New Series.—Vol. XVI., No. 3—issued May, 1930.
[Completing Vol. XVI.]
Price Twelve Shillings and Sixpence net.

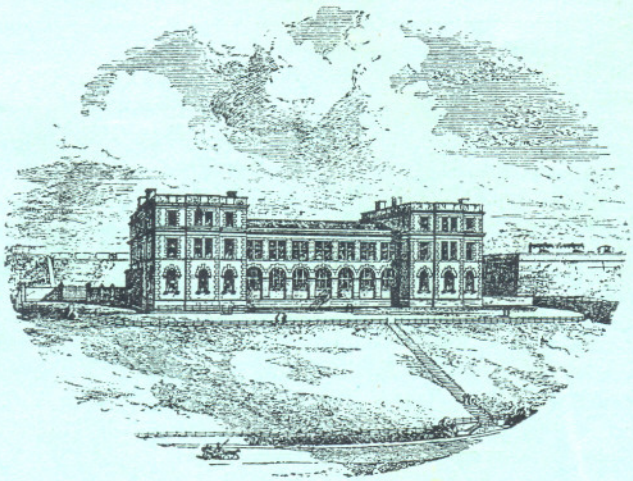
Journal

OF THE

MARINE BIOLOGICAL ASSOCIATION

OF

THE UNITED KINGDOM.



THE PLYMOUTH LABORATORY.

PLYMOUTH:
PRINTED FOR THE MARINE BIOLOGICAL ASSOCIATION AT THE MAYFLOWER PRESS
BY W. BRENDON & SON, LTD.,
AND
PUBLISHED BY THE ASSOCIATION AT ITS OFFICES ON THE CITADEL HILL.
SENT FREE BY POST TO ALL MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION:
ANNUAL SUBSCRIPTION FOR MEMBERSHIP, ONE GUINEA.
AGENTS IN LONDON: MESSRS. DULAU & CO., LTD., 32, OLD BOND STREET, PICCADILLY, W. 1.

PATRON.

HIS MAJESTY THE KING.

OFFICERS AND COUNCIL.

President.

Lieut.-Col. The Right Hon. WALTER GUINNESS, D.S.O., M.P.

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. Sir AUSTEN CHAMBERLAIN, K.G., M.P.
The Right Hon. NOEL BUXTON, M.P.
Sir W. B. HARDY, F.R.S.
GEORGE EVANS, Esq.
Sir NICHOLAS WATERHOUSE, K.B.E.
Prof. W. C. MCINTOSH, F.R.S.
G. A. BOULENGER, Esq., F.R.S.
J. O. BORLEY, Esq., O.B.E.

COUNCIL.

Elected Members.

Prof. J. BARCROFT, C.B.E., F.R.S.
ALEXANDER BOWMAN, Esq., D.Sc.
Prof. A. E. BOYCOTT, D.M., F.R.S.
Captain G. C. C. DAMANT, R.N., C.B.E.
Prof. J. STANLEY GARDINER, F.R.S.
RONALD D'OYLEY GOOD, Esq.
Prof. E. S. GOODRICH, D.Sc., F.R.S.
Prof. A. C. HARDY.
Prof. A. V. HILL, F.R.S.
C. F. A. PANTIN, Esq.
C. TATE REGAN, Esq., D.Sc., F.R.S.
A. D. RITCHIE, Esq.
G. C. ROBSON, Esq.
J. T. SAUNDERS, Esq.
Prof. D. M. S. WATSON, F.R.S.

Governors.

G. P. BIDDER, Esq., Sc.D.
E. T. BROWNE, Esq.
GEORGE EVANS, Esq.
H. G. MAURICE, Esq., C.B. (Ministry of Agriculture and Fisheries).
R. HOLLAND MARTIN, Esq., C.B. (Prime Warden of the Fishmongers' Company).
NIGEL O. WALKER, Esq. (Fishmongers' Company).
LOTHIAN D. NICHOLSON, Esq. (Fishmongers' Company).
Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).
J. GRAY, Esq., 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).

Chairman of Council: Prof. E. W. MACBRIDE, D.Sc., F.R.S.

Hon. Treasurer: GEORGE EVANS, Esq., 1 Wood Street, London, E.C. 2.

Secretary: E. J. ALLEN, Esq., D.Sc., F.R.S., The Laboratory, Citadel Hill, Plymouth.

SCIENTIFIC STAFF.

Director: E. J. ALLEN, Esq., D.Sc., F.R.S.

Head of Department of General Physiology: W. R. G. ATKINS, Esq., Sc.D., F.I.C., F.R.S.

Fisheries Naturalist: E. FORD, Esq., A.R.C.Sc.

Naturalist.
Miss M. V. LEBOUR, D.Sc.

Hydrographer.
H. W. HARVEY, Esq., M.A.

Physiologist.
C. M. YONGE, Esq., D.Sc., PH.D.

Director's Research Assistant.
Mrs. E. W. SEXTON, F.L.S.

Naturalist and Administrative Assistant.
F. S. RUSSELL, Esq., D.S.C., D.F.C., B.A.

Assistant Naturalists.
D. P. WILSON, Esq., M.Sc.
G. A. STEVEN, Esq., B.Sc.

Research Assistant.
B. DAWES, Esq., A.R.C.Sc., D.I.C.

TEES ESTUARY SURVEY.

Superintendent and Biologist: W. B. ALEXANDER, Esq., M.A.

Physiological Chemist: B. A. SOUTHGATE, Esq., B.A., PH.D.

Bottom Fauna and the Food of Fishes.

By

G. A. Steven, B.Sc.,

Assistant Naturalist at the Plymouth Laboratory.

With 1 Chart and 3 Figures in the Text.

In the waters off Plymouth there exists a definite inshore fishing-ground, approximately 13 square miles in area, locally known as the "corner." In order to obtain some idea of the Bionomic conditions prevailing on this ground an intensive study of the bottom fauna was undertaken. Quantitative seasonal observations extending over a period of one year (August, 1928–July, 1929 inclusive) have been made, using the 0·1 square metre Bottom Sampler and the "Agassiz" Trawl, a method having been devised for obtaining quantitative hauls with the latter instrument. Investigations into the food actually eaten by the fishes within the area have been carried on simultaneously, and the stomach contents of over 2000 fishes comprising 29 different species have been examined. On account of the length of time required for stomach examination, it was found impossible to make seasonal observations on them also, but comparable winter and summer examinations were made.

I am deeply indebted to Dr. Allen and the Staff of the Laboratory for much advice and other assistance throughout the course of this work. My very best thanks are also due to Capt. Lord and the crew of the s.s. *Salpa* for their invaluable co-operation and constant endeavour to reap the best results from all operations at sea.

Methods of Collection.

The quantitative faunistic observations were made in the first place by means of the Petersen 0·1 square metre bottom sampler (Petersen "grab"). Fifteen stations were fixed, more or less evenly distributed over the area—i.e. one station to rather less than one square mile (see Chart, p. 678). In autumn, 1928, and in winter, spring, and summer following, five bottom sampler hauls were taken at each of these stations.

Examination of the stomach contents of fishes from the same area soon disclosed the fact that a number of organisms—Pandalidæ, Crangonidæ,

Palæmonidæ, Hippolytidæ—were being preyed upon which were not represented at all in grab samples. A species of Portunus—*P. depurator*—also appeared frequently in stomach contents but not in grab hauls. An additional quantitative collecting method had therefore to be devised to supplement that of the bottom sampler. For this purpose the " Agassiz " trawl was eventually used in the following manner.

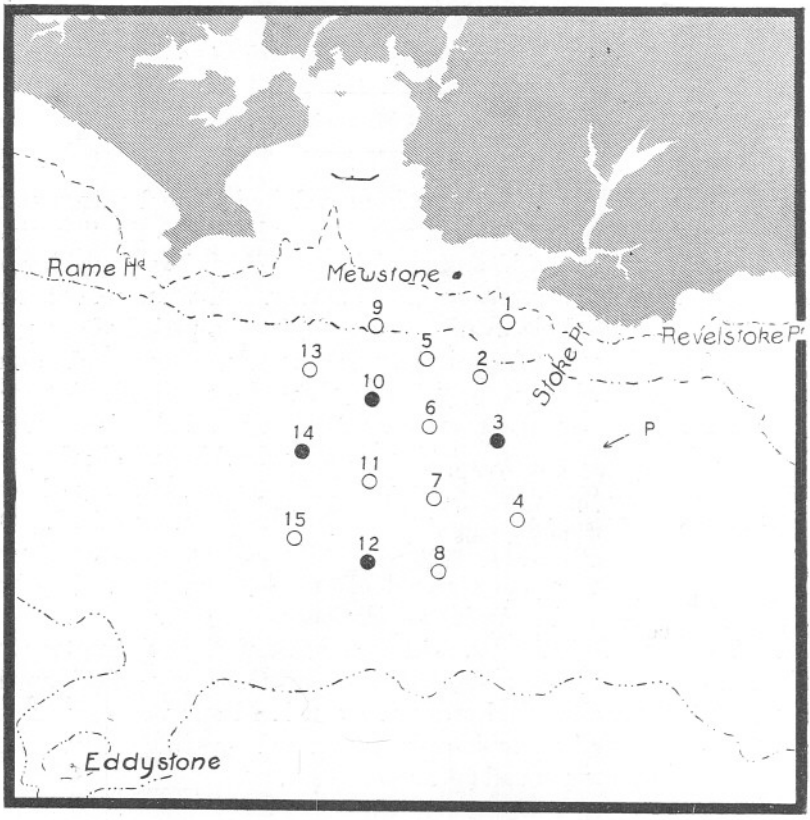


CHART of Bottom Sampler Stations and Trawl Centres on the " Corner " Fishing Ground off Plymouth, 1928–29.

o = Bottom Sampler Stations.
● = Bottom Sampler Stations also used as Trawl Centres.

Four representative grab stations—3, 10, 12, 14—were chosen as trawling centres. A trawler's " dan " was anchored on the station to be worked. The trawl was then shot so as to strike bottom as nearly as possible alongside the dan and towed in a straight line away from it for a distance of approximately 520 yards. Four hauls were taken around each trawl centre, towing in directions north, south, east, and west in turn from

the dan. The distance trawled was ascertained by using a range-finder* for observing the distance of the ship from the dan when the trawl was hauled clear of the bottom, due allowance being made for the length of warp paid out. The trawl used had a 7-foot beam—i.e. the mouth was 7 foot wide. By towing it over a distance of 520 yards, therefore, an area of approximately $\frac{1}{4}$ acre was covered at each haul. Thus a total area of roughly one acre was represented by the four trawl samples taken around each trawl centre. Unfortunately the trawl and range-finder were not brought into operation while the first (autumn) series of grab samples was being taken, so that trawl records are available only for the winter, spring, and summer seasons (Table IV).

By the use of the range-finder and dan one at least of the objections put forward by Petersen (**19**, p. 47) against the use of the trawl for quantitative estimation of the animal life on the sea bottom is overcome. He says, "If we wish to have accurate information regarding the amount of animal life, especially the number of individuals per unit of surface, we must rely upon other apparatus than the dredge and trawl; with these it is difficult to say what distance they have been dragged over the bottom, nor can we know how many animals they have left behind on the distance worked over: the number is often many times that taken up." The latter objection still holds. But even though it be impossible to estimate how many animals a trawl fails to capture, it is nevertheless permissible to hold the view that the animals it does bring up represent, at any rate, the minimum number of individuals present on the area covered. And this is all that can be claimed for the bottom sampler. It may and probably does bring up samples which represent fairly accurately the population of a sea bottom composed of soft mud or mire such as seems to be typical of much of the Limfjord (**19**, p. 14), for example. But on bottoms of a harder nature composed of sand or gravel, either with or without an admixture of mud, the performance of the bottom sampler is not so satisfactory. We can count the number of individuals it brings up, but have no way of knowing how many animals it leaves behind in their burrows beyond the reach of its "bite." Moreover, in such places as the Limfjord, active members of an epifauna, such as *Portunus depurator* which abounds on the "corner" grounds off Plymouth, appear to be present only in negligible numbers. Where such occur they too, more often than not, evade capture by the grab, probably scuttling out of its way as it descends upon them from above. Such species as *Pandalina brevirostris*, Palæmonidæ, and the Crangonidæ, important food animals in the "corner" area, do not come within its scope at all:† the trawl, whatever its limitations, is the most effective instrument for their capture. In order, therefore, to

* The instrument used was a Barr and Stroud range-finder, type F.T. 32. Base 80 cm.

† It is not designed to capture these animals.

acquire more complete data regarding the food animals present upon the ground under investigation than was possible with the bottom sampler alone, both sampler and trawl have been used in conjunction, the former for bringing up the sedentary infauna and the latter for the more active animals roaming on or above the sea bottom.

THE BOTTOM FAUNA.

In Table III is recorded the number of individuals of separate species or homogeneous groups per 0·5 square metre at each station as brought up in 5 hauls of the 0·1 square metre bottom sampler. Columns a, b, c, d are the data for autumn, 1928, and the following winter, spring, and summer respectively. Table IV records the number of animals brought up by the "Agassiz" trawl from $\frac{1}{4}$ acre of bottom N., S., E., and W. of each of the four stations 3, 10, 12, and 14. Only three seasons' observations (b, c, d) are available as explained above.

