly arrangement of the rhomboidal cells in rows. The arrangement of the cells in any species appears to be constant. In the group possessing micro-latero-frontal cilia the variation in the pattern in the various families is in marked contrast with the constancy of the general type of pattern found in the majority of the Eulamellibranchia.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART VII. LATERO-FRONTAL CILIA OF THE GILL FILAMENTS AND THEIR PHYLOGENETIC VALUE

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 80, 1937–8, *pp.* 345–436

Three types of latero-frontal tracts have been found in Lamellibranchs. The *first* is composed of large cilia, termed *eu-latero-frontal cilia*, together with subsidiary ones called *pro-latero-frontal cilia*, and is found in some or all of the three families of Protobranchia (presence of pro-latero-frontals doubtful in some families); in the Mytilidae and probably the Trigoniidae among the Filibranchia; and in the Eulamellibranchia (of Pelseneer, 1911). A list of the species investigated is given. The *second* is composed of small, tenuous cilia, termed *micro-latero-frontal cilia*, and is found in the Arcidae, Anomiidae, Pteriidae, Pectinidae, Spondylidae, Limidae, Pinnidae, and inferred to be present in the Amussiidae, Vulsellidae and Isognomonidae. A list of species examined is given. These forms were previously considered to lack latero-frontal cilia. The *third* is composed of moderate-sized cilia, termed *anomalous latero-frontal cilia*, together with subsidiary ones called *para-latero-frontal cilia*, and is found in the Ostreidae only.

In bivalves having eu-latero-frontal cilia the arrangement of the various ciliary tracts, frontal, latero-frontal and lateral is fairly constant, notable exceptions being a protobranch, *Nuculana*, and a filibranch, *Trigonia*. In bivalves having micro-latero-frontal cilia the arrangement of the various ciliary tracts is more or less constant.

The homology of the various types of latero-frontal cilia is discussed. The composition of the latero-frontal ciliated tracts has been found to be a constant character, and, as it is correlated with other characters, has taxonomic value.

It is suggested that the variations in the constitution of the latero-frontal tracts show that Ridewood's (1903) classification does not express genetic affinities, nor does Pelseneer's (1911) entirely, and that Pelseneer's order Filibranchia, and Ridewood's orders Eleutherorhabda and Synaptorhabda are not monophyletic.

Families possessing micro-latero-frontal cilia appear to be closely related, and form a group, which, with certain modifications, corresponds to "the Aviculidae and their allies" (Jackson), or the "sedentary" branch of lamellibranchs (Douvillé), previously established largely on shell characters. Thus the constitution of the latero-frontal tracts of the gills supports the findings of palaeontologists with regard to this group.

The relationship of forms with micro-latero-frontal cilia, and the evolution within the group of the eulamellibranchiate or synaptorhabdic gill are discussed. One family, the Ostreidae, which must be included on account of its relationship with either the Pteriacea or Pectinacea (based on other evidence) has anomalous, together with para-latero-frontal cilia. The anomalous latero-frontal cilia differ in certain respects from the eu-latero-frontal cilia characteristic of the majority of the Lamellibranchia, and are presumed to have arisen independently.

Common characters of the group with micro-latero-frontal cilia, in addition to the form of the latero-frontal cilia are: (1) shell characters of the prodissoconch, Arcidae excepted; (2) byssal fixation; (3) considerable free posterior region to the gill axes; (4) considerable development of the muscles of the gill axes, Ostreidae excepted; (5) method of division of the pallial cavity, Ostreidae excepted; (6) gills without a supra-axial extension to the outer demibranch; (7) presence of longitudinal currents at the free ventral edge of both inner and outer demibranchs, and of opposed frontal currents on all lamellae and frequently on the same filament, except in the Pinnidae; (8) absence of pallial sutures; (9) inner fold of mantle margin commonly well developed, especially in swimming forms; (10) insertion of retractor muscles of the mantle margin far from the shell edge, Arcidae excepted; (11) tendency for members to lie on the right valve, Ostreidae excepted; (12) abdominal sense organs on posterior adductor muscle; (13) intercommunication of auricles, Anomiidae excepted.

Two groups of Lamellibranchia are proposed provisionally; group I, Macrociliobranchia (latero-frontal tracts consisting of a row of eu-latero-frontal cilia, with also a row of pro-latero-frontal cilia in all or most members) with the orders Protobranchia (Pelseneer), Filibranchia (emended to contain only the Mytilacea and Trigoniacea), Eulamellibranchia (Pelseneer, 1911) and Septibranchia (Pelseneer): and group II, Microciliobranchia (latero-frontal tracts consisting characteristically of a row of micro-latero-frontal cilia) with the order Pseudolamellibranchia, emended to include the sub-orders Arcacea (less the Trigoniidae), Anomiacea, Pteriacea, Pectinacea, and Ostreacea. The Macrociliobranchia will need revision, for it is probable that the Filibranchia (emended), if not the Eulamellibranchia, are still not monophyletic.

D. A.

BIOCHEMISTRY OF THE ELECTRIC ORGANS OF *RAIA CLAVATA*

By Ernest Baldwin

Biochem. Journ., Vol. 32, 1938, *pp.* 888–94

A study was made of extracts from the electric tissue of *R. clavata* with reference to its power to catalyse the following reactions:

(1) Phosphoglyceric acid → phosphopyruvic acid;

(2) Phosphopyruvic acid + adenylic acid → pyruvic acid + adenylpyrophosphate;

(3) Adenylpyrophosphate + creatine → adenylic acid + creatine phosphoric acid;

(4) Adenylpyrophosphate → adenylic acid + phosphoric acid.

The power to catalyse these reactions is characteristic of all vertebrate muscles so far examined, and it has recently been shown that extracts from the electric organs of *Torpedo marmorata* contain enzymes capable of catalysing the same reactions. Extracts from *Raia clavata* have now been shown to possess the same catalytic properties.

Although, weight for weight, the electric organ of *Raia* is considerably less active than that of *Torpedo* and than muscle itself, the difference appears to be due to structural rather than to metabolic features, and it is probable that, in terms of the electrically active disc material, as opposed to connective tissue, the organ is no less active in *Raia* than it is in *Torpedo*.

There is thus reason to believe that in muscle itself, and in electric tissue derived by modification of muscular rudiments (as it is in *Raia* and *Torpedo* alike), we have a case in which different types of effector activity are subserved by common chemical mechanisms. Some preliminary experiments on the electric tissue of *Malapterurus electricus*, which arises from glandular rather than muscular sources, indicate that energy production is here attained by different chemical mechanisms. In electric organs of muscular and glandular origins, therefore, we have a case in which the same type of effector activity is subserved by different chemical mechanisms. E. B.

The Digestive System of *AMPHIOXUS* (*BRANCHIOSTOMA*) *LANCEOLATUS*

By E. J. W. Barrington

Phil. Trans. Roy. Soc. Lond. B, Vol. 228, *pp.* 269–311

In this paper an attempt is made to correlate structure and function in the digestive system of *Amphioxus*. A preliminary account of the cytology is given, and the ciliation is shown to give rise to a complex of ciliary tracts and currents. The cilia of the iliocolon ring set the food-cord into rotation along its longitudinal axis, and to the rotating cord are conveyed the digestive secretions produced in the "liver". These become mixed with the mass of food, together with secretions from the mid-gut, and portions of the mixed material are swept away from the rotating mass down the hind-gut, where absorption takes place. Some absorption probably takes place also in the mid-gut and in the "liver", but the general trend of the ciliation appears to be away from the latter region. It would seem that absorption, which is associated with the ingestion of solid material, can take place throughout most of the post-pharyngeal region, the limiting factor being the ciliary mechanisms. Some account is given of the nature and distribution of the digestive enzymes, and in conclusion the homology of the "liver" is discussed. It is suggested that it is at least as plausible to compare this organ with the intestinal diverticula of certain ammocoetes as with a true liver, and it is pointed out that these diverticula, which coexist with a well-developed liver, may themselves have some affinity with the pancreas of the higher Chordata.

E. J. W. B.

Oekologische und zellphysiologische Studien an Rotalgen der englischen Südküste

By R. Biebl

Beihefte zum Botanischen Centralblatt, Bd. 57, *Abt. A,* 1937, *pp.* 381–424

Die Lebensbedingungen an der Ebbelinie und in den Tidepools weichen stark von denen in grösserer Tiefe ab. In Uebereinstimmung damit zeigen die Rotalgen dieser Standorte eine verschiedene Resistenz gegen hypo- und hypertonisches Seewasser. Algen oberhalb der Ebbelinie besitzen eine osmotische Resistenzbreite von *ca.* 0·4–2·0 fach konzentriertes Seewasser, während Tiefenalgen nur einen Resistenzbereich von durchschnittlich 0·5–1·4 Seewasser aufweisen. Da die Rotalgen im allgemeinen sehr plasmolyseempfindlich sind, fällt meist die obere Grenze ihrer Resistenz gegen konzentriertes Seewasser mit der Grenzplasmolyse bewirkenden Konzentration zusammen. Die meisten Rotalgen der Ebbelinie und der Tidepools zeigen daher Grenzplasmolyse um 2·0 faches Seewasser, während die Tiefenalgen schon in 1·4–1·6 Seewasser zu plasmolysieren beginnen.

Nur *Ceramium ciliatum*, das seinen Standort an der Ebbelinie hat, besitzt trotz grosser Hypertonieresistenz einen niederen osmotischen Wert. Er entspricht 1·5 fach konz. Seewasser. Dieses Ceramium ist aber auch die einzige bekannte Rotalge, die Plasmolyse schadlos erträgt. In ähnlicher Weise zeigen plasmolyseunempfindliche Grünalgen (*Cladophora*) bei einer Resistenz gegen mehr als doppelt konzentriertes Seewasser einen niederen osmotischen Wert (1·3 Seewasser).

Sphondylothamnion multifidum stirbt schon bei Temperaturen unter +3° C. ab. Diese grosse Kälteempfindlichkeit wird als eine plasmatische Eigenschaft der Algen wärmerer Meere angesehen, die auch in anderen Verbreitungsgebieten beibehalten wird.

Die Untersuchungen wurden im Marine Biological Laboratory in Plymouth und an der Küste von Wembury (Süddevon) durchgeführt.