Seasonal observations were taken in order to determine what fluctuations, if any, of density or distribution of the bottom invertebrates take place in the course of a year. It will be seen from the tables that on the whole, both number and distribution of most of the organisms remained fairly constant. *Pandalina brevirostris* and some Crangonids were the only species which showed very definite migratory movements (Table IV). During the winter months Pandalina was more or less evenly distributed over the whole of the "corner" ground in depths of from 25–28 fathoms, with a tendency to be most numerous near the south-western edge where the water is deepest. In spring, Pandalina had moved shorewards and congregated in an immense shoal along the outer edge of the rough ground between Stoke Pt. and Revelstoke Pt. (see chart). They had then all but disappeared from most of the "corner" area west of stations 3 and 4, but were very numerous at those points and south-eastwards of them. A $\frac{1}{4}$-acre "Agassiz" haul taken in the month of April, towing from the point P on the chart in the direction indicated by the arrow, contained 537 individuals.

This shoreward migration in the spring seems to be a spawning migration into shallower water. In March, ovigerous females carrying eggs of a very pale pink colour became numerous in the catches. As the eggs ripen their colour changes to pale green, when they are ready to be shed. "Green-bellied" females became numerous in May and remained plentiful until the end of July. The main spawning season, therefore, seems to extend over a period of about three months. A certain amount of spawning evidently goes on for a longer time for the larvæ were abundant in the plankton until September and a few were still to be found at the time of writing (October, 1929).

Kemp (**12**) and Murie (**17**) describe a similar gregarious migratory habit in another Pandalid, *Pandalus montagui*. But in the case of this species the spawning migration is an off-shore one. Murie (p. 245) states that although nothing definite is known on this point, yet there is good reason for believing that around the long parallel sand-banks girding the outer arch facing Essex, the " pink shrimps " of the Thames estuary flock in the early spring to spawn. And the Humber shrimp trawlers " know quite well that the appearance of ' green-bellies ' is a sign that the prawns will soon be off to sea " (**12**, p. 88, footnote). It may be, then, that in estuarine regions such as those of the Thames and Humber, the large sand-banks and sand-flats at their mouths far off-shore, provide for *P. montagui* conditions suitable for spawning similar to those sought by *Pandalina brevirostris* in an in-shore migration from the deep and open sea.

Two species of the Amphipod genus Ampelisca—*A. spinipes* and *A. tenuicornis*—are present on the " corner " grounds. The former species is confined to bottoms of fairly clean sand or shell gravel—e.g. on and around Station 1. The latter with a preference for more muddy conditions is present over the whole area with the exception of Station 1. For convenience the two species are grouped together as Ampelisca spp. in Table III. From this table it will be seen that in autumn, 1928, these Amphipods were numerous on the western line of stations—13, 14, 15—and were also distributed in small numbers over the remainder of the area. In the following winter, however, they had almost entirely disappeared from the grounds, as recorded by the bottom sampler. Several additional hauls taken outside the area, both to seaward and to landward, also revealed a scarcity of Ampelisca. At first it was thought that, on the approach of winter, a great diminution in their numbers had taken place, either by natural death or otherwise. But this explanation had to be abandoned when young Rays (20–30 cm.) captured on the " corner " grounds at this time were found to have been feeding largely, and in some cases exclusively, on Ampelisca (Table II, p. 695). It is evident, therefore, that the Amphipods were still abundantly available to the fishes on the ground although, for some reason, the grab failed to capture them. Unfavourable weather and bad working conditions when the winter hauls were taken, which may suggest itself as a possible explanation, does not apply. Winter stations 13, 14, and 15 were worked in much more favourable conditions of wind and sea than were encountered at stations 9, 10, 11, and 12, for example, in the spring series of observations when 42, 109, 35, and 9 individuals respectively were taken off 0·5 square metres. Possibly Ampelisca may burrow deeply into the mud during the winter months, beyond the reach of the grab. In any case, whatever the explanation, the facts are interesting and important in so far as they serve to

illustrate the danger of assuming that a species is absent from the grounds when it is not to be found in the bottom sampler hauls.*

Perusal of Tables III and IV serves to show the great (numerical) richness of the organisms comprising the infauna as compared with those of the epifauna, even allowing for any discrepancy there may be in the sampling efficiency of the grab and trawl. The numbers as a whole, in both tables, are roughly of the same order of magnitude. But, where they represent the population of 0·5 square metre in the case of the grab samples (Table III) they represent the population of $\frac{1}{4}$ acre ($=0{\cdot}5$ sq. m. $\times 2023{\cdot}35$) for trawl samples (Table IV). Of *Upogebia deltaura*, for example, a burrowing crustacean found all over the "corner" grounds, totals of 11, 5, 14, and 18 individuals were taken at all stations in autumn, winter, spring, and summer respectively. These numbers captured over an area of $15 \times 0{\cdot}5$ square metres represent a calculated population of 1484, 674, 1888, 2428 individuals respectively per $\frac{1}{4}$ acre. For *U. stellata* the corresponding figures, as calculated, are 674, 674, 1349, and 1484 respectively. These numbers are far in excess of those for any species of the epifauna.

From Table III it will further be seen that the two species of Upogebia, considered together, are fairly uniformly distributed over the whole area. Calculating further on this basis, the Upogebia spp. population of the "corner" grounds exceeded 72 millions, 45 millions, 108 millions, and 130 millions in the autumn, winter, spring, and summer seasons respectively. These values, large though they be, probably fall far short of the actual numbers present, as, owing to the burrowing habit of this animal and the agility with which it darts into and along its underground passages, the bottom sampler is not likely to capture more than a small fraction of the total number of individuals present in the area from which it "bites."

The two species of Upogebia, therefore, form in themselves alone a vast potential food supply on the "corner" grounds. Nevertheless, although present in far greater numbers than *Portunus depurator*, for example, it does not necessarily follow that they are actually more important as a source of fish food. Prey, to be of service to any animal, must first of all be caught and eaten.

On this point, Ford (**7**, p. 532) remarks, "Before the potential value of a bed of Lamellibranchs as food for fishes can become known, the precise food value of the successive stages of the life-history of each lamellibranch must be determined. One species may never grow beyond a size which a medium-sized Dab could easily swallow whole, whereas another although it may be easily devoured in its early life will soon grow

* In this connexion, the relative inefficiency of every type of gear when compared with fishes as collectors, may be cited. In the waters off Plymouth, Sipunculus has never been taken in any collecting instrument. Nevertheless, this Gephyrean is commonly found in the stomachs of Rough Dogfishes (*Scyliorhinus canicula*) caught in these waters.

to a size quite beyond the largest of shell-eating fish and thus be relatively useless to fishes. In quantitative estimations of fish food similar to those made by the Danish investigators, this fact needs careful consideration." With sedentary hard-shelled organisms such as Lamellibranchs, size is the main consideration. But the burrowing habit of Upogebia and the alacrity with which it can scurry to safety, make its relatively great elusiveness as compared with that of Portunus, for example, a significant factor which must be taken into consideration in any attempt to estimate their relative values as sources of fish food.

This factor—*the comparative availability of the food animals present on or in the sea-floor*—is one the importance of which impresses itself upon the investigator, but except in certain cases—e.g. effect of size—he remains powerless to grapple effectively with it.* The availability of any animal for food, leaving out consideration of size, will depend upon :

1. The habits and activity of the organism itself ;
2. The habits and activity of the fish.

This will vary :

1. For the same organism with different fishes ; and
2. For different organisms with the same fish.

This variation of habit also affects grab samples, although it is impossible here also to obtain data by means of which its magnitude can be estimated and allowed for. A grab sample, in the opinion of the writer, must not be taken as a true or even approximate measure of the absolute numbers of animals present upon the sea bottom. In the Plymouth waters, at any rate, it is a *differential sample of the organisms*, ranging from 100 per cent (e.g. small Lamellibranchs and Gastropods, *Echinocyamus pusillus*, *Ophiothrix fragilis*) downwards (e.g. Upogebia, tubicolous Polychætes, *Portunus depurator*), according to their several abilities to elude the sampler. When considering grab results, this must always be borne in mind. In view of these facts, to work out the rough weights and dry weights of the organisms captured in the bottom sampler on the " corner " grounds, and to deduce therefrom the total amounts of the different types of food available over the area did not seem to be justified.

FOOD AND FEEDING HABITS OF FISHES.

General.

Examination of the stomach contents of fishes actually caught upon the grounds investigated by grab and trawl revealed that Ogilvie's statement with regard to post-larval herrings holds good in a general way

* See also **19**, p. 67, lines 7–10.

for all fishes—i.e. "within limits determined by size and suitability in other respects, the fish will eat what they can get" (**18**, p. 10). This fact is clearly demonstrated by examining fishes from grounds on which different bottom-dwelling animals predominate. For example, *Portunus depurator* is common on the "corner" grounds, while *Corystes cassivelaunus* and *Atelecyclus septemdentatus* are rarely found. But farther out in the direction of the Eddystone, Corystes and Atelecyclus, though not numerous, are fairly common and *P. depurator* less abundant. This change of fauna is reflected in the food of *Gadus luscus*, *Raia clavata*, and *Scyliorhinus canicula* trawled from those two areas (Table I).*

TABLE I.

DIFFERENCE IN FOOD OF *GADUS LUSCUS*, *RAIA CLAVATA*, AND *SCYLIORHINUS CANICULA* ON "CORNER" AND OUTSIDE GROUNDS.

		Stomachs containing *Portunus depurator*		Stomachs containing Corystes and/or Atelecyclus		Total number of stomachs examined
		Number	%	Number	%	
Gadus luscus	Corner	60	**36·8**	4	2·5	163
	Outside	19	25·7	16	**21·6**	74
Raia clavata	Corner	65	**38·9**	9	5·4	167
	Outside	12	24·5	18	**36·7**	49
Scyliorhinus canicula	Corner	18	11·8	1	0·7	152
	Outside	7	11·3	13	**21·0**	62

When, therefore, the food of the entire fish population of any particular area is considered as a whole, the organisms most commonly eaten are (with certain exceptions such as Echinodermata and Cœlenterata) found to be those most numerous and/or easily available. This does not apply, of course, to every species of fish considered individually, because for one reason or another some fishes are "selective" feeders: i.e. they are fitted by structure or habit to catch and eat certain animals and not others, when they are said to "select" the former and "reject" the latter.

A noteworthy feature of the "corner" grounds at the present time is the great scarcity of all kinds of Flatfishes except *Pleuronectes microcephalus* (the Lemon Dab) and *Arnoglossus laterna* (Scaldback). Only very occasionally are Sole, Brill, Turbot, and Flounder taken in the trawl, and Dab and Plaice are almost equally scarce. The absence of the last-named fish may be due to a corresponding paucity in the Lamellibranch, and in fact, the entire Molluscan fauna within the area. Although quantitative records are lacking, there is little doubt that during a

* See also **2**, p. 46, par. 2.

number of years immediately following the War *Aequipecten opercularis* (Queens)* at any rate was abundant. Plaice were then also numerous.

There is some indication that Queens are again on the increase. Should they once more populate the area it will be interesting and instructive to observe whether or not Plaice also return in numbers to the grounds.

The Lemon Dab (*Pleuronectes microcephalus*), though not abundant, is fairly numerous.† This may possibly be due to the fact that its diet consists mainly of Polychæta, the numbers of which probably have remained undiminished in spite of intensive trawling over the area.

The Scaldback (*Arnoglossus laterna*)—unfortunately not a marketable fish—is very plentiful. This again is probably to be explained by the presence of an abundant supply of suitable food organisms—Amphipoda, Schizopoda, Crangonidæ, Pandalidæ, and *Crystallogobius nilssonii*.

Periodic Change of Food.

As would be expected from the constancy of the constitution of the invertebrate fauna throughout the year, there is little obvious change of food in the summer and winter seasons. Nevertheless, there is, in certain cases at least, a definite *periodic* change. The Whiting, for example, normally feeds on a wide range of animals, its diet including large and small Crustaceans of all kinds, Worms and small Fishes (including the young of its own species), and an occasional Mollusc and Echinoderm. But Whiting of all sizes from 10 cm. in length upwards, caught in May and June, 1929, were found to be feeding almost exclusively on the Megalopa larvæ of *Corystes cassivelaunus*. Of fishes between 10 and 15 cm., twenty-five were examined. Two of those had their stomachs empty : all the others had been feeding on the larvæ. Of fishes over 15 cm. in length, fifty specimens were examined, forty-seven of which had been feeding on the Megalopas, *thirty-three of them exclusively*. In many cases the stomachs of the fish were simply gorged with the larvæ, some counts recording over 200 individuals per stomach.

The Whiting, in Plymouth waters, is a migratory species. Small fish appear in numbers from about May onwards, the larger fish following later in the season. A few may remain in the neighbourhood throughout the year. The fact that the time of their reappearance in numbers in the Plymouth area this year coincided with the presence of immense shoals‡

* Local fishermen state that trawling for Queens on and to the eastward of this area yielded very large hauls of the bivalves. Now they are so scarce that a whole day's takings would fall far short of an hour's catch in those years.

† This fish also is not quite so plentiful as formerly.

‡ One of these shoals was encountered in a small boat at sea about noon on the 20th May, 1929. For several miles the Megalopas were so numerous near the surface that two or three at a time could be scooped up in an ordinary cocoa-tin. A striking feature of the shoal was that all the larvæ were swimming rapidly, and all in the same direction.

of Corystes Megalopas in these waters, and that when caught the Whiting were found to be feeding almost entirely on the larvæ, suggests the possibility that the fish may have been attracted by this abundance of food. This view cannot definitely be put forward, however, without further evidence gleaned over a number of years.

Nineteen Whiting between 5 and 10 cm. in length were captured. Of these, two had empty stomachs, and seventeen had been feeding on small fishes, mostly *Crystallogobius nilssonii*, but one (9 cm.) had taken a Mackerel Midge (Onos sp.). Only two had eaten Megalopas, the stomach of one containing two and the other three individuals. The reason why these very small Whiting had not been feeding on the larvæ, as had the larger sizes, is not apparent.

Correlation of Habit and Structure with Food Eaten.

The habits of fishes—as of all animals—are inextricably bound up with structure and structure with habit. How the one affects the other does not concern us here. But both are important factors, influencing to a great extent the type of animal upon which a fish will normally depend for food. Because of their intimate relationship, therefore, the parts played by these two factors in determining the staple food of different fishes will be considered together.

The prey which a fish can capture is dependent to a large degree upon its feeding habits or foraging methods. These differ markedly in different fishes, and there is found always to be a corresponding difference in the type of organisms which form their staple food. This can best be illustrated by studying closely certain fishes with very typical and contrasting methods of feeding.

The **Lemon Dab** (*Pleuronectes microcephalus*). On the "corner" grounds the Lemon Dab feeds exclusively upon Annelids. This is entirely in keeping with the habits of the fish. It is a frequenter of muddy bottoms where worms are abundant and other organisms correspondingly scarce. Tubicolous Polychætes, which form the bulk of the Annelid fauna, cannot be captured by lying in wait for them : they have to be hunted and that discreetly, otherwise they disappear to safety down their tubes. So the Lemon Dab, if observed in an aquarium tank, is found to be of a very restless disposition. It is constantly on the move, swimming for short distances with intervening halts for brief periods. It comes to rest in a characteristic attitude, with the head and forepart of the body raised well off the substratum. Remaining perfectly still in this position, the fish, by means of its very prominent and exceedingly movable eyes, scans the bottom in its immediate neighbourhood (Fig. 1). Should it then observe a food organism—i.e. the anterior end of a worm cautiously emerging

from its burrow—the Lemon Dab suddenly pounces upon it like a true hunter with a kind of forward leap, bringing its mouth down almost vertically upon its victim by a strong arching of the anterior part of the

FIG. 1.—The Lemon Dab, *Pleuronectes microcephalus*.
Top ..... great range of eye movement.
Bottom..... typical attitudes of the fish when lying in waitf or prey.
(After Brightwell.)

body (Fig. 2). Foraging thus, it is not surprising that Todd (**29**, p. 104), during his researches upon the food of fishes in the Southern North Sea, should have found that the Lemon Dabs of that area were feeding to a considerable extent upon a species of Cerianthus.

It is somewhat strange, however, that of all these fishes from the "corner" grounds which have been examined, not one contained the slightest trace of a Lamellibranch. This may possibly be due to the great scarcity of these Molluscs in this area. On the other hand, there is every indication that the Lemon Dab does not "bite" its food. The nipped-off ends of tubicolous Polychætes are seldom or never found in its stomach: the whole worm is withdrawn unbroken from its burrow or tube. This being so, large Lamellibranchs perhaps are powerful enough to pull their siphons out of the fish's mouth even if they are caught. Small ones may

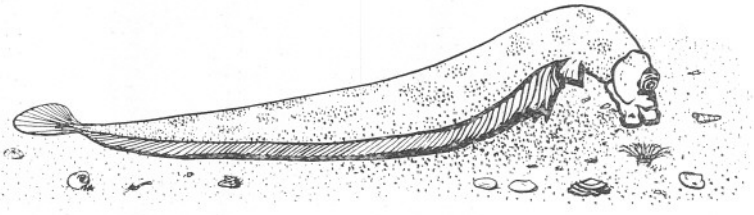


Fig. 2.—A Lemon Dab in the act of pouncing upon a tubicolous worm.

not be able to do so, but as the fish is not fitted for crushing hard shells, these are probably rejected when the valves are drawn into its mouth.

Ramsay Smith (**23**, p. 213) found that while Annelids formed the chief food of Lemon Dabs in the Firth of Forth, Hermit Crabs—*Eupagurus bernhardus* and *Anapagurus lævis*—also entered largely into their diet. In view of this statement, a number of small Hermits were introduced into aquarium tanks containing Lemon Dabs in order to observe what would happen. The fish immediately set about hunting the crabs in exactly the same manner as that described above for the capture of tubicolous Polychætes. With head raised well above the crab, the fish waits and watches until the Hermit ventures to appear at the mouth of its shell and then suddenly pounces upon it. Generally the crab shoots back to safety too quickly to be taken, as it usually walks about with only the tips of its walking legs and chelæ exposed. Moreover, the fish has to lie in wait facing the mouth of the shell, and the Hermits were frequently observed to dart back before emerging far enough even to crawl, having seen that danger threatened as soon as their eyes—conveniently placed on the tips of long eye-stalks—projected far enough to see up round the lip of the shell. The Lemon Dabs hunted more successfully, however, when a shell with its contained Hermit happened to be over-

turned. The crab is then obliged to expose much more of its body in its efforts to regain a normal position. In these circumstances, a fish was occasionally able to stalk and capture an unlucky Hermit. There seems then to be little doubt that small Pagurids would figure much more prominently in the diet of the Lemon Dab were it not for their extreme wariness and ability to beat a hasty retreat into the safety of their shells. On the " corner " grounds off Plymouth, the worm fauna appears to be large enough to support the Lemon Dabs of the area without their having to hunt such elusive prey. At any rate, small Hermits, though abundant, are not eaten.

The **Sole** (*Solea vulgaris*). The feeding habits of the ordinary Sole are very different from those of the Lemon Dab, and there is a corresponding difference in its diet. In foraging for prey the true Sole depends almost entirely on the tactile sense. The eyes, unlike those of the Lemon Dab which hunts by sight, are very small and scarcely movable. But the fish is provided with a dense mass of tactile villi on its lower cheek, which is thus equipped to function as a very sensitive tactile organ. When in search of food, the Sole creeps very slowly over the bottom using its lateral fins more for walking than for swimming, the fin spines in their motion resembling very much the legs of a centipede. As it moves along, the fish thoroughly explores the substratum by what may be described as a kind of patting and grubbing action of the snout, carefully feeling the objects in its path with the sensitive papillæ on its lower cheek. Bateson (**1**, p. 240) states that, so far as he could determine, the Sole is unable to find food which does not lie on the bottom, and will not succeed in finding food suspended in the water close above it unless it is lowered so that the fish is able to cover it with the lower surface of its head, when it is seized at once.

Unfortunately, *Solea vulgaris* was not obtainable in sufficient numbers from the " corner " to enable any definite conclusion to be drawn as to its staple food. But it may be significant that the few which were examined had been feeding on Eulalia, Phyllodoce, *Porcellana longicornis*, and Mollusca. Todd (**29**, p. 117), however, examined 212 stomachs containing recognisable food material. Of these, Polychæta were present in 59 per cent, Crustacea in 30 per cent, Pisces and Mollusca each in 11 per cent, Echinodermata in 9 per cent, Nemertinea in 3 per cent, and Polyzoa and Cœlenterata in less than 0·5 per cent. The principal food species were :—

Polychæta :	*Lagis koreni*, *Ophelia limacina*, Nephthys sp., and *Sabellaria spinulosa*.
Crustacea :	Ampelisca sp.
Mollusca :	*Scrobicularia* (=*Syndosmya*) *alba*.
Pisces :	*Pleuronectes limanda* (1·9–2·8 cm.), Ammodytes sp.
Echinoderms :	*Echinocyamus pusillus*.

It will at once be seen that all the above animals are such that a Sole, foraging for food in the manner described, might be expected to find and contrive to capture. The worms eaten, for example, are either free-living forms which creep over the sea bottom or, if tubicolous, are sluggish and vulnerable species such as the Pectinaridæ which inhabit shallow and friable tubes.

It has not been found possible to study the feeding habits of the other species of Sole, but it is probable that they all adopt essentially the same methods, all having sensitive papillæ developed to a greater or less extent on the lower cheek.

Besides the structural differences already mentioned, the Lemon Dab and Sole exhibit still other morphological modifications correlated with their modes of feeding. The Lemon Dab has a very small terminal mouth, with teeth on both sides, but best developed on the lower side. In the Sole, on the other hand, the mouth is not terminal, but curved down ventrally, and teeth are present only on the lower side. The Lemon Dab depends entirely upon the visual sense in foraging for its prey and is therefore a day feeder. The Sole is almost, if not quite, independent of vision for the finding and recognition of its food, and feeds mostly at night.

Dab and **Plaice** (*Pleuronectes limanda* and *P. platessa*). Both are visual feeders. The former forages in a manner similar to that of the Lemon Dab, but does not raise itself quite so far off the bottom or bring its mouth down upon its prey at such a steep angle. It shoots upon them more from a horizontal direction, and being an active and alert fish it is thus able to capture a greater range of organisms than the Lemon Dab, but is less successful when it comes to Polychætes alone. The hunting posture of the Plaice is still more nearly horizontal, the head being raised off the bottom even less than that of the Dab. Its food is therefore again more restricted in its range, approaching that of the Sole—i.e. Mollusca, errantiate Polychætes, and sometimes a few Crustaceans, including an occasional Upogebia.

Among Flatfishes, the direct effect of structure in determining the kind of food which is eaten is also clearly seen in the post-larval stages, which do not come within the scope of this work. Lebour (**13**, p. 443), however, has shown that young Pleuronectids fall into two groups according to the structure of the alimentary canal. One group includes *Solea vulgaris*, *S. variegata*, *S. lascaris*, *Pleuronectes limanda*, *Rhombus maximus*, *R. lævis*, *Zeugopterus punctatus*, *Z. unimaculatus*, and *Scophthalmus norvegicus*, each of which possesses a large mouth and short thick gullet and stomach. Very soon after hatching these fishes all feed upon small Copepoda and Cladocera. The second group includes *Pleuronectes flesus*, *P. microcephalus*, and *Arnoglossus laterna*, which have a small mouth and

long narrow gullet and stomach. These do not eat Copepods or any other Crustacea until a greater size is reached, subsisting at first largely on a vegetarian (Diatom) diet, and going on to Entomostraca only at a much later stage.

The **Gurnards.** Definite correlation between the habits of a fish and its staple food organisms is also well seen in the case of the Gurnards. Four species—*Trigla lineata*, *T. cuculus*, *T. gurnardus*, *T. hirundo*—are present in small numbers in the Plymouth area. If these four species be observed in aquarium tanks, they will be found to form a definite habitudinal series. *T. lineata* spends most of its time crawling over the bottom of the tank by means of its long finger-like pectoral filaments. In addition to their locomotor function, the filaments are also very efficient tactile organs used in the finding and identification of food. As the fish creeps slowly over the bottom, the filaments are kept in continuous motion thoroughly "fingering" the ground over which they pass. When anything which promises to be suitable as an article of diet is touched by one of the filaments, the fish suddenly wheels round upon it and either immediately swallows it, or subjects it to still further tactile "scrutiny." *T. cuculus*, *T. gurnardus*, and *T. hirundo* also possess pectoral filaments and use them in the manner described, but to a progressively less extent. These species depend more and more upon the visual sense for the recognition of their prey, and dart upon it from a distance. Thus we find that *T. lineata* feeds very largely upon *Porcellana longicornis*, and to a less extent upon Galathea, *Portunus pusillus*, and Amphipoda. Burrowing organisms such as Upogebia and those tubicolous Polychætes which retract with almost lightning-like rapidity on the slightest provocation do not figure in its diet any more than do such active swimmers as the Pandalidæ, Crangonidæ, Palæmonidæ, or Pisces. But those agile organisms which successfully elude capture by *T. lineata* fall easy victims to the three other species which are more active hunters, depending less upon the tactile than upon the visual sense in foraging for their prey.