R. B.

ZUR PROTOPLASMATISCHEN ANATOMIE DER ROTALGEN

By R. Biebl

Protoplasma, Vol. 28, 1937, *pp.* 562–81

Die Methoden der protoplasmatischen Anatomie (Resistenzversuche, Zentrifugierung, Beobachtung von Plasmolyseformen und -zeiten, etc.) ermöglichen es auch an zahlreichen Rotalgen deutlich physiologische Unterschiede morphologisch mehr minder gleichartig aussehender Zellen festzustellen. So zeigen eine Reihe von Rotalgen mit flächigem Thallus (*Polyneura Hilliae*, *Cryptopleura ramosum*, *Cryptopl. ram.* var. *uncinatum*, *Nitophyllum punctatum*) gegen verdünntes Seewasser und andere Lösungen auffallend resistente Randzonen, die in Zentrifugierungsversuchen eine höhere Viskosität des Plasmas erkennen lassen. Sie werden als physiologischer Schutzsaum gedeutet. Andere Algen besitzen wieder besonders empfindliche Thallusrippen (*Phycodris rubens*) oder zeigen in Resistenzversuchen verschiedene Empfindlichkeitsgradienten. Dabei erweisen sich bei manchen Algen die älteren, bei anderen wieder die jüngeren Zellen als die empfindlicheren. Zentrifugierungsversuche ergeben in einigen Algen auch ausgeprägte Viskositätsgradienten, in denen die Zähflüssigkeit des Protoplasmas stets mit dem Alter der Zellen zunimmt (*Callithamnion tetragonum* var. *brachiatum*, *Antithamnion tenuissimum*, *Polysiphonia urceolata*).
R. B.

SOME NOTES ON SEX RECOGNITION IN *CARCINIDES MAENAS* (L.)

By G. J. Broekhuysen

Arch. Néerl. de Zool., Tome III, *Livr.* 1, 1937, *pp.* 156–64

The object of the study was to establish whether the copulating crabs find each other as the result of a stimulating chemical substance produced by the female under certain physiological conditions or whether the sense of touch and the reaction of the female to it, is responsible for sex recognition.

The results indicate that in *C. maenas* there is no distinct sex recognition and that the copulation is probably determined by the reaction of the female to touch.
G. J. B.

SOME CONDITIONS GOVERNING THE SOLUBILITY OF IRON

By L. H. N. Cooper

Proc. Roy. Soc. London, B, Vol. CXXIV, 1937, *pp.* 299–307

Existing data on the solubility products of ferrous and ferric hydroxides and in the ion, $FeOH^{++}$, have been used to calculate the maximum activities of Fe^{++}, $FeOH^{++}$, and Fe^{+++} which may exist in sea water.

The maximum activity of ferrous ion is controlled both by the activity of the ferric ion and by the oxidation-reduction potential of the system.

The total quantity of iron in true solution in water after equilibrium has been attained does not exceed

3×10^{-8} mg. iron per cubic metre at *p*H 8·5
4×10^{-7} „ „ „ 8·0
4×10^{-5} „ „ „ 7·0
5×10^{-3} „ „ „ 6·0

and of this the greater part consists of ferrous and $FeOH^{++}$ ions. In more acid solutions ferrichloric acids may have to be taken into account.

These values apply to iron in sea water, in natural waters and in many physiological fluids. L. H. N. C.

SELENOCYSTIS FOLIATA (RAY) FROM *SCOLELEPIS FULIGINOSA* CLPDE. AND ITS IDENTITY WITH *HAPLOZOON* SP.

By M. J. Dibb

Parasitology, Vol. XXX, 1938, *pp.* 296–308

The so-called parasitic dinoflagellate occurring in the gut of the polychaete worm *Scolelepis fuliginosa* Clpde. at Plymouth, is really the sexual phase of the gregarine "*Selenidium foliatum*" Ray.

The gametocytes (often very unequal) associate by their posterior ends while *in situ*. One remains attached and its epimerite is transformed into a foot-like organ serving to attach the gametocyst to the host throughout the rest of development. The gametocyst is elongate and pyriform and its formation involves very little alteration in the shape of the gametocytes. Solitary encystment also occurs.

Flagellated isogametes are formed. The spherical spores contain four or eight spindle-shaped sporozoites.

A new genus *Selenocystis* is proposed for this organism, with *S. foliata* (Ray) as the type species. Although schizogony has not yet been found, the probability is that it may still be classified among the schizogregarines.

M. J. D.

THE STRUCTURE AND FUNCTION OF THE ALIMENTARY CANAL OF SOME TECTIBRANCH MOLLUSCS, WITH A NOTE ON EXCRETION

By Vera Fretter

Trans. Roy. Soc. Edin., Vol. LIX, 1938, *pp.* 599–646

In *Philine aperta*, *Scaphander lignarius*, *Haminea hydatis* and *Actaeon tornatilis* the muscular buccal cavity, lined by a glandular epithelium, contains a radula adapted for manipulating the type of food upon which the animal feeds. In *Actaeon* an odontophore is absent. Salivary glands secreting mucus, and in *Philine*, *Scaphander* and *Haminea* a diastatic enzyme, open laterally into the posterior end of the buccal cavity. The oesophagus leads from the dorsal food channel to the stomach and consists of, save in *Actaeon*, a crushing gizzard separating the anterior from the posterior crop. Here extracellular digestion occurs and in these forms the stomach is reduced in size. In *Actaeon* the oesophagus is a simple muscular tube and the stomach is well developed and provided with an extensive caecum in which digestion takes place. Opening into the stomach are the ducts of the digestive gland and from it the coiled intestine, provided with glands concerned in the elaboration of the faeces, leads to the anus. In *Philine*, *Scaphander* and *Haminea* the digestive gland contains a protease, diastase, glycogenase and lipase.

Soluble products and small particles, which are derived from the action of enzymes upon, and the mechanical force applied to the food in the oesophagus, are passed through the oesophageal sphincter to the stomach. They are ingested by the digestive cells of the digestive gland and within these digestion is completed. The digestive gland undergoes a rhythmical cycle involving phases of secretion, absorption and excretion. It also acts as a kidney in taking up waste matter from the blood and building it into a compact form which leaves the body with the faeces. V. F.

THE STRUCTURE AND FUNCTION OF THE ALIMENTARY CANAL OF AEOLID MOLLUSCS, WITH A DISCUSSION ON THEIR NEMATOCYSTS

By Alastair Graham

Trans. Roy. Soc. Edin., Vol. LIX, 1938, *pp.* 267–307

The food of *Eolidina alderi* (*Heliactis bellis*), *Facelina drummondi* and *Cratena glotensis* (hydroids) is bitten off by the jaws and raked into the buccal cavity by the radula lubricated by the secretion of salivary glands and by mucus secreted by the pedal gland. In the stomach it is exposed to a protease secreted by the digestive gland. Soluble products of digestion are absorbed by the cells of the stomach and digestive gland; particulate matter is ingested by the latter and digested intracellularly. Indigestible matter accumulates in these cells and is later extruded with the faeces. Ciliary currents bear food particles to the gland and secretion and waste to the stomach. Owing to the absence of a mantle cavity there are no intestinal glands and the faeces are expelled in an uncompacted condition. As nematocysts do not discharge spontaneously in sea water they can be ingested undischarged; secretion of mucus aids in preventing discharge and in protecting the aeolid. The *p*H of the gut is too high to cause explosion. The mechanism of their discharge by aeolids is concluded to be mechanical pressure exerted by the contraction of circular muscles around the cnidosacs or by a predator. A. G.

Studies in the Pigmentary System of Crustacea. IV. The Unitary versus the Multiple Hormone Hypothesis of Control

By L. H. Kleinholz

Biol. Bull., Vol. LXXV, 1938, *pp.* 510–32

Experiments were performed to determine whether one or more than one hormone is involved in the control of the crustacean pigmentary system. Blood transfusions from black- and from white-adapted individuals into white-adapted *Crangon* evoked darkening in about 25 % of the test animals; injection of rostral region extract was only slightly more effective. Superficial cautery of the rostral region had no permanent effect on colour mutability; deep cautery in sixty-nine animals resulted in nine individuals which became permanently pale. Because all of these nine individuals were abnormal in their swimming and equilibratory movements, it is suggested that the results were due to injury of the brain and consequent interference with the regulation of Hanström's sinus gland. The validity of the unitary hormone hypothesis was subjected to biological test by a study of the retinal and integumentary pigments in *Hippolyte*, which had been reported to undergo a diurnal rhythm in the activity of the integumentary effectors. No persistent activity could be found in the retinal pigments of *H. varians*; *H. pleuracantha* showed a persistent cyclic rhythm of the distal retinal pigment, but not in the phase expected in *H. varians*. Further study showed that the reported periodicity of colour change in *H. varians* was due to a direct effect of darkness on the body chromatophores. Threshold limits of the retinal and integumentary cells to eye-stalk hormones were determined in *Leander adspersus*. The lower threshold limit for the distal retinal pigment was found equivalent to 0·016 mg. (wet weight) of eye-stalk; that for the integumentary pigment was 0·0008 mg. These values do not support the unitary hormone hypothesis which requires that the minimal threshold for the retinal pigments be lower than that for the body chromatophores. The responses of the distal retinal pigment to various concentrations of stalk extract are plotted in curves which show a direct relation between response and the injected dosage. L. H. K.

THE FEEDING MECHANISM OF THE OYSTER. I. ON THE PALLIUM AND THE BRANCHIAL CHAMBERS OF *OSTREA VIRGINICA*, *O. EDULIS*, AND *O. ANGULATA*, WITH COMPARISONS WITH OTHER SPECIES OF THE GENUS

By Thurlow Christian Nelson

Journ. Morph., Vol. 63, 1938, *pp.* 1–61

This study forms the first part of an investigation of the feeding mechanism of the oyster. Anatomical features formerly overlooked or unknown are shown to be important in this process. Separation of the mantle from the visceral mass on the right side in deeply cupped species of oyster provides a shorter channel for egress of water from the right demibranchs. Correlated with this change is reduction in size of the right epibranchial chamber beneath the adductor together with backward displacement of the adductor itself. This water passage, designated the promyal chamber, develops during the first week after attachment of the oyster larva. The greatest displacement of the adductor and the largest promyal chamber occur in *O. frons*. The mantle border shows three reduplications of which the innermost, the pallial curtain, controls the amount and the place of entrance and egress of water. The importance of pallial curtains and promyal chamber to survival in turbid waters is discussed; oysters with the promyal chamber have invaded the river mouths, the flat oysters without this chamber have remained in the clear waters of high salinity near the sea. The bearing of these factors on the disappearance of fossil oysters is considered. It is proposed to relate to the genus *Ostrea* all flat, larviparous oysters which lack the promyal chamber and to raise the subgenus *Gryphaea* to generic rank to include all deeply cupped oviparous oysters with the promyal chamber. Anatomical and histological features of the pallium and branchial chambers are considered in detail.

T. C. N.

ENZYMIC PHOSPHORYLATIONS IN INVERTEBRATE MUSCLE

By Severo Ochoa

Biochem. Journ., Vol. XXXII, 1938, *pp.* 237–42

In enzyme preparations from muscle of the common lobster (*Homarus vulgaris*) adenylic acid is ineffective in activating the transfer of phosphate from phosphopyruvic acid to arginine whereas, in absence of the latter, it is readily phosphorylated to adenosine triphosphate. Addition of arginine to the muscle extract a few minutes after incubation with phosphopyruvic and adenylic acids, results in a synthesis of phosphoarginine of the same order as can be obtained with equivalent amounts of adenosine diphosphate or triphosphate. Thus the presence of arginine appears to inhibit the phosphorylation of adenylic by phosphopyruvic acid. Manganese can replace equivalent amounts of magnesium in the enzymic transfer of phosphate from phosphopyruvic acid to arginine in lobster muscle extract. Owing to the ineffectiveness of adenylic acid and cozymase in this enzymic reaction, the observation of von Euler that some adenosine diphosphate is set free on mild alkaline hydrolysis of cozymase has been confirmed by a biological method. Fish muscle extracts (*Raia clavata*) also phosphorylate readily adenylic acid in presence of phosphopyruvic acid, even if creatine be present, so that adenylic acid activates here (as in other vertebrate muscles) the transfer of phosphate from phosphopyruvic acid to creatine. Neither is arginine esterified by *Raia* muscle extracts nor is creatine by those of *Homarus*. S. O.