The **Dragonet** (*Callionymus lyra*). *Callionymus lyra*, too, is an interesting feeder whose habits are clearly reflected in its diet. This fish, a bottom dweller, is continually in a state of restless activity, in this somewhat resembling the Lemon Dab. For a few moments it will remain still, the anterior part of its body raised slightly off the ground as the fish rests poised upon its large pectoral fins. Then it skims along for a short distance, swimming usually less than a centimetre off the bottom, and again comes to rest. In this way Callionymus explores thoroughly a large and representative area of the sea floor, and few organisms escape its attention. Its food, therefore, is varied in the extreme. Ophiuroids, small Echinoids such as *Echinocyamus pusillus* and the young of larger species,

all the bottom-living Crustacea of suitable size—e.g. Amphipoda, Schizopoda, Porcellana, Galathea, Upogebia (occasionally), Paguridæ, *Portunus pusillus*, Ebalia, Inachidæ—small Mollusca of every description, and errantiate Polychæta are all to be found in the stomachs of Callionymus. Tubicolous Polychætes appear generally to elude it. Palæmonid, Crangonid, and Pandalid Crustaceans, too, it seldom captures, perhaps because they are too alert, but more probably because they live as a rule just above the bottom in a plane which Callionymus does not frequent (see also p. 693).

Other Fishes. The feeding habits of the other fishes from the " corner " have not been studied in detail. Of such forms as the Gadoids little can be

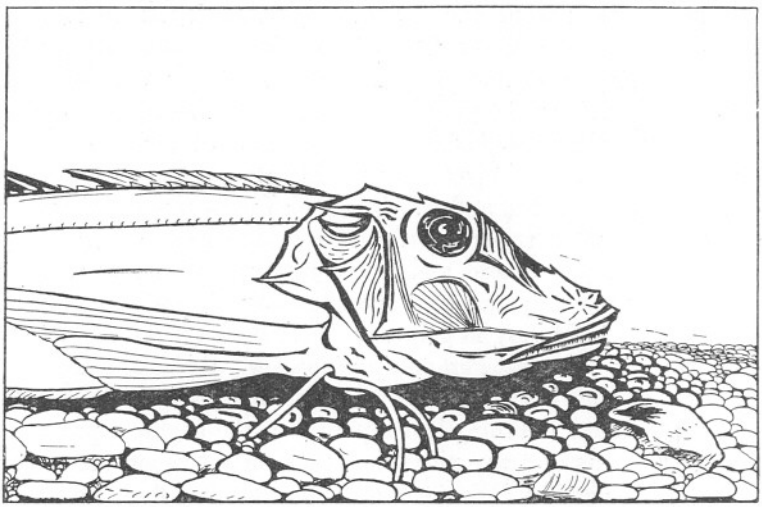


FIG. 3.—*Trigla hirundo* " feeling " its way along the sea floor by means of its long finger-like pectoral filaments.

added to what is already generally known. They are roving fishes which feed by sight, but some of them, such as the Pouting and Cod, appear to use their barbel as a tactile or gustatory organ. They will snap at almost anything which comes within their reach, whether on or off the bottom. Thus their food is almost as varied as the fauna of the area in which they are living. On the " corner " grounds only Whiting (*Gadus merlangus*), Whiting Pout (*G. luscus*), and the Poor-cod or Bib (*G. minutus*) are taken in any numbers. The first-named fish, while it feeds both on and off the bottom, confines its attention mostly to actively swimming pelagic organisms, while the two others graze more upon the bottom-dwelling animals (Table V).

Of the Dogfishes only two species have been taken during these

investigations. The feeding habits of these voracious members of the Shark tribe are also well known. The Rough Dogfish (*Scyliorhinus canicula*) feeds on anything which comes in its way. It hunts by scent, and although remaining for the most part in the lower layers also scours the sea from bottom to surface. The Spur Dog (*Squalus acanthias*), on the contrary, feeds while in Plymouth waters almost entirely on Herring. In fact it is present in numbers in the Plymouth area only during the winter months when Herrings are abundant. Todd (**29**, p. 132), however, states that in the North Sea its diet is much more comprehensive, including besides Pisces, Crustacea, Gephyrea, and often large quantities of *Pleurobrachia pileus*.

The four species of Ray examined feed almost entirely on the various Crustaceans available in their neighbourhood. Of their actual methods of feeding nothing has been seen.

Bionomics.

Elton (**6**, p. 59), in discussing food chains, states that they stop at certain points because there are very definite limits, both upper and lower, to the size of food an animal can eat. The size of the prey of carnivorous animals (both terrestrial and aquatic) is limited in the upward direction by their strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller organisms to satisfy their needs, the latter factor being also strongly influenced by the numbers as well as the size of the food animals. There is therefore an optimum size of food which is the one usually eaten. In the sea, however, another very important factor is involved which Elton does not mention possibly because it is very much less evident on the land. Animals of a suitable size for food, although living in the same area, may move in quite a different plane from that frequented by the carnivore and so, being inaccessible, remain outside a food chain from which size alone does not preclude them. During the time that the Megalopa Larvæ of Corystes were swarming in Plymouth waters, all the fishes which could catch them were feeding upon them to a greater or less extent. But *Callionymus lyra* was feeding on them not at all. There is no reason to suppose that this fish would not or could not eat the larvæ had they been available to it. The Megalopas, judging from the type and size of the other organisms which Callionymus will devour, are not too large or too small to suit it, nor is the fish too sluggish to catch them. But, so far as can be determined from observations on the habits of the fish, it never in ordinary circumstances leaves the bottom to feed. Therefore Megalopas swarming in the waters above it (**21**, p. 602) would not come within its range at all. Rays also are largely bottom feeders, but they will not infrequently rise off the ground in pursuit of food. Thus they,

the younger stages especially, made use of the Megalopas during the short time that they were abundant in the sea (Table II, p. 695).

Aquatic carnivores differ also from the majority of terrestrial forms in that they show a marked change of food (*prey*) with growth. This is due to at least two important factors. The first is that the larval fish must "fend for itself" from the time that the yolk-sac is absorbed, or even before, being entirely dependent upon its own efforts for the capture of its food. These little juvenile fishes must of necessity feed upon organisms proportionate to their size, which may be the young stages of the same food animals that support the adult fish or entirely different organisms. The food and feeding habits of the larval and post-larval stages of fishes have been very fully investigated by Lebour (*op. cit.*) and need not therefore be detailed here. Gradual change in the optimum size of food with growth continues until the adult size is reached. Todd (**29**) states that young Cod in the North Sea feed wholly on Crustacea, chiefly Ampelisca. With increase in size, their diet includes other groups, especially Pisces, Mollusca, and Polychæta. Young Plaice (<10 cm.) feed chiefly on Crustacea (Amphipoda, etc.) and Polychæta. With increase in size, Mollusca take first place. Such examples need not be multiplied. Among fishes captured on the "corner" grounds, change of food with growth was most obvious in two species of Ray—*Raia clavata* and *R. maculata*. The food of the young stages (20–40 cm.) consisted mainly of small Crustacea, chiefly Ampelisca.* Larger fish fed less upon Ampelisca and depended more upon other larger Crustacea. Eventually, in the largest fish, Amphipoda disappear entirely from their diet (Table II).

The prey of many terrestrial carnivores, on the other hand, changes but little or not at all during their growing period for the simple reason that they do not hunt. To begin with, the young of predatory mammals, for example, are fed upon maternal milk. Later on, the parents forage on their behalf, carrying home prey to the lair to feed them. Thus the growing animal does not have to hunt for itself until, from the point of view of foraging for food, it has become an adult and can catch the normal prey of the species. This applies also to birds. The nestlings are fed either upon semi-digested regurgitations from the stomach of the parent (e.g. Penguins) or are supplied liberally with food brought back by the old birds to the nest. In short, the higher terrestrial carnivores at least, do not have to depend upon their own efforts from the moment of their birth. This the little fish is obliged to do or die.

In the sea, another important factor bringing about change of food with growth is, in many cases, the change of level or environment frequented by the growing fish at different stages of its development. It

* During the time that Corystes Megalopas were abundant, young Rays (20–30 cm.) were feeding largely upon them (Table II).

TABLE II.*

Food of *Raia clavata* and *Raia maculata*.

Total number of Organisms in all Stomachs Examined.

	Season.	Length of Fish (in cm.).	Ampelisca.	Other Amphipoda.	Corystes Megalopas.	Schizopoda.	Isopoda.	Porcellana longicornis.	Annelida.	Hippolytidæ.	Portunus pusillus.	Crangonidæ.	Pandalidæ.	Galathea.	Upogebia.	Amphioxus.	Pisces.	Inachidæ.	Eupagurus.	Atelecyclus & Corystes.	Portunus depurator.	Total Number of Fishes Examined.
Raia clavata	Winter.	>10	**11**	–	–	**15**	–	–	2	3	–	–	5	–	1	–	–	–	–	–	–	8
		>20	**236**	3	–	1	–	6	–	1	–	1	1	1	1	–	–	–	–	–	–	11
		>30	**167**	–	–	–	–	–	1	2	2	7	**29**	–	**11**	–	2	–	–	–	2	19
		>40	2	–	–	–	–	–	–	1	8	1	**25**	–	4	–	–	–	–	–	7	8
		>50	1	–	–	–	–	–	–	–	1	1	9	6	**14**	–	2	–	**13**	3	**76**	25
		>60	–	–	–	–	–	–	–	–	–	–	–	–	2	–	4	–	5	1	**23**	9
	Summer.	>10	8	–	**78**	5	1	–	1	1	2	1	–	–	–	–	–	–	–	–	–	12
		>20	3	–	**89**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
		>30	**69**	–	**477**	–	–	–	3	1	4	4	8	1	–	–	–	–	–	–	2	23
		>40	**11**	–	**183**	–	–	–	–	–	3	1	7	**13**	9	–	1	–	–	2	**11**	16
		>50	–	–	**29**	–	–	–	3	–	–	–	4	**19**	**14**	–	1	–	9	2	**49**	25
		>60	–	–	–	–	–	–	–	–	–	–	–	**11**	7	–	–	–	4	1	2	6
Raia maculata	Winter.	>20	**15**	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	2
		>30	**296**	–	–	–	**30**	–	–	2	2	1	1	2	4	–	–	–	–	–	–	13
		>40	3	–	–	–	–	–	–	–	–	–	1	–	1	–	3	–	–	–	8	5
		>50	1	–	–	–	–	–	–	–	–	–	3	–	2	–	3	–	–	–	4	5
		>60	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	2	8	3
	Summer.	>20	3	2	**13**	–	–	–	2	–	2	–	–	–	–	–	–	–	–	–	–	1
		>30	**113**	3	**150**	4	2	4	6	–	–	4	–	–	–	–	–	–	–	–	–	6
		>40	**13**	1	**209**	1	–	–	4	–	–	1	–	–	–	**10**	–	–	–	–	–	3
		>50	3	–	–	–	–	1	–	–	1	–	–	2	5	–	–	2	**14**	3	9	11
		>60	–	–	–	–	–	–	–	–	–	–	–	–	3	–	3	5	4	1	2	6

* This table shows :—

(a) Gradual change of food with growth.
(b) That Ampelisca was abundantly available to the Rays in the winter season when few were taken in the bottom sampler.
(c) That the younger stages preyed largely upon Corystes Megalopas when these larvæ were swarming in the area in summer.

will suffice to quote one example. Young Pleuronectidæ before metamorphosis are active members of the marine macro-plankton, feeding greedily upon other plankton organisms of suitable size. Later, when metamorphosis sets in, they descend to the sea bottom and there remain lying on one side for the rest of their lives. It is obvious, therefore, that apart altogether from any change imposed by increase in size, there must follow a complete change of food due to change of environment and therefore of available food organisms.

BIBLIOGRAPHY.

1. Bateson, W. The Sense-organs and Perceptions of Fishes; with Remarks on the Supply of Bait. Jour. Mar. Biol. Assoc., N.S., Vol. I, No. 3, p. 225, 1890.

2. Blegvad, H. On the Food of Fish in the Danish Waters within The Skaw. Rep. Danish Biol. Sta., XXIV, p. 17, 1916.

3. —— Continued Studies on the Quantity of Fish Food in the Sea Bottom. Rep. Danish Biol. Sta., XXXI (1925), p. 27, 1926.

4. —— Quantitative Investigations of Bottom Invertebrates in the Limfjord 1910–1927 with Special Reference to the Plaice-Food. Rep. Danish Biol. Sta., XXXIV (1928), p. 33, 1928.

5. Cunningham, J. T. A Treatise on the Common Sole (*Solea vulgaris*). Mar. Biol. Assoc., Plymouth, 1890.

6. Elton, Charles. Animal Ecology. Sedgwick & Jackson, London, 1927.

7. Ford, E. On the Growth of some Lamellibranchs in Relation to the Food-supply of Fishes. Jour. Mar. Biol. Assoc., N.S., Vol. XIII, No. 3, p. 531, 1925.

8. Hertling, H. Untersuchungen über die Ernährung von Meeresfischen. I. Quantitative Nahrungsuntersuchungen an Pleuronektiden und einigen anderen Fischen der Ostsee. Ber. deutsch. wiss. Komm. Meeresforsch., Berlin, N.F./Bd. IV/Heft 2, p. 25, 1928.

9. Hunt, O. D. The Food of the Bottom Fauna of the Plymouth Fishing Grounds. Jour. Mar. Biol. Assoc., N.S., Vol. XIII, No, 3, p. 560, 1925.

10. Jensen, P. Boysen. Valuation of the Limfjord. I. Studies on the Fish-food in the Limfjord 1909–1917, its Quantity, Variation, and Annual Production. Rep. Danish Biol. Sta., XXVI, p. 1, 1919.

11. JENSEN, AAGE J. C. The Relation between the Size of the Plaice Stock and the Quantity of "First Class Plaice-Food" in certain Parts of the Limfjord. Rep. Danish Biol. Sta., XXXIV, p. 87, 1928.

12. KEMP, STANLEY. The Decapoda Natantia of the Coasts of Ireland. Fisheries, Ireland, Sci. Invest., 1908, I, (1910).

13. LEBOUR, M. V. The Food of Post-Larval Fish. Jour. Mar. Biol. Assoc., N.S., Vol. XI, No. 4, p. 433, 1918.

14. —— Feeding Habits of Some Young Fish. Jour. Mar. Biol. Assoc., Vol. XII, No. 1, p. 9, 1919.

15. —— The Food of Post-Larval Fish. No. II (1918). Jour. Mar. Biol. Assoc., Vol. XII, No. 1, p. 22, 1919.

16. —— The Food of Young Fish. No. III (1919). Jour. Mar. Biol. Assoc., Vol. XII, No. 2, p. 261, 1920.

17. MURIE, JAMES. Report on the Sea Fisheries and Fishing Industries of the Thames Estuary. Waterlow Bros. & Layton, London, 1903.

18. OGILVIE, HELEN S. Observations on the Food of Post-Larval Herring from the Scottish Coast. Fisheries, Scotland, Sci. Invest., 1927, I, 1927.

19. PETERSEN, C. G. JOH., and P. BOYSEN JENSEN. Valuation of the Sea. I. Animal Life of the Sea-bottom, its Food and Quantity. Rep. Danish Biol. Sta., XX, p. 3, 1911.

20. PETERSEN, C. G. JOH. The Sea Bottom and its Production of Fish-Food. Rep. Danish Biol. Sta., XXV, p. 1, 1918.

21. RUSSELL, F. S. The Vertical Distribution of Marine Macroplankton. V. The Distribution of Animals Caught in the Ring-trawl in the Daytime in the Plymouth Area. Jour. Mar. Biol. Assoc., Vol. XIV, No. 3, p. 557, 1927.

22. SCOTT, THOMAS. Observations on the Food of Fishes. Twentieth Annual Rept. Fish. Bd. for Scotland, Pt. III, p. 486, 1902.

23. SMITH, W. RAMSAY. On the Food of Fishes. Tenth Annual Rept. Fish. Bd. for Scotland, Pt. III, p. 211, 1892.

24 SÖMME, JACOB D. Faunistische und Quantitative Studien über Polychaeten aus dem Lenefjord und dem Grönsfjord (südliches Norwegen). Medd. Zool. Mus. Oslo, Nr. 11, p. 103, 1927.

25. Tchugunov, N. L. Essay on the Quantitative Exploration of the Benthos-production in the North part of the Caspian Sea and of the Typical Basins of the Volga-delta. Rep. Ichthyol. Lab. Astrachan, V, No. 1. (Original paper in Russian.)

26. Titcomb, John W., and C. M. McCay. The Nutritional Requirements and Growth Rates of Brook Trout. Trans. Amer. Fish. Soc., Vol. 58, p. 205, 1928.

27. Todd, R. A. Notes on the Invertebrate Fauna and Fish-food of the Bays between the Start and Exmouth. Jour. Mar. Biol. Assoc., N.S., Vol. VI, No. 4, p. 541, 1903.

28. —— Report on the Food of Fishes Collected during 1903. Internat. Fish. Investigations. Mar. Biol. Assoc., Report I (Southern Area), 1902–1903 (Cd. 2670), p. 227, 1905.

29. —— Second Report on the Food of Fishes (North Sea, 1904-1905). Internat. Fish. Investigations. Mar. Biol. Assoc., Report II (Southern Area), Pt. I, 1904–1905, (Cd. 3837), p. 49, 1907.

30. Wilson, Gregg. Notes on How Fish find Food. Rept. Brit. Assoc., 1893, p. 548, 1894.

APPENDIX.

TABLES III, IV, AND V.

EXPLANATION OF TABLES.

TABLE III. BOTTOM SAMPLER HAULS.

In this table is recorded the number of individuals or homogeneous groups of animals brought up from 0·5 square metre of bottom in five hauls of the 0·1 square metre bottom sampler at all stations 1–15. (See Chart, p. 678.)

The type of soil* at each station is indicated. Seasonal observations are tabulated under the heading a, b, c, d for autumn 1928, and the following winter, spring and summer respectively.

Points of special interest in this table are :—

(a) The relatively large Polychæte fauna of the area (see p. 689).

(b) The almost complete absence of Ampelisca in the winter season in bottom sampler hauls (see p. 681).

(c) The more or less uniform distribution of Upogebia spp. over the whole area as recorded by the bottom sampler—probably only a small fraction of the whole population (see p. 682).

(d) Mollusca are poorly represented on this ground.

(e) *Portunus depurator* is not recorded at all by the bottom sampler.

(f) That there is little or no change in the infauna as a whole over the year.

In this and the following table, where for various reasons actual counts were impracticable or impossible, the following signs have been used.

+ =Fragments only of the animal were obtained.
⊕ =Present, but not counted.
‡‡ =Present.

TABLE IV. TRAWL SAMPLES.

This table records the number of individuals or homogeneous groups of the epifauna per ¼ acre of bottom as brought up by the "Agassiz" trawl. Four ¼-acre hauls are given for each of stations 3, 10, 12, and 14 towing north, south, east, and west (N.S.E.W.) in turn from each of these centres. Three seasons' observations are indicated, as explained for Table III, by the letters b, c, d at the heads of the columns.

Points of special interest brought out by this table are :—

(a) The relative abundance of *Pandalina brevirostris*, and the migratory movements thereof (see p. 680).

* Detailed analyses of the soils have not been made, but samples are preserved so that this can be done later if necessary.

(b) *Portunus depurator* is very common on the ground, although not one was captured by the bottom sampler.

(c) A sudden appearance of *Acanthodoris pilosa* around station 3 when the summer series of observations was taken; other Nudibranchs also more numerous.

(d) *Crangon vulgaris* is most numerous on the ground in winter, having left its summer haunts closer inshore. *Pontophilus spinosus* is also present in greatest numbers at this season.

(e) Scarcity of *Corystes cassivelaunus* and *Atelecyclus septemdentatus*. In this connection, cf. Table I, page 684.

TABLE V. FOOD OF FISHES.

Here are tabulated the results of detailed examinations of stomach contents of fishes taken in an "Otter" Trawl within the "corner" area. The number of stomachs containing different organisms is given for different sizes of each fish, as well as the total number of each size-group examined. The numbers have not been worked out as percentages as this would tend to give a false value to observations on small numbers of fish. Although an attempt was made to examine at least twenty-five specimens of each species, this was possible only in the case of fishes which are sufficiently numerous on the ground. Of other species, less common or rare, the numbers examined were determined by the numbers caught.

Comparable winter and summer observations have been made, and are recorded separately in the upper and lower (italicised) columns respectively, opposite each size-group.

This table shows :—

(a) The food organisms preyed upon by the different fishes of the area (reading across).

(b) The various fishes which feed upon any particular animal (reading vertically).

(c) That the food of some fishes is restricted to certain organisms. This is determined by their structure or methods of foraging as explained in the text (p. 686).

(d) The importance of Corystes Megalopas as food for Whiting (over 10 cm.) and young Rays when these larvæ are available; small Whiting under 10 cm. in length did not feed to any extent upon the larvæ at a time when all the larger sizes were doing so.

TABLE III.