COZYMASE IN INVERTEBRATE MUSCLE

By S. Ochoa and C. G. Ochoa

Nature, Vol. 140, 1937, *p.* 1097

A comparative study of the quantitative distribution of cozymase in muscle from marine invertebrates. Both the oxidized (CO) and reduced (COH_2) forms have been determined in fresh muscle and after 4 hr. autolysis at 18°. The strong tail muscle of *Homarus vulgaris*, the adductors of *Ostrea* and *Pecten* and the swiftly contracting mantle muscle of *Sepia* contain as much cozymase as mammalian muscle does (0·24–0·45 mg. per g.). Very little was found to be present in the less active muscles of *Metridium*, *Holothuria* and *Echinus*. The ratio CO/COH_2 is fairly constant (30–45% COH_2) in all the muscles examined and of the same order as in mammalian muscle. The amount of autolytic inactivation ranges from 30 to 50% of the cozymase originally present and is definitely lower than in mammalian muscle where it ranges from 80 to 95%. A certain parallelism was found between the content of cozymase and other phosphorus compounds particularly adenylpyrophosphate which is chemically and functionally related to cozymase.

S. O.

THE STOLONIZATION AND THE SEXUAL CHARACTERS OF THE STOLON IN THE SYLLIDIAN POLYCHAETES (Studies on the Syllidae. III)

By Yô K. Okada

Japanese Journ. Zool., Vol. VII, 1937, *pp.* 441–90

In this part of the serial study of Syllidian Polychaetes the process of schizogamy is investigated. The author has first made a general survey of the methods of stolonization in this group of animals, and has distinguished two different types of gemmation having distinct origin in *Trypanosyllis*, the synchronous plural formation of stolons in *Syllis ramosa* and the lineal successive production of new individuals in *Myrianida* and *Autolytus* beside the simple division of the body in two in other forms. The stolonization is compared with the process of regeneration, new animals being produced in the Syllinae on the median ventral surface of the last segment (sometimes more than one segment) of the stock with as many centres of proliferation as the number of resulted stolons, whereas in the Autolytinae the formation of new animals is limited to the posterior end of the stock with a common source for all individuals.

The position of stolonization is sometimes fixed. It varies in the Autolytinae only according to the rule of fragmentation. In any case, however, stolonization never occurs in the extremely anterior (before the 13th set. segment) or posterior part of the body.

Finally the development of the sexual characters in the stolon is analysed. The modification of the eyes and the cephalic appendages are intimately related (through humoral agents) with the ripening of the sexual elements in the gonad, whereas the change of parapodia including the elongation of setae, though it takes place likewise in close connexion with the ripening of the gonad, has no humoral connexion with the latter. Y. K. O.

THE RATES OF CONDUCTION OF NERVE FIBRES OF VARIOUS DIAMETERS IN CEPHALOPODS

By R. J. Pumphrey and J. Z. Young

Journ. Exp. Biol. Vol. 15, 1938, *pp.* 453–66

The rates of conduction of nerve fibres of *Sepia* and *Loligo* varying from 30 to 718 μ in diameter have been estimated from records of their action potentials, and the limits of conduction velocity found to be 2·2–22·8 m./sec. at 20° C. Although the fibres examined have different functions, and come from animals which differ considerably in structure and mode of life, yet the conduction rates of all of them can be expressed approximately as a single function of the diameter. That is to say they do not differ greatly from each other except in size. The exact relationship of conduction velocity to diameter cannot yet be determined, but is such that the velocity increases with a power of the diameter somewhat higher than the square root but less than the first power.

The possession of giant fibres produces a significant saving of time for the animal, it being calculated that the reaction time of a squid is about half that which it would be in a similar animal which possessed no giant fibres. The presence of rapidly conducting fibres is also an advantage in that it decreases the discrepancies between the times of contraction of parts of the mantle at varying distances from the central nervous system. In *Loligo* there is a graded series of fibres with the larger in the longer nerves, and this is apparently a further device for ensuring more nearly simultaneous contraction.

J. Z. Y.

A Revision of the Genus *Campanulina* van Beneden, 1847

By W. J. Rees

Ann. Mag. Nat. Hist., Ser. 11, *Vol.* 3, 1939, *pp.* 433–47

The revision of the genus *Campanulina* van Beneden, 1847, has resulted in the almost complete dismemberment of the genus. *C. tenuis* van Beneden 1847 (non 1866) has been shown to be the sole species of the genus. The other subsequently described species of "*Campanulina*" have been referred to other genera. The medusa-bearing species have been referred to four genera, viz. *Aequorea*, *Campomma*, *Phialella*, and *Eirene*, while the species with fixed gonophores have been placed in *Opercularella*. Species whose gonosomes are unknown are placed provisionally in *Opercularella*. W. J. R.

Further Observations on the Effect of Trematode Parasites on *Peringia ulvae* (Pennant) 1777

By Miriam Rothschild

Novitates Zoologicae, Vol. XLI, 1938, *pp.* 84–102

The sampling of large collections of *Peringia ulvae* from different localities and habitats established several additional points regarding the relationship of this mollusc and its trematode parasites. The study is complicated by the great variation which is found in size (growth), shell colour, shell shape and shell texture of the snail—probably due to environmental rather than genetic factors. In all collections, however, irrespective of growth conditions, trematode parasites were found to produce relative gigantism in the host, which involves both soft and hard portions of the body.

The normal sex ratio of *P. ulvae* also varies from sample to sample, but female specimens consistently outnumber males in the largest size groups and also attain greater dimensions. More males than female snails are infected with trematodes, sometimes the ratio was found to be as high as 16: 1. This fact in conjunction with the gigantism produced by the parasites, can combine to obscure or even reverse the normal difference in size usually displayed by the sexes. The penis of all infected males is abnormal, being greatly reduced in size, and it is possible that some infected snails without a penis are totally castrated males. There is also some evidence to support the theory that infected females grow a penis. This would explain the apparent excess of parasitized males, over females. M. R.

THE EXCRETORY SYSTEM OF *CERCARIA CORONANDA* N.SP., TOGETHER WITH NOTES ON ITS LIFE-HISTORY AND THE CLASSIFICATION OF CERCARIAE OF THE SUPERFAMILY OPISTHORCHIOIDEA VOGEL 1934 (TREMATODA)

By Miriam Rothschild

Novitates Zoologicae, Vol. XLI, 1938, *pp.* 148–63

The excretory system of a typical pleurolophocercous cercaria from *Peringia ulvae* (Pennant) 1777 was found to be of an extremely aberrant type. The main collecting tubes divide about the level of the ventral sucker and the flame cell pattern is $2\,[(2+2)+(2+2)]=16$. This illustrates once again that the greatest caution is necessary when using the excretory system as a basis for a natural classification.

Closely allied cercariae are notoriously difficult to distinguish specifically. The most important characters for differentiating between the pleurolophocercous cercariae from *P. ulvae* were found to be: (1) Shape and size of the body under a coverslip *at death*. (2) The precise extent, position and shape of the caudal fin-folds. (3) Pigmentation of the body. (4) Behaviour and length of life of the cercaria.

In the laboratory *Gobius ruthensparri* Euphras. serves as a second intermediate host. The cysts are situated in the lateral muscles of the body. The metacercaria develops a crown of 15 spines round the oral sucker and the anterior cornua of the excretory vesicle extend anteriorly into the oesophageal region. A gonotyl is present. Feeding experiments were unsuccessful, but from the morphology of the metacercaria it is thought that the fluke pertains to the subfamily Neochasminae Van Cleave and Mueller. M. R.

OCCURRENCE OF YOUNG *OPHIOTHRIX FRAGILIS* WITHIN THE GENITAL BURSA OF THE ADULT

By J. E. Smith

Nature, Vol. 141, 1938, *p.* 554

Recently metamorphosed *O. fragilis* are, on occasions, to be found within the genital bursa of the adult. The presence of young within the bursa of an adult ophiuroid has frequently been taken to indicate a viviparous habit. This is clearly an unjustified assumption since, in an oviparous species such as *O. fragilis*, the young forms must have entered the bursa after metamorphosing elsewhere. J. E. S.

LES MOUVEMENTS PROTOPLASMIQUES AU COURS DE LA FÉCONDATION DE L'ŒUF D'ASCIDIE

By G. Vandebroek

Arch. f. exper. Zellf. Vol. XIX, *pp.* 411–19

In this preliminary note on researches on the development of Ascidians, it is shown that from the moment of penetration of the spermatozoon till the first segmentation, deformations and protoplasmic movements occur in the egg of ascidians (*Ascidia aspersa* and *scabra*). Certain of these phenomena may be followed by the simple observation of eggs from which the membranes have been removed; others are only visible if stained marks have been made on the surface of the egg.

During this period, the egg exhibits bilateral symmetry four times. Stained marks show that this bilateral symmetry coincides exactly with the bilateral symmetry of the tadpole. The first of these deformations consists in the flattening of a lateral face immediately after penetration of the spermatozoon. This flat face will give rise to the mesoblastic face of the blastule. The occurrence of the same phenomenon after activation (by overstaining) indicates that the plan of bilateral symmetry pre-exists in the unfertilized egg. The formation of a flat face must be ascribed to a change of the surface tension on a heterogeneous mass. The three other deformations respectively coinciding with the emission of the first and the second polar bodies, and with the first karyokinesis, are correlated with the appearance of the spindle and aster figures.

Protoplasmic movements may be observed twice: (1) immediately after the penetration of the spermatozoon, whilst a constriction wave is being propagated from the animal to the vegetative pole; (2) on the moment of conjugation of the pronuclei. The first seems to be due to the change of surface tension already mentioned; the second to the displacement of the attraction sphere at the time of conjugation of the pronuclei.

Identical phenomena have been observed in *Ciona*, *Corella* and *Molgula*.

G. V.

THE PHOTIC CONTROL OF PIGMENTARY RESPONSES IN TELEOST FISHES

By Ursula Wykes

Journ. Exp. Biol. Vol. XIV, 1937, *pp.* 79–86

Many shallow water teleosts, e.g. *Gobius paganellus* and *G. ruthensparri*, *Ctenolabrus rupestris*, *Lepadogaster gouani* and *Phoxinus phoxinus*, when blinded, show a pigmentary response to photostimulation.