Station.	1				2				3				4				5			
Type of Soil.	Clean shelly gravel.				Medium shell gravel, mixed with mud and pebbles.				Rough shell gravel mixed with mud and pebbles.											
Season.	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Asteroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiuroidea	–	–	1	–	–	–	2	1	–	–	–	3	–	–	–	–	–	–	–	1
Echinoidea	1	1	2	–	–	–	–	1	4	–	–	1	5	–	2	–	–	–	–	–
Holothuroidea	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	2	–	–	1
Nemertinea	1	–	1	–	1	–	–	–	2	1	–	+	1	1	–	–	1	+	+	+
Polygordius	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Aphrodite aculeata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Harmothoë lunulata	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	–
Scalisetosus assimilis	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Sthenelais boa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais limicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllodoce sp.	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–
Eulalia ornata	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Ophiodromus flexuosus	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys cæca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys hombergii	2	2	2	–	–	1	–	–	–	–	–	–	2	–	–	–	2	–	–	–
Glycera convoluta	4	3	–	1	1	2	1	1	2	4	2	1	1	2	–	–	1	1	–	–
Goniada maculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Nematonereis unicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Hyalinœcia bilineata	–	1	–	1	3	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–
Lumbriconereis spp.	2	–	–	1	1	–	3	–	4	–	2	2	8	4	4	5	2	–	4	1
Aricia cuvieri	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Laonice cirrata	–	1	–	1	–	–	–	–	1	–	–	–	1	–	1	–	–	–	1	–
Magelona papillicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllochætopterus anglica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Heterocirrus spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scalibregma inflatum	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Notomastus latericeus	–	–	–	–	+	–	4	–	5	–	3	+	+	1	5	3	1	1	1	1
Clymene sp.	–	–	–	–	–	–	–	–	–	–	–	+	1	–	–	+	–	–	–	–
Owenia fusiformis	2	2	4	–	2	–	–	–	–	1	–	–	9	–	2	–	8	–	4	9
Pectinaria auricoma	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	2	1	2	–
Amphicteis gunneri	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	3	–	–	–
Melinna palmata	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	3	1
Loimia medusa	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Lanice conchilegica	–	–	1	–	1	–	–	–	–	1	2	2	1	1	–	–	–	–	–	1
Thelepus cincinnatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Polycirrus caliendrum	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Terebellides strœmi	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–
Sabella pavonina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Dasychone bombyx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydroides norvegica	–	–	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomatoceros triqueter	–	–	–	–	⊕	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gephyrea	–	–	–	–	1	1	–	–	2	–	–	1	–	–	–	1	1	–	–	–
Scalpellum vulgare	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	⊕
Ampelisca spp.	2	–	4	1	6	1	2	1	2	1	2	1	2	1	–	–	3	–	–	–
Perioculodes longimanus	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Cheirocratus sundevalli	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maera othonis	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erichthonius brasiliensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Conilera cylindracea	–	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Diastylis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Squilla larva	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alpheus ruber	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Processa canaliculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea nexa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–
Galathea intermedia	2	–	1	–	1	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
Upogebia stellata	1	–	2	–	1	1	1	2	–	1	–	2	–	–	3	2	1	1	1	–
Upogebia deltaura	–	–	1	–	–	–	–	–	1	1	3	–	–	1	–	2	1	1	1	3
Callianassa subterranea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paguridæ	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Porcellana longicornis	–	–	–	–	–	1	–	–	–	3	–	–	–	–	–	1	–	–	–	–
Ebalia cranchii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	–
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Macropodia longirostris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	1	–	–	–	2	1	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Craspedochilus onyx	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–
Turritella communis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Nucula nucleus	1	3	–	–	3	–	2	2	1	4	5	–	1	–	1	–	–	–	1	1
Nucula nitida	–	–	1	–	1	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Nucula radiata	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glycymeris glycymeris	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Æquipecten opercularis	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palliolum tigerinus	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Astarte sulcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina spinifera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina borealis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Syndosmya alba	1	–	–	1	–	–	–	–	–	2	–	–	1	–	–	–	–	–	–	–
Tellina crassa	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Tellina donacina	–	–	–	–	1	1	–	–	1	–	1	–	–	1	–	–	–	–	–	–
Lucinopsis undata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dosinia exoleta	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–
Clausinella fasciata	2	1	1	–	–	1	1	1	–	–	–	–	–	2	–	–	–	–	–	–
Ventricola casina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Timoclea ovata	–	–	–	–	1	–	11	2	–	2	1	–	5	–	2	–	–	–	–	–
Chamelæa gallina	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Cardium sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Psammobia tellinella	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corbula gibba	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Solecurtus antiquatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cultellus pellucidus	–	–	3	–	–	–	–	–	–	–	–	–	1	–	3	–	–	–	–	–
Natica alderi	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Station.	6				7				8				9				10			
Type of Soil.	Medium gravel mixed with mud. Some pebbles.				Fine silty sand, with pebbles, shells, and shell fragments.												Very fine muddy sand.			
Season.	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Asteroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiuroidea	–	–	1	1	1	1	1	1	–	–	1	1	–	–	4	–	2	–	–	2
Echinoidea	–	–	–	–	1	1	–	–	–	–	1	1	–	–	–	–	–	–	–	–
Holothuroidea	–	1	1	–	–	–	1	1	–	–	–	1	–	–	1	3	–	1	1	1
Nemertinea	–	+	–	–	1	–	–	+	–	–	3	–	–	1	–	1	–	–	1	1
Polygordius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphrodite aculeata	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Harmothoë lunulata	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
Scalisetosus assimilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais boa	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–
Sthenelais limicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllodoce sp.	–	–	–	–	1	–	1	–	1	–	–	1	–	–	–	–	1	–	–	–
Eulalia ornata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiodromus flexuosus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Nephthys cæca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys hombergii	–	1	–	1	3	2	3	–	4	3	6	–	2	3	3	3	4	1	1	5
Glycera convoluta	4	1	2	–	2	–	3	2	4	–	3	–	4	–	2	2	3	3	4	1
Goniada maculata	–	1	–	–	–	–	1	–	–	–	1	–	–	–	–	3	–	–	–	1
Nematonereis unicornis	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Hyalinœcia bilineata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lumbriconereis spp.	5	1	–	3	5	–	5	–	4	–	1	5	–	1	4	–	4	1	1	2
Aricia cuvieri	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–
Laonice cirrata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Magelona papillicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Phyllochætopterus anglica	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterocirrus spp.	–	–	–	1	1	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–
Scalibregma inflatum	1	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–
Notomastus latericeus	2	–	+	4	+	–	+	2	2	–	2	6	+	3	3	4	+	+	4	2
Clymene sp.	2	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–
Owenia fusiformis	7	8	5	5	6	10	3	14	5	5	7	5	3	2	8	–	12	2	5	–
Pectinaria auricoma	1	–	–	–	1	1	–	–	–	–	–	–	1	–	3	–	–	1	–	–
Amphicteis gunneri	1	–	–	–	–	1	–	–	–	–	3	–	–	–	1	–	2	–	1	1
Melinna palmata	6	–	1	3	–	–	–	1	–	1	–	–	–	–	15	10	5	2	4	3
Loimia medusa	4	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–
Lanice conchilegica	–	–	–	–	2	–	1	–	–	1	2	4	–	–	1	–	1	–	–	–
Thelepus cincinnatus	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Polycirrus caliendrum	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Terebellides strœmi	–	–	–	–	–	1	–	–	1	–	1	–	–	–	–	–	–	–	–	1
Sabella pavonina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dasychone bombyx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydroides norvegica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomatoceros triqueter	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gephyrea	2	–	1	–	1	–	1	2	–	–	–	–	–	–	–	1	–	–	–	–
Scalpellum vulgare	–	–	–	–	–	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	–
Ampelisca spp.	2	–	2	5	1	–	1	13	4	7	7	5	9	–	42	2	7	–	109	30
Perioculodes longimanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cheirocratus sundevalli	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maera othonis	–	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Gammarus sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata	1	–	–	3	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–
Erichthonius brasiliensis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	6	–
Conilera cylindracea	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Diastylis sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1
Squilla larva	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alpheus ruber	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–
Processa canaliculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea nexa	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea intermedia	–	–	–	1	1	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–
Upogebia stellata	1	1	2	–	–	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–
Upogebia deltaura	1	2	4	1	–	–	1	–	–	–	–	1	3	–	–	1	–	–	1	–
Callianassa subterranea	–	–	–	–	–	–	–	–	–	–	–	1	2	1	9	9	–	–	7	1
Paguridæ	–	–	–	–	1	–	–	–	1	4	–	1	–	–	1	–	–	–	–	–
Porcellana longicornis	–	–	–	3	–	1	–	–	–	–	–	–	2	–	1	–	–	–	1	–
Ebalia cranchii	2	–	1	–	–	3	–	–	1	1	–	–	–	–	2	1	–	–	–	–
Ebalia tuberosa	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Macropodia longirostris	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	–	–	–	–	1	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1	–	1	–	–
Craspedochilus onyx	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	–	–	–	–	3	1	–	4	–	–	2	–	5	3	6	8	1	–	1	–
Nucula nucleus	9	–	1	1	4	–	–	–	1	7	1	–	–	–	–	–	–	–	–	–
Nucula nitida	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nucula radiata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glycymeris glycymeris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Æquipecten opercularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Palliolum tigerinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astarte sulcata	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina spinifera	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–
Lucina borealis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Syndosmya alba	–	1	–	–	–	1	–	2	–	4	–	1	–	–	–	–	1	–	–	–
Tellina crassa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tellina donacina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucinopsis undata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dosinia exoleta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clausinella fasciata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ventricola casina	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Timoclea ovata	3	–	–	–	1	–	1	–	3	1	1	–	–	–	2	–	–	–	–	–
Chamelæa gallina	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
Cardium sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Psammobia tellinella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corbula gibba	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Solecurtus antiquatus	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	1
Cultellus pellucidus	–	1	–	–	–	4	3	1	–	3	–	5	–	1	3	3	–	–	1	–
Natica alderi	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Station.	11				12				13				14				15			
Type of Soil.	Very fine muddy sand.								Mud, containing some very fine sand.											
Season.	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Asteroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ophiuroidea	1	–	3	–	–	–	2	1	–	–	–	1	2	–	–	–	3	–	1	–
Echinoidea	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	3	–	–	–
Holothuroidea	–	–	1	1	3	–	1	–	4	+	1	2	–	1	–	1	2	1	–	3
Nemertinea	–	1	+	2	–	–	1	–	+	–	–	1	1	+	+	–	–	+	–	1
Polygordius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aphrodite aculeata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Harmothoë lunulata	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Scalisetosus assimilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sthenelais boa	–	1	–	–	–	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Sthenelais limicola	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllodoce sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eulalia ornata	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiodromus flexuosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nephthys cæca	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Nephthys hombergii	2	3	5	10	6	3	2	5	3	3	–	1	4	3	4	3	8	3	9	4
Glycera convoluta	3	–	–	–	–	–	1	1	2	2	1	4	4	1	–	3	4	3	–	2
Goniada maculata	–	1	–	1	–	–	–	–	8	–	1	1	–	1	–	1	3	–	–	3
Nematonereis unicornis	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyalinœcia bilineata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lumbriconereis spp.	8	–	–	–	1	–	3	–	–	–	–	–	–	–	2	1	–	–	–	1
Aricia cuvieri	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Laonice cirrata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Magelona papillicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phyllochætopterus anglica	2	2	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterocirrus spp.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–
Scalibregma inflatum	–	–	–	–	–	–	–	–	3	–	1	–	1	–	–	–	–	–	–	–
Notomastus latericeus	1	–	2	–	1	+	3	3	1	3	3	11	5	–	1	5	2	2	–	9
Clymene sp.	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Owenia fusiformis	11	4	3	3	6	3	6	–	3	–	1	5	5	1	6	1	5	2	3	6
Pectinaria auricoma	–	–	–	–	–	–	–	–	3	–	–	6	3	–	1	3	5	–	–	–
Amphicteis gunneri	–	–	1	1	–	–	1	–	4	–	1	–	–	–	1	–	–	–	–	–
Melinna palmata	3	–	3	4	1	–	5	–	6	–	1	5	4	–	–	–	–	1	4	3
Loimia medusa	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lanice conchilegica	3	1	–	3	2	1	1	–	–	–	–	1	–	–	–	–	–	–	1	–
Thelepus cincinnatus	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polycirrus caliendrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Terebellides strœmi	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sabella pavonina	–	–	–	–	2	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
Dasychone bombyx	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydroides norvegica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pomatoceros triqueter	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gephyrea	1	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Scalpellum vulgare	⊕	–	–	⊕	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ampelisca spp.	5	2	35	–	2	2	9	25	30	–	30	20	53	–	79	21	49	–	8	30
Perioculodes longimanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cheirocratus sundevalli	–	–	1	–	–	–	–	–	1	–	–	–	2	–	–	–	1	–	–	–
Maera othonis	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erichthonius brasiliensis	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conilera cylindracea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diastylis sp.	1	–	–	–	–	–	1	–	5	–	1	–	–	–	–	–	2	1	–	–
Squilla larva	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Alpheus ruber	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
Processa canaliculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea nexa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galathea intermedia	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Upogebia stellata	–	–	–	1	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	2
Upogebia deltaura	–	–	1	2	–	–	–	1	2	–	2	–	1	–	–	2	2	–	–	5
Callianassa subterranea	–	–	3	3	–	–	–	5	5	3	1	10	4	1	1	4	–	–	1	6
Paguridæ	1	–	2	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1
Porcellana longicornis	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	1	–	–	–
Ebalia cranchii	–	1	1	–	–	–	–	–	1	–	–	1	–	–	1	1	3	1	–	1
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Macropodia longirostris	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	3	–	–	–
Atelecyclus septemdentatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1
Craspedochilus onyx	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	–	–	–	–	–	1	–	–	3	2	–	4	–	–	2	–	3	4	1	3
Nucula nucleus	3	1	–	–	–	2	2	–	–	–	–	–	–	1	–	–	–	–	–	–
Nucula nitida	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–
Nucula radiata	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glycymeris glycymeris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Æquipecten opercularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palliolum tigerinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astarte sulcata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucina spinifera	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Lucina borealis	–	–	–	6	–	–	–	1	2	–	–	1	–	–	–	–	–	–	–	–
Syndosmya alba	2	1	–	1	–	–	1	–	11	1	–	–	5	–	–	1	3	1	–	–
Tellina crassa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tellina donacina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucinopsis undata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Dosinia exoleta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clausinella fasciata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ventricola casina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Timoclea ovata	–	–	–	–	1	9	2	–	1	–	–	–	–	–	–	–	–	–	1	–
Chamelæa gallina	–	–	–	–	–	–	–	–	1	5	–	–	2	1	–	–	–	–	–	–
Cardium sp.	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Psammobia tellinella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corbula gibba	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Solecurtus antiquatus	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1	–	–	–
Cultellus pellucidus	1	1	4	–	2	–	–	1	7	1	1	2	3	1	1	1	7	2	2	3
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE IV.

Station.	3											
Direction Towed.	N.			E.			S.			W.		
Season.	b	c	d	b	c	d	b	c	d	b	c	d
Hydractinia echinata	–	–	–	–	–	–	–	–	–	–	–	–
Sertularella gayi	–	–	–	–	–	–	–	–	–	–	–	‡‡
Hydrallmania falcata	–	–	–	–	–	–	–	–	–	–	–	–
Antennularia antennina	–	–	–	–	–	–	–	–	‡‡	–	–	‡‡
Plumularia catharina	–	–	–	–	–	–	–	–	–	–	–	–
Alcyonium digitatum	–	–	–	–	–	–	–	–	–	–	–	–
Metridium senilis	–	–	–	–	–	–	–	–	–	–	–	–
Astropecten irregularis	–	–	–	–	–	–	1	–	–	–	–	–
Palmipes membranaceus	–	–	2	1	–	–	–	–	2	1	–	1
Solaster papposus	–	–	–	–	1	1	–	–	–	–	–	–
Henricia sanguinolenta	–	–	–	–	–	–	–	–	–	–	–	–
Stichastrella rosea	–	–	1	–	–	–	–	–	–	–	–	–
Asterias rubens	–	–	–	–	–	–	–	–	–	–	–	–
Marthasterias glacialis	3	2	3	2	2	–	1	–	2	–	4	1
Ophiothrix fragilis	3	–	1	2	2	3	4	–	7	1	5	6
Amphiura filiformis	–	–	–	–	–	–	–	–	–	–	–	–
Ophiura texturata	8	–	10	6	–	–	3	–	1	1	–	–
Echinus esculentus	1	–	–	–	–	–	3	–	–	–	–	–
Spatangus purpureus	–	–	–	–	–	–	–	–	–	–	–	–
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	–	–	–
Phascolion strombi	–	–	–	–	–	–	–	–	–	–	–	–
Balanus sp.	⊕	⊕	⊕	–	⊕	⊕	–	⊕	⊕	–	⊕	–
Scalpellum vulgare	⊕	–	–	–	–	–	–	–	–	–	–	–
Conilera cylindracea	6	–	1	–	–	–	1	–	–	–	–	–
Schizopoda	–	–	–	–	3	–	–	6	–	–	7	–
Pandalus montagui	11	–	3	2	2	29	3	3	–	–	–	6
Pandalina brevirostris	21	121	50	24	116	421	–	429	6	18	377	173
Hippolyte varians	–	1	–	–	1	14	–	2	–	1	–	–
Spirontocaris cranchi	–	–	1	–	–	–	–	3	–	–	1	–
Leander serratus	–	–	–	–	–	–	–	4	–	–	–	–
Crangon vulgaris	8	–	–	–	1	–	2	–	–	5	–	–
Philocheras sculptus	1	2	–	–	2	4	–	8	2	1	–	2
Philocheras bispinosus	–	1	–	–	2	4	–	2	–	1	2	2
Pontophilus spinosus	–	2	2	–	1	1	–	2	–	6	1	–
Galathea nexa	9	–	4	1	2	11	6	8	15	4	13	9
Galathea intermedia	8	–	–	2	–	2	3	–	10	1	–	–
Munida bamffica	–	–	–	–	–	–	–	1	–	–	2	–
Porcellana longicornis	1	3	10	4	3	7	16	10	20	4	14	1
Eupagurus bernhardus	–	–	–	–	–	–	–	–	–	–	–	–
Eupagurus prideauxi	24	2	4	7	5	16	10	21	53	14	12	–
Anapagurus lævis	12	–	–	3	–	–	–	–	–	–	–	5
Portunus puber	–	–	–	–	–	–	–	–	–	–	–	1
Portunus pusillus	6	–	2	–	–	–	2	–	5	–	–	2
Portunus holsatus	1	2	3	2	2	4	1	3	6	–	2	–
Portunus depurator	21	26	30	4	10	23	6	11	22	8	15	35
Cancer pagurus	–	–	–	–	–	–	–	–	1	–	–	1
Atelecyclus septemdentatus	–	1	1	–	–	–	1	–	1	–	–	1
Corystes cassivelaunus	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	–	–	–	–	1	–	1
Ebalia tuberosa	3	1	1	–	–	1	2	–	1	–	–	–
Ebalia cranchii	–	–	1	–	–	–	–	–	–	–	1	–
Maia squinado	–	–	–	–	–	–	–	–	–	–	2	–
Eurynome aspera	–		–	–	–	–	–	–	–	–	–	–
Hyas araneus	–	–	–	–	–	2	–	–	–	–	–	1
Inachus dorsettensis	13	6	10	4	2	11	4	2	8	–	–	15
Macropodia longirostris	25	10	31	24	8	107	1	16	16	13	12	64
Macropodia rostratus	3	1	5	4	2	9	–	3	1	–	2	–
Phoxichilus spinosus	–	2	–	–	–	–	–	–	–	–	–	–
Ovula patula (on Alcyonium)	–	–	–	–	–	–	–	–	–	–	–	–
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	–	–	–	–	–	–	–	–	–	–	–	–
Oscanius membranaceus	–	–	–	–	–	4	–	1	2	–	2	4
Amphorina cærulea	–	–	–	–	–	–	–	–	–	–	–	–
Galvina tricolor	–	1	1	–	–	–	–	–	–	–	–	–
Antiopella hyalina	–	–	1	–	–	–	–	–	–	–	–	1
Lomanotus sp.	–	–	–	–	1	–	–	–	–	–	–	–
Dendronotus frondosus	–	1	–	–	–	–	–	2	–	–	–	–
Pleurophyllidia loveni	–	–	–	–	–	–	–	–	–	–	–	–
Archidoris tuberculata	–	–	–	–	–	–	–	2	–	–	–	–
Jorunna johnstoni	–	–	–	–	–	1	–	–	1	–	–	2
Platydoris testudinaria	–	–	–	–	–	–	–	–	–	–	–	–
Polycera quadrilineata	–	–	–	–	–	–	–	–	1	–	1	–
Acanthodoris pilosa	–	–	1	–	–	14	–	–	2	–	–	21
Lamellidoris oblonga	–	–	–	–	–	–	–	–	–	–	–	–
Ancula cristata	–	–	–	–	–	5	–	–	–	–	–	–
Lamellibranchs	16	–	17	2	2	13	10	–	22	3	4	6
Sepia officinalis	–	–	–	–	–	–	–	–	–	–	–	–
Sepiola atlantica	1	1	2	–	–	–	–	1	2	–	–	–
Eugyra arenosa	–	–	4	–	–	1	–	–	–	–	–	–
Ascidiella scabra	1	–	–	–	–	1	–	–	–	–	–	3
Polyzoa	–	–	–	–	–	‡‡	–	–	–	–	–	‡‡
Amphioxus lanceolatus	1	–	–	–	–	–	–	–	–	–	–	–