This response was analysed quantitatively in *Lepadogaster gouani*. The melanophores of the blinded animal contract in darkness and expand when illuminated by a 100 W. light. In the normal animal on a light background the latter response is checked by a secondary contraction.

The dermal response of these animals is thus closely comparable to that of the chameleon, and it is possible that it may be similarly controlled. No such dermal response was observed in *Pleuronectes platessa*.

It is evident from the experiments, however, that many colour-changing teleosts do exhibit pigmentary responses which are independent of visual stimulation and which depend on the intensity of the incident light.

U. W.

The Nature and Significance of the Membranes surrounding the Developing Eggs of *HOMARUS VULGARIS* and other Decapoda

By C. M. Yonge

Proc. Zool. Soc. Lond., A, Vol. 107, *pp.* 499–517

The developing eggs of *Homarus* are surrounded by two secreted membranes. The inner of these is of chitin and is secreted by the walls of the oviduct when the eggs descend. The outer membrane is identical in all respects with the cuticle which constitutes the outermost layer of the integument. This membrane is secreted by the numerous cement glands present in the pleopods of the female. These glands resemble in all respects the tegumental glands which secrete the cuticle. The eggs are attached to the non-plumose setae on the pleopods by strands of the same "cement". There is good evidence that the ducts of the cement glands open on these setae. The limited permeability of the outer membrane renders osmotic hatching possible. In *Homarus* fertilization is almost certainly external and the complicated nature of the spermatozoa is probably correlated with the necessity for penetrating the inner membrane. In decapod Crustacea there is an intimate association between ecdysis and egg-laying, the sequence of events being outlined. Egg attachment in the Decapoda thus represents the exploitation of a substance which forms the outer layer of the integument. The properties of this substance—low surface tension, slow solidification in water, final hardness and limited permeability—make it ideal for this purpose. C. M. Y.

NOTICES OF BOOKS

The Journal of Endocrinology

Volume 1, Number 1, June, 1939, pp. 1–116. Oxford University Press, England. Price 10s. net.

The rapid increase in knowledge of the physiology of reproduction, growth and allied subjects has greatly augmented the volume of research in this field in recent years. In America, *Endocrinology* has, for over twenty years, provided a special vehicle for the publication of papers dealing with this branch of science. In this country the literature has hitherto been scattered among physiological and medical publications. A separate periodical was clearly needed, and the *Journal of Endocrinology*, the first number of which appeared in June, fulfils this need. The new journal is published in attractive format by the Oxford University Press, and, under a distinguished Council of Management, it promises to occupy an important place in biological literature.

A. S.

Ecological Animal Geography

An Authorized rewritten edition based on *Tiergeographie auf oekologischer Grundlage* by Richard Hesse. Prepared by W. C. Allee and Karl P. Schmidt. New York: John Wiles and Sons. Inc. London: Chapman and Hall, Ltd. 1937

Those who know Prof. Hesse's *Tiergeographie auf oekologischer Grundlage* know how useful it is and the present authors have conferred a boon on those who read German with difficulty—moreover it has been rendered to a certain extent up to date since the German edition was published in 1926. The study of animal geography is now mainly concerned with the ecological side and this has advanced enormously during the last few years. Strictly scientific ecological studies are always being produced relating to every variety of habitat and to animals of all groups. To summarize such studies and to bring them together into a whole is a gigantic task and the authors besides translating the original work have incorporated much new material. That there should be important omissions is inevitable in such a work—notably the absence of reference to Yonge's studies of corals in the Great Barrier Reef (1931), especially with reference to the use of zoöxanthellae. One is tempted also to criticize certain passages, the term "sea-weed" for instance being applied solely to *Zostera* and its relatives, the life in the *Zostera* beds being described on page 180 and no mention being made of the larger algae (seaweeds in the ordinary sense) until page 201, which is misleading and confusing to the uninitiated. A few careless slips are in evidence, among others Figs. 103 and 133 describe respectively *Daphnia* and *Stygodytes* as copepods. Apart from such trifling errors, however, the work is most valuable and a splendid book of reference which should be in every library both public and private.

M. V. L.

Between Pacific Tides

By Edward F. Ricketts and Jack Calvin.

Stanford University Press, 1939. London: Humphrey Milford, Oxford University Press. xxii + 320 pp. 112 figs. + XLVI plates. 27*s*.

This book is an introduction to life between tide-marks along the Pacific coast of North America. The arrangement is on ecological lines, the text being divided into four main sections: Protected Outer Coast; Open Coast; Bay and Estuary; Wharf Piling. These sections are subdivided into rocky shores, sandy beaches, etc. under which headings animals are described more or less in the order in which they occur from high to low water mark. This latter part of the arrangement is not entirely satisfactory on account of the difficulties involved, but it is nevertheless a commendable idea that may be capable of improvement. Full accounts are given of the chief features and habits of several hundreds of species, the authors frequently referring to Atlantic and European species when these are better known than their Pacific counterparts. Plant life is for the most part ignored.

The numerous illustrations, photographs and line drawings, are gathered together for easy reference into four series of plates inserted after the sections of text to which they relate. While the half-tone reproduction leaves something to be desired it is clear that the original photographs themselves vary considerably in quality. The better ones are of living animals in their environments, but some are all too obviously pictures of dead specimens, while the photographic technique itself is sometimes none too good. The drawings likewise appear to have been made with differing degrees of care.

There is a comprehensive and annotated bibliography which, while not up-to-date as the authors themselves admit, is likely to be really useful to all students of sea-shore biology. An unfortunate error attributes books of the late Prof. James Johnstone to D. W. Johnson, the author of *Shore Processes and Shoreline Development*.

In spite of all criticisms this book is well worth reading, even by those not likely to reach the shores of the Pacific. The authors are evidently steeped in the natural history lore of shore animals, much of their knowledge being derived at first hand. Their text can hardly fail to stimulate many readers to go out and observe for themselves and that is perhaps the highest purpose that can be claimed for such a book as this.

D. P. W.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1938

The Council and the Officers.

Four ordinary meetings of the Council were held during the year in the Rooms of the Royal Society, London, at which the average attendance was eighteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used.

At the request of the Development Commission a meeting was held on October 17 1938, between the Commissioners and representatives of the Council. The meeting was called to consider ways in which the private income of the Association could be increased, for the view taken by the Commissioners is that the grant from the Development Fund, given primarily for fisheries research, is disproportionately large in comparison with the income derived from other sources. The Commissioners recognized that, apart from income, the Association has in recent years received considerable sums from non-Government sources for the purchase of special apparatus and equipment, as contributions towards the cost of publications, and in payment of the salary of an additional member of the staff, but they pointed out that the steady rise in the amount of the Government grant was not accompanied by a similar rise in private income. A careful examination of the position appeared to indicate that no large additions to the private income could be expected, but that if the Association were to receive the support of all working marine biologists a considerable increase would be made in the list of members. A note asking for increased support from biologists in this country has since been prepared and distributed.

Articles of Association.

At a special general meeting of the Association held on October 26 1938, in the Rooms of the Royal Society, London, a special resolution was passed which effected certain alterations in the Articles of Association. By the terms of the new Article 28, the Annual General Meeting of the Association will in future be held at such time and place as the Council shall from time to time determine, instead of being fixed for the month of April as heretofore. The new Article 21 determines that the annual contribution by members of the Association shall become due on the 1st of April, in advance, instead of on the 1st of January.

The E. T. Browne Bequests.

Under the Will of the late Mr E. T. Browne the following bequests are made free of death duties to the President and Council of the Association:

(i) £1500 to be held in Trust to cover the cost of the monograph on British Medusae now in course of preparation by Mr F. S. Russell, any balance after publication to be applied to the cost of publishing similar books on the British marine fauna.

(ii) £2000 to the building fund of the Association.

(iii) £2000 to be held in Trust for the provision out of the income of a special fund for the purchase of apparatus.

(iv) £1000 to be held in Trust for the provision out of the income of a special fund for the purchase of books for the library.

(v) All instruments and apparatus from his laboratory in Berkhamsted and all books that the Association may wish to select from his library.

Provision is also made in the Will for the payment of the salary of Mr W. J. Rees for the year 1938.

The Plymouth Laboratory.

The new constant temperature rooms, built with the aid of a grant from the Rockefeller Foundation and a gift from the estate of the late Dr Florence Buchanan, were completed in March. One room is at present kept at 7° C. and the other at 13° C., the variations from these temperatures not exceeding 1° C.

During the year the technical staff of the Laboratory has been increased by the addition of a Workshop Assistant. The store-room, situated above the packing shed, has been converted to serve as a workshop by raising the roof and inserting a window on the north side.

The room on the second floor of the main building, formerly the workshop, has been renovated and will be used for research. It will be known as the Browne Memorial Room, in memory of the late Mr E. T. Browne, and will contain furniture from Mr Browne's laboratory and the valuable reference library on Coelenterata which he bequeathed to the Association.

A scheme for the renovation of the old laboratory building and for the construction of a new floor has been approved by Council and the work began in November. When completed this scheme will give more rooms for research workers and greatly improved accommodation for some of the permanent members of the staff. The existing experimental salt-water tanks on the first floor will be reconstructed on more convenient lines, and the old heating system which serves all the buildings will be renewed. The service lift will be refitted, space and suitable cases for the reference collection of the British marine fauna will be provided, and the old library will be converted into a common room for the use of members of the staff and visiting workers. The cost of the scheme is estimated at £7250 and the Association has been promised a Government grant of £3000 from the Development Fund for the heating installation, furnishing and equipment, provided that the remaining £4250 can be met from other sources. The Council has allotted £1000 from the Browne bequest towards the building scheme and wishes to express its grateful thanks for the generous subscriptions shown on p. 452.

During the work of reconstruction, members of the staff affected have been accommodated in the north building, but it is hoped that the first floor will be ready for reoccupation by the end of March 1939 so that the normal influx of visiting workers at Easter will not create any difficulty. It will be necessary, however, to close the public tank room for a short period during the winter for the erection of new steel pillars.

The Aquarium.

The Aquarium has been well stocked throughout the year; it has been well attended by visitors and numerous parties of school children. There has been no change in the general character of the exhibit and the circulating plant has remained in good order throughout the year. The general health of the fishes has been very good, most of those now present, together with many of the invertebrates, having been in the aquarium for several years.

The Ship and Motor Boat.

The steam-drifter *Salpa* and the motor-boat *Gammarus* have given continuous and satisfactory service throughout the year.

The Staff.

At the meeting of the British Association held in Cambridge Dr S. Kemp presided over the Zoological Section. He attended the meeting of the International Council for the Exploration of the Sea, held at Copenhagen in May, on the invitation of the Council, and was also present at a Committee meeting in November.

During the year Mr F. S. Russell was elected a Fellow of the Royal Society.

Dr M. V. Lebour was granted one year's leave of absence in May; during this period she is continuing her studies of molluscan and crustacean development at the Bermuda Biological Station.

Arrangements have been made for Mr W. J. Rees, whose salary has hitherto been met by the late Mr E. T. Browne, to continue his work at the Laboratory until the end of the year 1939. Mr P. R. Crimp has been appointed Student Probationer in place of Mr P. H. T. Hartley and began work at Plymouth on February 1 1938.

With the consent of the Treasury a superannuation scheme for the senior laboratory assistants and technical staff of the Laboratory has now been introduced, and the senior members of the crews of the *Salpa* and *Gammarus* after long and satisfactory service will henceforth be eligible to a gratuity on retirement. Mr J. T. B. Martin, leading deck-hand in the *Salpa*, has been obliged to retire owing to ill-health, and a small gratuity has been obtained for him.

Mackerel Investigations.

A meeting of a subcommittee appointed by the International Council for the Exploration of the Sea to study technical methods in mackerel research was held at the Plymouth Laboratory on December 8 and 9 1937, and was attended by representatives from France, Germany, Denmark, Portugal, Eire and England. A profitable discussion was held in the course of which the work in progress at Plymouth was explained and demonstrated. At the meeting arrangements were made for collaboration between France, Eire and England in mackerel investigations to the west of the entrance to the English Channel, and a joint programme of research was undertaken by research ships from the three countries during April 1938.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

H. R. Barer, London (Force-velocity relationships of marine animals).
Dr E. J. W. Barrington, Nottingham (Digestion in *Amphioxus*).
R. Bassindale, Manchester (Nervous system of *Balanus*).
Miss F. L. Beanland, Southsea (Shore fauna).
Dr A. M. Bidder, Cambridge (Library).
Dr E. C. Bullard, Cambridge (Testing apparatus at sea).
M. D. Burkenroad, Yale, U.S.A. (*Ligia*).
C. Cheng, China (Parasites from marine fishes).
H. A. Cole, Conway (Library).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
D. J. Crisp, Cambridge (*Protodrilus*).
Dr G. E. R. Deacon, "Discovery" Committee (Library).
Miss M. J. Dibb, London (Gregarine parasites of polychaete worms).
J. E. Forrest, London (Anatomy and physiology of nudibranchs).
H. C. Gilson, Cambridge (Mollusca).
Dr H. Gohar, Edinburgh (Library).
R. Goode, Cambridge (Nervous organization in *Calliactis*).
Prof. E. S. Goodrich, Oxford (polychaetes).
Dr H. Pixell-Goodrich, Oxford (Protozoa).
Dr L. Gravel, Quebec (Library).
Miss R. F. Griffith, Birmingham (Movements of crown of serpulids).
J. A. Harpman, London (Nervous system of jellyfish and *Actinia*).
Dr J. E. Harris, Cambridge (Development of swimming in embryo dogfish).
Dr B. Havinga, Amsterdam (*Zostera*).
G. A. C. Herklots, Hong Kong (General).
W. Holmes, Oxford (Colour change in cephalopods).
C. F. Hickling, Lowestoft (Pilchard fishery).
Dr G. F. H. Houben, Amsterdam (*Zostera*).
H. H. Howells, Bristol (Digestion and mantle currents in tectibranchs).
F. Hsüch, Liverpool (Herrings).
Dr M. W. Jepps, Glasgow (Foraminifera).
R. R. M. Jones, Anglesey (Museum).
Miss I. C. Ledingham, London (Physiology of *Arenicola*).

Dr O. Löwenstein, Exeter (Physiology of the labyrinth).
Dr A. Lysaght, London (*Littorina*).
E. G. MacGregor, Cambridge (Nervous organization in *Calliactis parasitica*).
D. W. le Mare, Oxford (Library and methods).
Miss M. F. Mare, Cambridge (Microfauna and flora of mud deposits).
J. S. Marr, "Discovery" Committee (Library).
D. J. Matthews, London (Chemistry of seawater).
H. D. Metten, London (Ovulation in *Scyllium*).
Father W. B. Murphy, Dublin (General biology).
Dr E. H. and Mrs Myers, La Jolla, California (Foraminifera).
Dr C. L. Oakley, London (Parasitic Copepods).
Dr and Mrs A. Örström, Stockholm, Sweden (Metabolism of eggs of *Echinus*).
Miss M. R. Osborn, Cambridge (Locomotion in *Asterias*).
Dr N. K. Panikkar, London (General biology).
Dr and Mrs C. F. A. Pantin, Cambridge (Feeding in *Anemonia*).
D. A. Parry, Bristol (Feeding and digestion in *Sagitta* and *Spadella*).
W. Neil Paton, Oxford (Library).
Miss M. L. Popham, Bristol (Studies on the Leptonidae).
Miss E. A. Potter, Tetbury (Fertilization of *Gammarus*).
Mrs A. Raunkier, Lyngby, Denmark (General zoology).
Dr C. J. A. Reigersman, Amsterdam (*Zostera*).
D. M. Ross, Cambridge (Neuromuscular transmission in sea anemones).
Miss A. Rothschild, London (Life cycle of trematodes).
The Hon. M. Rothschild, London (Parasitic trematodes).
Dr W. A. H. Rushton, Cambridge (Nervous system in cephalopods).
Dr O. H. Schmitt, St Louis, U.S.A. (Nervous system of cephalopods).
B. Sievers, Stockholm, Sweden (General biology).
Miss F. A. Stanbury, Plymouth (Silica in diatoms).
Miss E. M. Stephenson, Exeter (Measurements of light intensity).
Miss O. F. Tassart, London (Library).
H. J. Thomas, Bristol (Development, feeding and digestion of *Balanus*).
I. M. Thomas, Cardiff (General).
T. G. Tutin, Cambridge (*Zostera*).
A. M. Vardy, London (Library).
Prof. M. Watanabe, Japan (Library).
G. Weaver, Sandown (Library).
G. P. Wells, London (Physiology of *Arenicola*).
H. P. Whiting, Cambridge (Development of swimming in the embryo dogfish).
Prof. H. Woollard, London (Nervous system of jelly-fish and *Actinia*).
Dr K. S. Wu, Nanking, China (Physiology of *Arenicola*).
Prof. C. M. Yonge, Bristol (Biology of *Nucula*. Mantle cavity of Gastropoda and Amphineura).
J. Z. Young, Oxford (Nervous system of cephalopods).

Mr D. P. Wilson and Mr G. A. Steven conducted the usual Easter Vacation Course in Marine Biology which was attended by forty-two students from the Universities of Oxford, Cambridge, London, Edinburgh, Liverpool, Birmingham, Bristol and Exeter, and Wycliffe College, Gloucester.

A course of Marine Biology was conducted by Prof. J. H. Orton during the Summer Vacation; this was attended by twelve students from Cambridge, London, Leeds and Wellingborough.

During the Easter Vacation, Mr J. M. Branfoot brought three students from Oundle School, Mr P. H. F. White three from Harrow, Mr B. W. H. Coulson and Mr I. Hamilton eight from Dauntsey's School, Mr A. H. Wood three from Bradfield College, Mr M. A. Moore two from Shrewsbury School, Dr W. L. Francis two from Repton School, Mr H. C. W. Wilson three from Malvern College, Mr A. H. Lewis two from Wellington College, Mr J. M. Bennett five from Monkton Combe School, Mr R. H. Pott and Mr B. A. Barr four from Stowe School.

The yacht *Culver*, which has recently been bought and equipped by the Royal Society for oceanographical work at Bermuda, called at Plymouth in June and was inspected by members of the Royal Society Committee. In July Prof. Helland Hansen and Dr Mosby called at the Laboratory on their return from a hydrographical expedition in the Atlantic in the *Armauer Hansen*.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment

The British Medical Association held their Annual Meeting in Plymouth during July and delegates visited the laboratories to see the exhibits and demonstrations arranged for the Section of Physiology and Biochemistry. Dr W. R. G. Atkins acted as a Vice-President of this Section and opened a discussion on Light in Relation to Climate and Health. Earlier in the year Dr Atkins lectured at the four Dutch Universities.

The Report of the Sub-Committee of the International Council for the Exploration of the Sea dealing with the measurement of submarine daylight has now appeared. Dr H. H. Poole and Dr W. R. G. Atkins contributed to it, and they have continued to collaborate in further work at Plymouth on the angular distribution of light in the sea. With a new photometer, it has even been possible to measure the green and blue light coming upwards at a depth of 70 m. at Station E1. Photo-electric cells have been standardized for workers in South Africa and in Burma, and measurements of nocturnal illumination have been made in connexion with Miss E. M. Stephenson's work on the colour changes of shrimps.

Dr Atkins has shown that neither the sunshine records of the British Isles for the last forty years, the total radiation measurements for a much shorter period, nor his own measurements of daylight at Plymouth, support the suggestion that the wasting disease of *Zostera marina* is in any way due to lack of light. He has also contributed a review of our knowledge of the illumination in algal habitats to the Kylin Number of *Botaniska Notiser*.

Dr L. H. N. Cooper and Mr A. Milne have applied the Pulfrich photometer with its eight spectral filters to the measurement of under-water illumination in the Tamar estuary. They found that the estuary was invariably more turbid than the open sea and that the zonation of algae on buoys is closely related to the amount of light received. Subsequently more accurate figures appeared for the extinction coefficient of red light in distilled water, required as a correction term, and a revision of the results for red light has therefore been made. Red light of wave-length around 600 mμ penetrates best. That part of the absorption due to dissolved and suspended solids is inversely proportional to the wave-length.

The uncertainty which surrounded the salt error in determinations of phosphorus in sea water has been largely resolved by Dr Cooper so that he has now been able to compare the routine phosphate observations at International Station E1 during the last six years with his own and Dr Atkins' earlier observations. In the nineteen-twenties the winter maximum for phosphate, representing the stock available for plant growth in the following spring, averaged 0·67 mg.-atom P per cu. m. Since 1930 it has averaged only 0·47 mg.-atom and the fall shows a close correlation with the decrease in abundance of summer spawning young fish in the English Channel observed by Mr F. S. Russell, and with the decrease in the easting of the residual current at the Varne lightship in the Straits of Dover observed by Dr J. N. Carruthers. Comparison with Mr D. J. Matthews' analyses made on water taken near the Knap Buoy in 1916 and 1917 supports the view that the rich phosphate of the nineteen-twenties was carried in by the inflow of warm Atlantic water in 1921. There is as yet no evidence of any enrichment of phosphate in the English Channel which might lead to better survival conditions for the plant and animal plankton and young fish and would ultimately result in improvement in the commercial fisheries of the south-west.

Further advance in the studies of the iron cycle awaits a fuller knowledge of the physical chemistry of 2:2′-dipyridyl and of the intensely coloured complex it forms with ferrous-ion. Dr Cooper finds dipyridyl to be a very weak base, its first dissociation constant being about $1{\cdot}2 \times 10^{-10}$. Its second dissociation constant is only slightly smaller, but uncertainty as to the activity coefficients involved in the second stage dissociation has so far prevented its accurate evaluation. These results confirm the view that the sudden reduction in the rate of formation of the ferrous-dipyridyl complex from its components in solutions more acid than *p*H 3 is due to the formation of dipyridylium ions from the neutral molecule which alone can react with ferrous ions.