Station.	10											
Direction Towed.	N.			E.			S.			W.		
Season.	b	c	d	b	c	d	b	c	d	b	c	d
Hydractinia echinata	–	–	–	–	–	–	–	–	–	–	–	–
Sertularella gayi	–	–	–	–	–	–	–	–	–	–	–	–
Hydrallmania falcata	–	–	–	–	–	–	–	–	–	–	–	–
Antennularia antennina	–	–	–	–	–	–	–	–	–	–	–	–
Plumularia catharina	–	–	–	–	–	–	–	–	–	–	–	–
Alcyonium digitatum	–	–	–	–	–	–	–	–	–	–	–	–
Metridium senilis	–	–	–	–	–	–	–	–	–	–	–	–
Astropecten irregularis	–	–	–	–	1	–	–	–	–	–	1	–
Palmipes membranaceus	–	–	–	–	–	–	–	–	–	–	–	–
Solaster papposus	–	–	–	–	–	–	–	–	–	–	–	–
Henricia sanguinolenta	–	–	–	–	–	–	–	–	–	–	–	–
Stichastrella rosea	–	–	–	–	–	–	–	–	–	–	–	–
Asterias rubens	–	–	–	–	–	–	–	–	–	–	–	–
Marthasterias glacialis	7	1	5	14	3	5	8	1	4	3	4	4
Ophiothrix fragilis	2	2	4	–	–	17	1	–	1	1	1	–
Amphiura filiformis	–	–	–	–	–	–	–	–	–	–	–	–
Ophiura texturata	–	–	1	2	1	1	2	–	1	1	–	–
Echinus esculentus	–	–	–	–	–	–	–	–	–	–	–	–
Spatangus purpureus	–	–	–	–	–	–	–	–	–	–	–	–
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	–	–	–
Phascolion strombi	–	–	–	–	–	–	–	–	–	–	–	–
Balanus sp.	⊕	–	⊕	–	⊕	⊕	⊕	–	–	–	⊕	–
Scalpellum vulgare	–	–	–	–	–	–	–	–	–	–	–	–
Conilera cylindracea	–	–	–	–	–	–	–	–	–	–	–	–
Schizopoda	–	–	–	–	–	–	–	–	–	–	–	–
Pandalus montagui	–	2	–	–	4	–	–	1	–	–	–	1
Pandalina brevirostris	16	1	7	19	18	4	62	1	–	10	1	7
Hippolyte varians	–	–	–	–	–	–	1	–	1	1	–	–
Spirontocaris cranchi	–	–	–	–	–	–	–	–	–	–	–	–
Leander serratus	–	2	–	–	2	–	–	1	–	–	2	–
Crangon vulgaris	28	–	–	36	–	1	23	–	–	25	–	–
Philocheras sculptus	–	–	–	–	–	–	–	–	–	–	–	–
Philocheras bispinosus	–	–	–	–	–	–	–	–	–	1	–	–
Pontophilus spinosus	20	–	4	45	2	2	20	–	1	5	–	–
Galathea nexa	9	6	9	7	8	12	21	4	15	9	2	7
Galathea intermedia	4	–	2	–	–	3	6	–	1	3	–	3
Munida bamffica	–	–	1	–	–	–	–	–	–	–	–	–
Porcellana longicornis	12	8	7	4	12	23	14	2	–	1	–	4
Eupagurus bernhardus	–	–	3	–	–	2	–	1	–	–	–	–
Eupagurus prideauxi	12	2	–	68	2	–	75	1	–	30	40	–
Anapagurus lævis	–	–	–	–	–	8	–	–	–	–	–	–
Portunus puber	1	1	1	–	–	–	–	2	–	–	1	–
Portunus pusillus	–	–	–	1	–	–	1	–	–	1	–	–
Portunus holsatus	–	–	–	–	2	1	–	1	1	–	1	–
Portunus depurator	41	14	15	56	29	35	80	51	42	40	45	7
Cancer pagurus	–	–	–	–	–	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	1	–	–	–	–	1	–	1	–	–	–
Corystes cassivelaunus	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	–	–	–	1	–	–	1	1	–	–
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	1
Ebalia cranchii	–	–	–	–	–	2	–	–	–	–	–	–
Maia squinado	1	–	–	–	–	–	–	–	–	–	1	–
Eurynome aspera	–	–	–	–	–	–	–	–	–	–	–	–
Hyas araneus	–	–	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	11	2	2	27	2	5	8	3	6	4	2	7
Macropodia longirostris	21	4	11	61	6	16	40	4	15	34	4	13
Macropodia rostratus	3	1	1	2	1	3	3	2	1	1	4	3
Phoxichilus spinosus	–	–	1	–	–	1	–	–	1	–	–	1
Ovula patula (on Alcyonium)	–	–	–	–	–	–	–	–	–	–	–	–
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	3	1	7	5	6	2	2	4	1	–	–	–
Oscanius membranaceus	2	–	–	–	–	–	–	–	1	–	–	1
Amphorina cærulea	–	–	–	–	–	2	–	–	–	–	–	–
Galvina tricolor	–	–	–	–	–	–	–	–	–	–	–	–
Antiopella hyalina	–	–	–	–	–	–	–	–	–	–	–	–
Lomanotus sp.	–	–	–	–	–	–	–	–	1	–	–	–
Dendronotus frondosus	–	–	–	–	–	–	–	–	–	–	–	–
Pleurophyllidia loveni	–	–	–	–	–	–	–	–	–	–	–	–
Archidoris tuberculata	–	–	–	–	–	–	–	–	–	–	–	–
Jorunna johnstoni	–	–	1	–	–	–	–	–	–	–	–	–
Platydoris testudinaria	–	–	1	–	–	–	–	–	–	–	–	–
Polycera quadrilineata	–	–	–	–	–	–	–	–	–	–	–	–
Acanthodoris pilosa	–	–	–	–	–	–	–	–	–	–	–	–
Lamellidoris oblonga	–	–	–	–	–	–	–	–	–	–	–	–
Ancula cristata	–	–	3	–	–	–	–	–	–	–	–	–
Lamellibranchs	–	–	2	2	–	2	1	1	1	–	–	–
Sepia officinalis	–	–	–	–	–	–	–	–	1	–	–	–
Sepiola atlantica	–	–	–	–	–	–	2	–	–	1	1	–
Eugyra arenosa	–	–	–	–	–	–	–	–	–	–	–	–
Ascidiella scabra	–	–	–	–	–	–	–	–	–	–	–	–
Polyzoa	–	–	‡‡	–	–	–	–	–	–	–	–	–
Amphioxus lanceolatus	–	–	–	–	–	–	–	–	–	–	–	–