Plankton

Dr H. W. Harvey has, during the past year, worked on the growth of the diatom *Ditylum brightwelli* in natural and artificial sea water. It was found to make a moderate vegetative growth in offshore sea water, collected between October 1937 and the early summer of 1938 and enriched with phosphate, nitrate and iron. Waters collected before and after this period, similarly enriched, would not allow a vegetative growth to take place. Nor would "winter-collected" waters, which had been stored for several months in glass vessels and similarly enriched, support a growth of the diatom. It has been found that the inability of these stored waters to support growth is primarily due to lack of manganese. If this is added in the form of a manganous salt, bringing the concentration to that found by Thompson and Wilson in Pacific waters, the diatom would make a moderate vegetative growth in the stored waters. The addition of manganese was also found to allow growth in a freshly collected offshore water (November 1938), in which the diatom would make no growth without such addition.

In artificial sea water, containing Na, Ca, Mg, K, Fe, Mn, silicate, nitrate, phosphate, chloride and sulphate, the diatom would make no growth, or very little growth. On adding a water extract of soil or marine algae, it would grow vigorously and yield a moderate crop, producing 1000–2000 cells per c.c. The active principles in the algal extract were separated into two groups, by adsorption on carbon and by continuous extraction with butyl alcohol. The activity of the fraction adsorbed on carbon appears due to an organic acid having either basic properties or many hydroxyl groups. An active preparation has also been prepared from winter-collected offshore sea water by adsorption on carbon. It has been found that several compounds containing the $—SCH_2CH(NH_2)COOH$ group have a similar effect upon the growth of *Ditylum*. The activity of the other fraction, not adsorbed on carbon and extracted by butyl alcohol, appears due, in part at least, to organic compounds. Several breakdown products of living organic matter, as lactic acid, gluconic acid and alanine, have shown activity. Adding a preparation containing either fraction only to artificial sea water has little or no effect; a vigorous growth results only if both are added.

In experiments with stored winter-collected sea water, enriched with nitrate, phosphate and iron, but deficient in manganese, the addition of soil or algal extracts allows vigorous growth and a considerable crop of the diatom. Both fractions were necessary. If a compound containing the —*SR* group and gluconic acid were added, both to the extent of 2 mg. per litre, a moderate crop was produced, the growth being limited finally through lack of manganese. With 0·02 mg. per litre of manganese added to the water these two compounds when added in addition, increased the growth due to the addition of manganese only; the growth was then limited through lack of silica. With these two compounds, manganese and an ample supply of colloidal silica, very heavy growths exceeding 20,000 cells per c.c. were obtained.

Samples of water collected during the course of the late summer and autumn of 1938, after similar enrichment with phosphate, nitrate and irons, did not behave alike. Some would allow a moderate growth of the diatom after the addition of —*SR* only, others would not. It has not been determined whether the latter lacked the second organic accessory or manganese or both. An offshore water collected in November 1938 allowed a moderate growth on the addition of manganese only, the cells growing abnormally long in comparison with their diameter, which is symptomatic of lack of the —*SR* accessory.

Mr F. S. Russell has continued to keep watch on the changes in the animal plankton off Plymouth as shown by the weekly ring-trawl collections. The results for the year 1937 have been published and the 1938 collections have been examined up to date. The year 1938 has been remarkable for the almost complete absence of *Sagitta elegans* at all times.

Mr Russell has devoted much time to work on the monograph of British medusae. In this connexion he has been making a study of the nematocysts of medusae and their value as characters for use in classification. A report on the nematocysts of twenty species has been published. While the affinities of various species of Anthomedusae are clearly shown by their nematocysts, it seems doubtful at present whether they will afford any help in tracing the phylogenetic relationships of the Leptomedusae. The nematocysts have, however, proved of value in distinguishing certain species of *Aequorea* which have always been a source of considerable difficulty.

Mr W. J. Rees has continued his work on hydroids and medusae. The dismemberment of the genus *Perigonimus*, resulting from the discovery that the medusa of *P. muscoides* (the genotype) is a *Bougainvillia*, has necessitated the devotion of much time to the study of hydroid literature. The genus *Rhizorhagium* has also been revised and a new species, *R. album*, has been described from the Cornish Coast. Variations in the form of the hydroid of the medusa *Leuckartiara octona* have been studied and it has been shown by rearing the medusa that the hydroid previously known as *Perigonimus sessilis* is this species. A medusa obtained from the hydroid *P. abyssi* belongs to the family Pandeidae and is almost certainly a species of *Leuckartiara*. The above results, together with observations on *Boreohydra simplex*, *Campanulina paracuminata* n.sp., *Corymorpha aurata*, *Rhizorhagium roseum*, *Stauridium productum* and *Thamnostoma russelli* n.sp., have now been published in the *Journal*.

A small hydroid of the *Syncoryne* type, living on and in the substance of a sponge, liberated young medusae in the Laboratory and these have proved to be young specimens of the medusa *Dipurena halterata*. The hydroid of this interesting medusa was previously unknown.

In connexion with his work Mr Rees went to Valentia Harbour, Co. Kerry, for six weeks during the summer and brought back a representative collection of the medusae to be found there. Among these were several specimens of the little known medusa *Bougainvillia pyramidata* and a specimen of *Phialidium hemisphaericum* with five radial canals. Mr Rees received a grant from the Royal Society to cover his expenses at Valentia.

Fauna of the Sea Floor (Ecology, Physiology, Genetics)

Further progress has been made in investigations on the estuarine fauna. A series of papers on the ecology of the Tamar Estuary has been started, of which three have so far been published. Investigations on the intertidal macrofauna are being prepared for publication in the next number of the *Journal* by Mr G. M. Spooner.

Mr Spooner has begun investigations on a populous but hitherto somewhat neglected section of the estuarine fauna, which seeks the cover of clumps of weed and deposits of leaves, and is apt to be overlooked by the more usually employed methods of collecting. It was found that crustaceans of the genus *Gammarus* form by far the most numerous and widespread element of this fauna, and special attention has been given to them. Evidence is growing that they are quite as, if not more, important than shrimps and mysids as food for bottom-feeding fish.

The genus colonizes the whole range of estuarine and brackish waters from the sea to fresh water, from near high water mark to the permanent channel. Several species are involved, each with its own salinity preference, or other environmental requirements, and there are enough of them to cover the whole range of environment provided in the estuarine zones. It has been shown that their ranges are extremely clear cut. *G. locusta* penetrates from the sea up the river channels and lower tidal zone to a point at which the salinity at low water falls to about 7 parts per thousand. *G. marinus* lives in the upper and middle tidal zone considerably higher up the estuary, until in fact the tidal range has become so reduced that there is scarcely sufficient intertidal zone for it to colonize. *G. locusta* is replaced, with some overlapping, by a variety of *G. zaddachi* and *G. chevreuxi*, and these latter in turn by *G. pulex* in purely fresh water. All these species occupy identical habitats and occur alike in extremely muddy surroundings, as in the Tamar, or on clean sand, as in the South Devon Avon. The limits of their ranges are clearly decided by the salinity conditions alone. *G. duebeni* also occurs widely in brackish ditches, streams flowing into the tidal area of estuaries, splash pools on the coast, etc., but does not enter into the estuarine series.

Special attention has been given to the strictly estuarine *G. zaddachi*. It was found that specimens from the more saline part of the species' range could be distinguished from the typical form inhabiting waters of lower salinity by certain conspicuous though superficial characters. Investigation showed that the two types do not intergrade, but keep quite distinct even in the region of overlapping. Experiments in the laboratory were conducted to test the nature of this morphological difference. These have already progressed far enough to show that both forms bred perfectly true in a wide range of salinities, and moreover that they cannot produce eggs capable of developing into embryos when crossed. The biological problem presented has further points of interest and is being followed up. The possibilities of using samples of *Gammarus*, sieved from weeds or other debris near low-water mark, as "biological indicators" of the salinity conditions prevailing at different points in an estuary are considerable.

Examination of large numbers of *Gammarus* has led to a closer appreciation of the systematic characters and data have been collected for a revision of the genus, which has long been badly needed in this country. This side of the work is being conducted in collaboration with Mrs Sexton. Three undescribed species, discovered by Mrs Sexton some years ago, have been rediscovered in numbers on the coast near Plymouth, and another species imperfectly described from Scotland, has also been obtained in numbers.

In February 1938, an investigation of the microfauna of the intertidal muds in the River Tamar estuary was begun by Mr P. R. Crimp. The mud flats, which form such a conspicuous feature of this estuary, harbour in their surface layers a rich fauna of small organisms such as free-living nematodes, copepods of the suborder Harpacticoida, and ostracods, as well as of the more minute flagellates, Infusoria, etc., which however do not come within the scope of the present work.

A quantitative study of the distribution of the microfauna is of obvious interest from the point of view of the ecology of the estuary, but no previous work has been done on these lines. A technique has now been devised for the quantitative estimation of the fauna, and samples are being collected regularly from a number of stations spaced out so as to cover the whole area of the estuary.

In this way it is hoped to obtain a complete picture of the distribution and density of population of the more important species in the microfauna, which may be comparable with the results of similar quantitative estimations of the macrofauna of the same region.

Results so far obtained show that the nematodes are the most abundant group, giving a population density of the order of two million individuals per square metre at a typical station. As would be expected, the mud microfauna is rich in numbers of individuals, but comparatively poor in numbers of species.

During the summer Mr D. P. Wilson has had considerable success in rearing larvae of *Nephthys hombergi*. Regularly every year for several years past attempts have been made to rear this species but the larvae have always died at a very early stage. This year two cultures have been kept alive for more than six weeks, the larvae by the end of that time apparently having accomplished the first half of their pelagic development. These reared larvae have enabled both similar and later stages to be recognized in the plankton. Sufficient material has by these means been obtained to enable a start to be made on a detailed study of the development, and for this purpose larvae are now being sectioned.

Mrs E. W. Sexton and Miss A. R. Clark have been engaged in testing new stocks of *Gammarus chevreuxi* obtained from the River Tavy district.

Briefly stated, heterozygosity has been definitely proved in eighteen cases. There is one doubtful instance, in a very small stock, of two bright reds occurring, but as these became black before reaching maturity, the probability is that the red appearance was due to premature extrusion rather than to changes in the retinal pigment. This stock, and six of the heterozygous are still being tested, but the results of their crosses have not yet come through. In the eighteen proved heterozygous stocks a great diversity was noted, both in the coloured retinal pigment, and in the white inter-ommatidial pigment.

The recessives were as follows: bright-red eyes in seven stocks; one of which was found by crossing, to be identical with Stock II (r_2 gene) from Chelson: bright reds and dark reds in one stock, neither of them carrying r_2: black nowhites in five other cases, one proved not genotypic: and five stocks in which both pigments were affected, viz. two with bright red nowhites: one with dark red normals, and bright red nowhites: two with black nowhites and bright red nowhites (one of which has not yet given results from crossing). Four of these stocks have been crossed, each with four different stocks including the original Stocks I and II, and shown to be distinct.

As far as the work has gone, all the Nowhites of the new stocks (like the Nowhite Reds of a previous mutation M.LVII) have given *normal-eyed* offspring in every cross with genotypic nowhites from other experiments.

In addition to work with the new Tavy stocks, the old Chelson stocks have been maintained. These include the original red-eyed 1912 Stock I and 1922 Stock II with their variations, in particular the D LIII with its two red genes, bright red (r_2) and ruby.

Another brackish water species of *Gammarus*, as yet undescribed, is being investigated. It was found by Prof. Munro Fox in 1932 in various places in the Droitwich district. Through the kindness of Miss M. F. Mare and Mr Spooner, who took samples of amphipods at Droitwich and Wyken Slough in the summer, enough living specimens were obtained with which to start experiments in the Laboratory. This new species is of remarkable appearance. The body is coloured green and yellow, with a longitudinal band of pinkish orange, and numerous transverse dark stripes running across the back and down the sides and appendages. It is hoped to publish a description and figures in the near future. A great deal of time has been devoted to the work of putting the records and charts of the *Gammarus* experiments on a permanent basis, and this is still being carried on.

Fish and Fisheries

The investigation begun last year by Dr A. Sand on the Ampullae of Lorenzini of elasmobranchs has been completed and published in the *Proceedings of the Royal Society*. This work forms a part of his studies on the physiology of the sense organs of fishes. It was discovered that the ampullary sense organs are temperature receptors, and their responses with respect to temperature changes constitute a most unusual type of sensory activity, which, moreover, bears an interesting relation to the mode of activity of lateral-line and labyrinthine receptors.

During the course of the year Dr Sand again collaborated with Dr Lowenstein of Glasgow in continuing work on the labyrinth. The discovery that the isolated labyrinth of the Ray can survive for several hours made possible the analysis of the individual activity of each one of the three pairs of semicircular canals with respect to angular displacement. All six canals are, broadly speaking, concerned in the response to any given movement, but the integrated pattern of sensory response is specific for every plane of angular displacement. This work will be published in due course.

In July Dr Sand read a paper and gave a demonstration before the Physiological Section of the British Medical Association, and in August he attended the International Physiological Congress at Zurich where he read a paper on Sensory Rhythms in Fishes.

Opportunities for Mr E. Ford to continue his studies of vertebral variation in teleostean fishes have been limited on account of his administrative duties as Assistant Director of the Laboratory. Progress has been made, however, in the preparation of a report on the form of the backbone in clupeoid fishes, including the herring, to which reference was made in last year's report.

The winter drift-net fishery for herrings at Plymouth, which has been falling off in yield from season to season since about 1931, virtually collapsed during the winter of 1937–38, and for the first time since Mr Ford began his routine survey of the fishery in 1924, no samples were obtainable for examination. The only consolation which can be drawn from this failure of the Plymouth fishery is that there is reason to believe that the loss may not be a permanent one. Sooner or later, a more favourable phase in the cycle of physical conditions which control the life and movements of herrings in south western waters may be expected to restore the productivity of the local fishing grounds to its former value.

Researches into the biology of the mackerel in western waters have been continued by Mr G. A. Steven and Mr P. G. Corbin. During the year biometrical data from a further 2200 fish have been collected, particular attention having been paid to devising and perfecting a routine method of age determination. The otolith method has been adopted as being less tedious and more satisfactory than scale readings for this fish, and scales are now no longer collected.

Much progress has been made in interpreting the otolith readings. Certain considerations seemed to suggest that fish of 20–21 cm. in length are in their second year, although their otolith and scales carry no trace of the winter ring which is normally laid down in the scales and otoliths of most fishes in the winter of their first year of life. This interpretation has now been confirmed from data derived from samples of small fish, down to 9 cm. in length, collected in quantity for the first time at the end of last year. It can now tentatively be stated, therefore, that the mackerel inhabiting the English Channel and the fishing grounds off its western entrance reach approximately the following lengths at ages 2–7 years inclusive.

Length at	2	years about	27 cm.
,,	3	,,	31·5 cm.
,,	4	,,	33·5 cm.
,,	5	,,	35 cm.
,,	6	,,	35·5 cm.
,,	7	,,	36 cm.

Preliminary analyses of the age composition of the mackerel landings do not as yet reveal any dominating year class; that is to say recruitment over the last four or five years has been fairly uniform. Routine analyses of the age composition of the population over a number of years will have to be made, however, in order to detect fluctuations in recruitment and discover their effect upon the fish stock. As yet data for only two seasons are available.

Examination of skeletons with a view to ascertaining whether mackerel from different localities, or from the same locality at different times, will reveal distinctive racial characteristics has been continued. The data have not as yet been fully worked up but preliminary analyses appear to indicate that the only variant which can be found—the number of thoracic vertebrae with "open" haemal arches—is not an expression of racial difference.

Three plankton cruises have again been made this year in connexion with the mackerel research, in April, May and July. They were made on dates as near those of last year as possible so that comparison may be made between the two years' data. The April cruise was again made in the Ministry of Fisheries' research ship *George Bligh*; the May and July cruises in the steam trawler *Elk*. During the April cruise the S.S. *Muirchu*, from the Fisheries Department of Eire, and the S.S. *Quentin Roosevelt* from France were also carrying out simultaneous plankton cruises to the north and south respectively of the ground worked by the *George Bligh*. From the additional data thus collected it is hoped to obtain a more complete picture of the spawning activities of the mackerel in April—the main spawning month—than would be possible from the work of a single vessel.

In general the 1938 observations confirm the findings of 1937. These showed that a diminution from a maximum spawning activity in early April occurs as the fishing season advances and is accompanied by a coastward movement of the locality of spawning, so that in July only slight spawning is taking place and does not extend westwards beyond the Scilly Islands.

Westwards of the areas of abundant mackerel eggs, encountered in April both in this year and in 1937, considerable numbers of mackerel post-larvae were found, and this indicates that spawning starts farther westward and earlier than actual plankton investigations have yet shown.

Temperature, salinity and phosphate data have again been collected on the cruises when possible.

At Newlyn selected drifters have continued throughout their season to collect plankton samples from the fishing grounds and to keep daily log-book records of catches. From this material it is hoped to ascertain whether a plankton-mackerel correlation exists or not, but observations over a considerable period will be necessary before this question can be satisfactorily settled.

The seasonal observations on the abundance of young fish in the plankton have been continued throughout the year by Mr Russell. The year 1938 has been similar in most respects to the two preceding years, the numbers of all species of young fish being very low. It has been the worst year yet experienced as regards the survival of the young of spring spawners, whose usual spring peak of abundance has now been absent for three years. There are indications that a scarcity of adult fish is now becoming apparent.

Mr Wilson has continued his work on seasonal variations in the fat-content of the flounder and a paper embodying the main results has been prepared for publication. Some early findings were recorded last year; these have been confirmed and extended, particularly as regards spawning flounders caught at sea. Large maturing flounders have a relatively big fat content when they first enter the sea; this fat is rapidly lost during the spawning season, February to April, when little or no feeding takes place. Those females which return to the estuaries after spawning quickly make good this fat loss. Special attention has been paid to the occurrence of minute fat droplets within the fibres of the superficial lateral muscle. They are generally absent during the summer, but in the winter are present in some immature and in most mature fish, and are especially prominent in sea-caught fish during the spawning period. They do not disappear from the fibres until after spawning has taken place and are therefore present in quantity while the fat reserves of the adipose tissues are being depleted.

Advisory work has been continued in connexion with the preservation of nets and ropes and the prevention of fouling. Dr Atkins has had a number of nets, trawl twines and ropes exposed in the Cawsand fish pond. The tests had to be interrupted when the premises were handed back to the Army during the recent crisis, but it is probable that they can shortly be resumed.

The Library.

The thanks of the Association are again due to numerous Foreign Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those authors who have sent copies of their books or papers, which are much appreciated.

During the year very important additions have been made under the terms of the Will of the late Mr E. T. Browne. Many valuable books and serials from his extensive library have now been transferred to Plymouth, including the whole of his reference collection of books and papers on the Coelenterata.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the *Journal* of the Association.

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MOORE, H. B., 1938. Algal production and the food requirements of a limpet. *Proc. Malac. Soc.* Vol. XXIII, pp. 117–118.

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Membership of the Association.

Governors. Upon his retirement from the office of Fisheries Secretary to the Ministry of Agriculture and Fisheries, Mr H. G. Maurice, C.B., ceases to be a Governor of the Association. His place is taken by the new Fisheries Secretary, Mr A. T. A. Dobson, C.B., C.V.O., C.B.E.

Lord Hollenden has taken the place of Col. the Hon. Angus McDonnell, C.B., as the new Prime Warden of the Fishmongers' Company.

Founders. The name of Col. E. T. Peel, D.S.O., M.C., has been added to the list of Founders.

Annual Members. The total number of annual members on Jan. 1 1939 was 286, of whom 12 were elected during the year. This is a net increase of two over the total of 284 annual members on Jan. 1 1938.

Finance.

General Fund. The Council have again to express their thanks to the Development Commissioners for their continued support of the general work of the Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52. 10*s*.), London (£105), Bristol (£25), Birmingham (£15. 15*s*.), Manchester (£10. 10*s*.), Leeds (£10. 10*s*.), Sheffield (£5), the Imperial College of Science and Technology (£10), Royal College of Surgeons (£52. 10*s*.), and the Cornwall Sea Fisheries Committee (£10). They are pleased to note that London University is now renting two tables at the Laboratory instead of one as in former years, and that the Royal College of Surgeons has rented one table for 1939.

Special grants. The Council wish to thank the Rockefeller Foundation for a grant of £200 for the provision of a cathode ray equipment and the Royal Society for £50 for the purchase of a research microscope.

Building Scheme.

The Council gratefully acknowledge receipt or promise of the following donations towards the cost of the new building scheme:

	£	s.	d.
Grant from the Development Fund ...	3000	0	0
Grant from the Rockefeller Foundation ...	2000	0	0
Legacy from the late Mr E. T. Browne ...	1000	0	0
Dr G. P. Bidder	500	0	0
The Fishmongers' Company	250	0	0
Lord Moyne [two donations]	150	0	0
Col. E. T. Peel	100	0	0
The Duke of Bedford	50	0	0
Viscount Astor	50	0	0
Anonymous	50	0	0
The Earl of Iveagh	10	0	0
Major Dorrien Smith	5	0	0
The Hon. J. H. Parker	3	3	0
Messrs E. Hardman and Co.	2	2	0
The Earl of Stradbroke	2	2	0
	£7172	7	0

President, Vice-Presidents, Officers and Council.

The Council greatly regret that Lord Moyne is now unable to continue as President, and wish to place on record their high appreciation of the services he has rendered to the Association during the past nine years. In his place they have nominated Dr G. P. Bidder, whose deep interest in their work and generous benefactions to the Plymouth Laboratory are well known to all members.

The following is the list of gentlemen proposed by the Council for election for the year 1939–40.

President

G. P. BIDDER, Esq., Sc.D.

Vice-Presidents

The Duke of BEDFORD, K.G.
The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Lord ST LEVAN, C.B., C.V.O.
The Right Hon. W. S. MORRISON, M.C., K.C., M.P.
Lord NOEL-BUXTON, P.C.
Sir SIDNEY HARMER, K.B.E., F.R.S.
Sir NICHOLAS WATERHOUSE, K.B.E.
Sir P. CHALMERS MITCHELL, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. PEEL, D.S.O., M.C.
Lord MILDMAY OF FLETE, P.C.
The Right Hon. Sir REGINALD DORMAN-SMITH, M.P.

COUNCIL

To retire in 1940

Prof. H. Graham Cannon, Sc.D., F.R.S.
Capt. G. C. C. Damant, R.N., C.B.E.
H. Muir Evans, Esq., M.D.
Prof. F. E. Fritsch, D.Sc., F.R.S.
C. F. A. Pantin, Esq., Sc.D., F.R.S.
J. Z. Young, Esq.

To retire in 1941

R. S. Clark, Esq., D.Sc.
A. C. Gardiner, Esq.
Prof. A. C. Hardy, D.Sc.
Prof. A. V. Hill, O.B.E., Sc.D., F.R.S.
Prof. D. L. Mackinnon, D.Sc.

To retire in 1942

H. G. Maurice, Esq., C.B.
Lord Rothschild
J. R. Norman, Esq.
Morley Neale, Esq.

Chairman of Council

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer

Guy Wood, Esq., M.B., M.R.C.P., The Charterhouse, London, E.C. 1

Secretary

Stanley Kemp, Esq., Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Esq., Sc.D.
The Lord Moyne, P.C., D.S.O.
A. T. A. Dobson, Esq., C.B., C.V.O., C.B.E. (Ministry of Agriculture and Fisheries)
The Lord Hollenden, C.M.G. (Prime Warden of the Fishmongers' Company)
Guy Wood, Esq., M.B., M.R.C.P. (Fishmongers' Company)
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O. (Fishmongers' Company)
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society)
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society)
E. J. Allen, Esq., C.B.E., D.Sc., F.R.S. (*Honorary*)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 MARCH 1939

	£	*s.*	*d.*	£	*s.*	*d.*
To Salaries, including Association's Contributions to Superannuation				8144	18	11
,, Laboratory Wages, including National Insurance and Association's Contributions to Superannuation				2684	8	7
,, Depreciation of Library				516	12	10
,, Scientific Publications, *less* Sales				464	0	1
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	295	7	10			
Electricity, Gas, Coal, Oil and Water	371	5	7			
Chemicals and Apparatus	388	7	10			
Rates, Taxes and Insurance	100	12	5			
Travelling Expenses	153	3	5			
Stationery, Postages, Telephone, Carriage and Sundries	322	8	10			
Specimens	129	5	1			
				1760	11	0
,, Maintenance and Hire of Boats:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1684	2	11			
Coal, Water, Oil, Petrol, etc.	313	15	11			
Maintenance and Repairs, with Nets, Gear and Apparatus	457	1	3			
Purchase of Material for Nets for Sale, excluding Labour	326	11	11			
Boat Hire and Collecting Expenses	5	17	2			
Insurance	262	9	0			
				3049	18	2
,, Transfer to "Salpa" Depreciation Fund				322	16	11
,, Transfer to Repairs and Renovation Fund				300	0	0
,, Balance, being Surplus for the Year				766	9	0
				£18,009	15	6

	£	*s.*	*d.*	£	*s.*	*d.*
By Grants:						
Ministry of Agriculture and Fisheries Grant from Development Fund	13908	0	0			
Fishmonger's Company	600	0	0			
Royal Society	50	0	0			
British Association	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				14,648	0	0
,, Subscriptions (excluding Subscriptions received in advance)				271	4	4
,, Donations				23	12	6
,, Sales:						
Specimens	1030	5	8			
Fish (*less* Expenses)	132	18	9			
Nets, Gear and Hydrographical Apparatus	564	10	11			
				1727	15	4
,, Table Rents (including Universities of Cambridge £105; London £105; Oxford £52. 10*s*.; Bristol £25; Birmingham £15. 15*s*.; Leeds £10. 10*s*.; Manchester £10. 10*s*.; Sheffield £5; Royal College of Surgeons £52. 10*s*.; Imperial College £10; Trustees of Ray Lankester Fund £20)				576	5	6
,, Tank Room Receipts				560	12	0
,, Interest on Investments, *less* Tax:						
General Fund	7	14	6			
Salpa Depreciation Fund	45	12	1			
Composition Fee Fund	2	15	6			
,, Interest on Bank Deposit Account, *less* Bank Charges	2	1	2			
				58	3	3
,, Sale of Dr M. V. Lebour's Book				2	11	2
,, Sale of "Marine Fauna of Plymouth"				5	9	6
,, Income Tax Recoverable				20	17	8
,, Transfer from E. T. Browne's Scholarship Grant Fund				100	0	0
,, Transfer from Mackerel Research Fund				15	4	3
				£18,009	15	6

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31 MARCH 1939

	£	s.	d.	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
On Open Account							70	6	10
PROPORTION OF SUBSCRIPTIONS RECEIVED IN ADVANCE							145	3	2
E. T. BROWNE'S SCHOLARSHIP GRANT FUND:									
As at March 31 1938				24	0	2			
Grant Received				225	0	0			
	£	s.	d.	249	0	2			
Less: Expenditure	149	0	2						
Amount charged to Income and Expenditure Account at March 31 1938, now written back	100	0	0						
				249	0	2	–	–	–
AQUARIUM GUIDE PRINTING FUND:									
As at March 31 1938				26	14	6			
Sale of Aquarium Guides				7	16	6			
				34	11	0			
Less: Expenditure				1	10	0			
							33	1	0
J. MARTIN'S PENSION FUND:									
Grant Received				93	15	0			
Less: Payments to J. Martin				11	0	0			
							82	15	0
SPECIAL APPARATUS FUND:									
Grants Received				250	0	0			
Less: Expenditure				176	7	5			
							73	12	7
MACKEREL RESEARCH FUND:									
Grant Received				899	16	11			
Less: Expenditure	883	15	9						
Adverse balance charged to Income and Expenditure Account at March 31 1938, now written back	15	4	3						
				899	0	0			
								16	11

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at March 31 1931						
S.S. *Salpa*	2000	0	0			
Motor Boat	150	0	0			
Nets, Gear and General Equipment	27	0	0			
				2177	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost						
As at March 31 1938	1150	6	5			
Additions during the year	159	9	9			
				1309	16	2
LIBRARY:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost *less* Depreciation						
As at March 31 1938	2295	4	11			
Additions during the year	574	4	9			
	2869	9	8			
Less: Depreciation	516	12	10			
				2352	16	10
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS:						
As estimated by the Director				565	0	0
SUNDRY DEBTORS:						
Sale of Specimens, Journals, Nets, Gear and Apparatus				223	0	3
INCOME TAX RECOVERABLE				19	4	5
PREPAYMENTS				64	4	9
GENERAL FUND INVESTMENT at Market Value as at March 31 1931:						
£352. 2*s.* 3*d.* Local Loans 3%				232	7	10
(Market value at date £279. 18*s.* 7*d.*)						
"SALPA" DEPRECIATION FUND INVESTMENTS at Cost:						
£590. 6*s.* Local Loans 3%	506	10	9			
£1832. 14*s.* 3*d.* Conversion Loan 3%	1851	6	9			
(Market value at date £2237. 17*s.*)				2357	17	6

BUILDING EXTENSION FUND:			
Donations Received		2560 5 0	
Transfer from E. T. Browne Bequests Fund		1000 0 0	
Transfer from Repairs and Renovation Fund		118 0 0	
		3678 5 0	
Less: Expenditure		2126 6 0	
			1551 19 0
E. T. BROWNE BEQUESTS FUND:			
Bequest Received		6500 0 0	
Bank Interest on Deposit Account		5 16 4	
		6505 16 4	
Less: Donation to Building Extension Fund	1000 0 0		
Expenditure	49 16 0		
		1049 16 0	
			5456 0 4
"SALPA" DEPRECIATION FUND:			
Balance transferred from Reserve for Depreciation of Boats and Machinery as at March 31 1938		2035 0 7	
Transfer from Income and Expenditure Account		322 16 11	
			2357 17 6
COMPOSITION FEE FUND:			
As at March 31 1938			126 0 0
REPAIRS AND RENOVATION FUND:			
Transfer from Income and Expenditure Account		300 0 0	
Less: Expenditure	131 3 3		
Transfer to Building Extension Fund	118 0 0		
		249 3 3	
			50 16 9
CONSTANT TEMPERATURE ROOMS FUND:			
As at March 31 1938		133 4 8	
Less: Expenditure		91 14 0	
			41 10 8
SURPLUS:			
As at March 31 1938		6322 6 7	
Add: Surplus for the year, as per Income and Expenditure Account		766 9 0	
			7088 15 7
			£17,078 15 4

REPAIRS AND RENOVATION FUND INVESTMENTS at Cost:		
£51. 4*s*. Conversion Loan (Market value at date £49. 8*s*. 2*d*.)		50 0 0
COMPOSITION FEE FUND INVESTMENTS at Cost:		
£18. 8*s*. 6*d*. Local Loans 3%	15 15 0	
£108. 6*s*. 5*d*. Conversion Loan 3%	110 5 0	
(Market value at date £119. 3*s*. 5*d*.)		126 0 0
BUILDING EXTENSION FUND INVESTMENT at Cost:		
£1019. 0*s*. 11*d*. Conversion Loan 3% (Market value at date £983. 7*s*. 7*d*.)		1000 0 0
BROWNE BEQUESTS INVESTMENTS at Cost:		
£5604. 14*s*. 11*d*. Conversion Loan 3% (Market value at date £5408. 11*s*. 7*d*.)		5500 0 0
CASH AT BANK AND IN HAND:		
Coutts & Company—Current Account	591 18 6	
Lloyds Bank Limited—Current Account	397 16 11	
Lloyds Bank Limited—Deposit Account *re* J. Martin	82 15 0	
Cash in hand	28 17 2	
		1101 7 7
		£17,078 15 4

E. J. ALLEN } *Members of Council.*
M. BURTON }

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs according to the best of our information and the explanations given to us and as shown by the Books of the Association.

PRICE, WATERHOUSE AND CO.

34 *and* 35 *Bedford Street,*
Plymouth. May 24 1939.

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM is a corporate body of subscribing members founded to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its members.

The Association was founded in 1884 at a meeting held in the rooms of the Royal Society of London with Professor T. H. Huxley in the chair. Amongst distinguished scientific men present on that occasion were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester, who was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £16,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Resident Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter and in September, and marine animals and plants are supplied to educational institutions.

Research work at sea is undertaken by the steam drifter "Salpa" and by a motor boat, which also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	*s.*	*d.*
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this *Journal* excepting when those statements are contained in an official report of the Council.

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