Station.	12											
Direction Towed.	N.			E.			S.			W.		
Season.	b	c	d	b	c	d	b	c	d	b	c	d
Hydractinia echinata	–	–	–	–	–	–	–	–	–	‡‡	–	–
Sertularella gayi	‡‡	–	–	–	–	–	‡‡	–	–	–	–	–
Hydrallmania falcata	–	–	–	–	–	–	‡‡	–	‡‡	–	–	–
Antennularia antennina	‡‡	–	–	–	–	–	‡‡	–	‡‡	–	–	–
Plumularia catharina	–	–	–	–	–	–	–	–	–	–	–	–
Alcyonium digitatum	–	–	–	–	–	–	–	–	‡‡	–	–	–
Metridium senilis	–	1	–	–	–	–	–	–	1	–	2	–
Astropecten irregularis	1	–	–	–	–	2	–	–	–	–	1	–
Palmipes membranaceus	–	–	–	–	–	–	–	–	–	–	–	–
Solaster papposus	–	–	–	–	–	–	–	–	–	–	–	–
Henricia sanguinolenta	–	–	–	–	–	–	–	–	–	–	–	–
Stichastrella rosea	–	–	–	–	–	–	–	–	–	–	–	–
Asterias rubens	–	–	–	–	–	–	–	–	–	–	–	–
Marthasterias glacialis	2	1	–	–	–	–	–	2	–	1	–	1
Ophiothrix fragilis	20	–	1	9	5	–	15	–	2	38	1	9
Amphiura filiformis	–	–	–	–	–	–	3	–	–	–	–	–
Ophiura texturata	–	–	–	–	2	–	–	–	–	–	2	1
Echinus esculentus	–	–	–	–	–	–	–	–	–	1	–	–
Spatangus purpureus	–	–	–	–	–	–	–	–	–	–	–	–
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	–	–	–
Phascolion strombi	–	–	–	–	–	–	–	–	–	–	–	–
Balanus sp.	⊕	⊕	–	–	⊕	⊕	–	–	–	–	⊕	–
Scalpellum vulgare	–	⊕	–	–	–	–	⊕	⊕	–	–	–	⊕
Conilera cylindracea	–	–	–	–	–	–	–	–	–	–	–	–
Schizopoda	–	–	–	–	–	–	–	2	–	–	–	–
Pandalus montagui	–	–	–	–	–	–	–	–	–	–	–	–
Pandalina brevirostris	24	4	–	12	2	–	12	2	2	14	5	7
Hippolyte varians	–	–	–	–	–	–	1	–	–	–	–	–
Spirontocaris cranchi	19	1	–	2	–	–	2	1	–	7	–	–
Leander serratus	–	–	–	–	–	–	–	–	–	–	–	–
Crangon vulgaris	29	–	–	7	1	–	5	1	–	7	1	–
Philocheras sculptus	–	–	–	1	–	–	–	–	–	2	–	–
Philocheras bispinosus	–	2	1	–	–	–	–	3	1	–	2	2
Pontophilus spinosus	1	2	–	–	–	–	–	1	2	–	2	1
Galathea nexa	23	6	2	5	11	2	20	8	9	29	4	5
Galathea intermedia	–	–	–	–	–	–	–	–	–	–	–	3
Munida bamffica	1	–	–	–	–	–	–	–	–	–	–	1
Porcellana longicornis	193	6	1	15	29	4	249	49	14	230	22	139
Eupagurus bernhardus	1	–	–	–	–	1	–	–	–	1	1	1
Eupagurus prideauxi	12	15	5	5	12	3	7	7	4	8	24	7
Anapagurus lævis	–	–	–	–	–	4	–	–	6	–	–	6
Portunus puber	–	–	–	–	–	–	–	–	–	–	–	–
Portunus pusillus	–	–	–	–	–	–	–	–	–	–	–	–
Portunus holsatus	–	–	2	2	4	5	2	1	3	–	–	–
Portunus depurator	8	7	4	5	51	8	5	8	12	3	3	3
Cancer pagurus	–	–	–	–	–	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	1	–	–	1	1	–	2	–	–	3	1
Corystes cassivelaunus	–	–	–	–	–	1	–	1	–	–	–	1
Gonoplax rhomboides	–	–	–	–	–	–	–	–	–	–	–	–
Ebalia tuberosa	–	–	–	–	1	–	–	–	–	–	1	–
Ebalia cranchii	–	–	–	–	–	–	–	–	–	–	–	1
Maia squinado	–	–	–	–	–	–	–	–	–	–	1	–
Eurynome aspera	–	–	–	–	–	–	–	–	–	1	–	–
Hyas araneus	–	–	–	–	–	–	–	–	–	–	1	–
Inachus dorsettensis	5	6	4	1	9	13	3	12	6	6	6	9
Macropodia longirostris	9	13	9	12	11	7	37	9	11	11	18	29
Macropodia rostratus	5	2	1	2	2	3	4	1	–	3	1	7
Phoxichilus spinosus	–	–	–	–	–	–	–	1	–	–	–	2
Ovula patula (on Alcyonium)	–	–	–	–	–	–	–	–	1	–	–	–
Natica alderi	–	–	–	–	–	–	–	1	–	–	–	–
Turritella communis	1	1	2	–	–	–	–	1	–	–	–	–
Oscanius membranaceus	–	–	–	–	–	–	–	2	–	–	–	–
Amphorina cærulea	–	–	–	–	–	–	–	–	–	–	–	–
Galvina tricolor	–	–	6	–	–	1	–	–	–	–	–	–
Antiopella hyalina	–	–	–	–	–	–	–	1	–	–	–	–
Lomanotus sp.	–	–	–	–	–	–	–	–	–	–	–	–
Dendronotus frondosus	–	–	–	–	–	–	–	1	–	–	–	–
Pleurophyllidia loveni	–	–	–	–	–	–	–	–	–	–	1	–
Archidoris tuberculata	–	–	–	–	–	–	–	1	–	–	–	–
Jorunna johnstoni	–	–	–	–	–	–	–	–	–	–	–	–
Platydoris testudinaria	–	–	–	–	–	–	–	–	–	–	–	–
Polycera quadrilineata	–	–	–	–	–	–	–	–	–	–	–	–
Acanthodoris pilosa	–	–	–	–	–	–	–	–	–	–	–	–
Lamellidoris oblonga	1	–	–	–	1	–	8	–	15	5	–	4
Ancula cristata	–	–	4	–	–	–	–	–	–	–	–	–
Lamellibranchs	Small Aequipecten numerous, attached to Cellaria											
Sepia officinalis	–	–	–	–	–	–	–	–	–	–	–	–
Sepiola atlantica	–	–	–	1	1	–	3	1	–	3	1	–
Eugyra arenosa	–	–	–	–	–	–	–	–	–	–	–	–
Ascidiella scabra	–	–	–	1	–	–	–	–	–	–	–	–
Polyzoa	Cellaria spp. very abundant at this station											
Amphioxus lanceolatus	–	–	–	–	–	–	–	–	–	–	–	–

Station.	14											
Direction Towed.	N.			E.			S.			W.		
Season.	b	c	d	b	c	d	b	c	d	b	c	d
Hydractinia echinata	–	–	–	–	–	–	–	–	–	–	–	–
Sertularella gayi	–	–	–	–	–	–	–	–	‡‡	‡‡	–	–
Hydrallmania falcata	–	–	–	–	–	–	–	–	–	‡‡	–	‡‡
Antennularia antennina	–	–	–	‡‡	–	–	‡‡	–	–	‡‡	–	–
Plumularia catharina	–	–	–	–	–	–	–	–	–	–	–	‡‡
Alcyonium digitatum	–	–	–	–	–	–	–	–	–	–	–	–
Metridium senilis	2	–	–	–	–	–	–	–	1	1	–	2
Astropecten irregularis	–	–	–	–	–	–	–	–	–	–	–	–
Palmipes membranaceus	–	–	–	–	–	–	–	–	–	–	–	–
Solaster papposus	–	–	–	–	–	–	–	–	–	–	–	–
Henricia sanguinolenta	–	–	–	–	–	–	–	–	–	–	–	–
Stichastrella rosea	–	–	–	–	–	–	–	–	–	–	–	–
Asterias rubens	–	–	–	–	–	–	1	–	–	–	–	–
Marthasterias glacialis	3	2	5	4	6	2	1	6	3	9	1	2
Ophiothrix fragilis	1	2	–	4	1	2	–	–	–	7	1	4
Amphiura filiformis	–	–	–	–	–	–	–	–	–	1	–	–
Ophiura texturata	–	2	2	1	–	1	–	1	1	1	–	–
Echinus esculentus	–	–	–	–	–	–	–	–	–	–	–	–
Spatangus purpureus	–	–	–	–	–	–	–	–	–	–	–	–
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	–	–	–
Phascolion strombi	–	–	–	–	–	–	–	–	–	–	–	–
Balanus sp.	–	–	–	–	–	⊕	–	–	–	–	–	–
Scalpellum vulgare	–	–	–	–	–	–	–	–	–	⊕	–	–
Conilera cylindracea	–	–	–	–	–	–	–	–	–	–	–	–
Schizopoda	–	–	–	–	–	–	–	1	–	–	1	–
Pandalus montagui	–	–	–	–	–	1	–	–	–	–	1	–
Pandalina brevirostris	42	46	3	211	20	2	45	13	7	65	9	5
Hippolyte varians	–	–	–	–	–	–	–	–	–	–	–	–
Spirontocaris cranchi	–	–	–	1	–	–	4	–	–	–	–	–
Leander serratus	–	–	–	–	–	–	–	–	–	–	–	–
Crangon vulgaris	6	–	1	9	1	1	22	3	–	8	–	1
Philocheras sculptus	–	–	–	–	–	–	–	–	–	–	–	–
Philocheras bispinosus	–	1	–	–	2	–	–	3	1	1	3	–
Pontophilus spinosus	10	2	–	5	–	1	2	1	1	19	1	2
Galathea nexa	13	4	2	8	6	11	4	5	3	20	9	6
Galathea intermedia	–	–	–	–	–	–	1	–	1	–	–	–
Munida bamffica	1	2	4	1	1	2	–	–	1	–	–	2
Porcellana longicornis	9	–	–	7	4	31	14	13	11	25	2	30
Eupagurus bernhardus	–	–	2	–	–	–	–	–	1	–	–	1
Eupagurus prideauxi	3	4	1	17	5	–	2	5	1	2	–	–
Anapagurus lævis	–	–	13	–	–	45	–	–	20	–	–	8
Portunus puber	–	2	–	6	–	–	1	–	–	1	–	2
Portunus pusillus	–	–	–	–	1	–	–	–	–	–	–	–
Portunus holsatus	–	–	–	1	1	1	–	–	1	–	–	–
Portunus depurator	31	21	12	18	38	38	18	32	19	35	13	21
Cancer pagurus	1	–	–	–	–	–	–	–	–	–	–	–
Atelecyclus septemdentatus	–	–	–	–	–	–	–	1	–	–	–	–
Corystes cassivelaunus	–	–	–	–	–	–	–	–	–	–	–	–
Gonoplax rhomboides	–	–	1	–	–	–	–	–	–	–	–	1
Ebalia tuberosa	–	–	–	–	–	–	–	–	–	–	–	–
Ebalia cranchii	–	–	–	2	–	–	–	–	–	–	–	–
Maia squinado	–	–	–	–	–	–	–	–	–	–	–	–
Eurynome aspera	–	–	–	–	–	–	–	–	–	–	–	–
Hyas araneus	–	2	–	–	–	–	–	–	–	–	–	–
Inachus dorsettensis	6	4	5	–	1	4	2	2	4	6	–	4
Macropodia longirostris	8	7	4	6	14	30	3	6	16	17	2	23
Macropodia rostratus	3	1	2	4	2	6	–	1	–	1	–	2
Phoxichilus spinosus	–	–	–	–	–	1	–	2	–	–	–	–
Ovula patula (on Alcyonium)	–	–	–	–	–	–	–	–	–	–	–	–
Natica alderi	–	–	–	–	–	–	–	–	–	–	–	–
Turritella communis	–	–	–	–	–	–	1	–	1	1	1	1
Oscanius membranaceus	1	4	1	1	1	3	–	2	1	1	1	2
Amphorina cærulea	–	–	–	–	–	–	–	–	–	–	–	–
Galvina tricolor	–	–	–	–	–	4	–	–	1	–	–	2
Antiopella hyalina	–	1	–	–	–	–	–	1	–	–	–	–
Lomanotus sp.	–	1	–	–	–	–	–	–	–	–	–	–
Dendronotus frondosus	–	–	–	–	–	–	–	–	–	–	–	–
Pleurophyllidia loveni	–	–	–	–	–	–	–	–	–	–	–	–
Archidoris tuberculata	–	–	–	–	–	–	–	–	–	–	–	–
Jorunna johnstoni	–	–	–	–	–	–	–	–	–	–	–	–
Platydoris testudinaria	–	–	–	–	–	–	–	–	–	–	–	–
Polycera quadrilineata	–	–	–	–	–	–	–	–	–	–	–	–
Acanthodoris pilosa	–	–	–	–	–	–	–	–	–	–	–	–
Lamellidoris oblonga	–	–	–	–	–	–	–	–	–	–	–	–
Ancula cristata	–	–	–	–	–	–	–	–	–	–	–	1
Lamellibranchs	1	3	2	–	–	–	–	1	–	1	–	2
Sepia officinalis	–	–	–	–	–	–	–	–	–	1	–	–
Sepiola atlantica	3	–	–	1	–	–	1	–	1	–	–	–
Eugyra arenosa	–	–	–	–	–	–	–	–	–	–	–	–
Ascidiella scabra	2	–	4	–	–	–	–	–	–	–	–	–
Polyzoa	–	–	–	–	–	‡‡	–	–	–	–	–	‡‡
Amphioxus lanceolatus	–	–	–	–	–	–	–	–	–	–	–	–

TABLE V.

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ.	Alpheidæ.	Crangonidæ.	Processa.	Galathea.	Upogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Atelecyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Trigla lineata	>5	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	–	–	–	–	–	–	–	–	2
		–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	*1*	–	–	*1*	–	–	–	–	–	–	–	–	–	*1*	–	*3*
	>10	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
		–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	–	–	–	*2*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	1	–	–	–	–	–	–	–	–	2
		–	–	–	–	–	*1*	–	*1*	–	–	–	–	*1*	–	*2*	–	–	*1*	–	–	*1*	–	–	*1*	*1*	–	–	–	–	*2*
Trigla cuculus	>5	–	–	–	–	–	4	–	3	–	5	2	–	–	–	6	–	–	7	–	–	–	–	–	–	–	–	–	–	3	21
		–	–	–	–	–	*3*	–	*1*	–	*4*	–	–	–	–	*5*	–	–	*9*	*1*	–	*1*	–	–	–	–	–	–	–	–	*17*
	>10	–	–	–	–	–	7	–	–	–	12	1	–	11	–	6	1	–	–	–	–	8	2	–	–	–	–	–	2	5	28
		–	–	–	–	5	*15*	–	–	–	–	–	–	*5*	–	*4*	–	*1*	*16*	*1*	–	–	–	–	–	–	*1*	–	*1*	–	*24*
	>15	–	–	–	–	–	7	–	–	–	4	–	–	1	–	3	–	–	8	–	–	2	–	–	–	–	–	–	–	–	12
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	*4*	–	–	*1*	*2*	–	–	–	–	–	–	–	–	*1*	*1*	*6*
	>20	–	–	–	–	–	5	–	–	–	10	–	–	12	1	3	–	–	1	–	–	7	–	1	–	–	–	–	3	2	17
		–	–	–	–	–	*1*	–	*1*	–	*2*	–	–	*3*	–	*8*	*1*	*1*	*3*	–	–	*1*	–	–	–	–	*1*	–	*2*	–	*10*
Trigla hirundo	>15	–	–	–	–	–	1	–	–	–	1	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	*1*	–	–	–	*1*	–	–	*2*	–	*2*	–	–	*1*	–	–	–	–	–	–	–	–	–	–	*1*	*3*
	>20	–	–	–	–	–	1	–	–	–	2	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4
		–	–	–	–	–	–	–	–	–	*1*	–	–	*2*	–	*3*	–	–	*3*	*2*	–	*2*	–	–	–	–	–	–	–	–	*5*
Trigla gurnardus	>5	–	–	–	–	1	7	–	–	9	6	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13
		–	–	–	–	–	*9*	*1*	–	7	*3*	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*10*
	>10	–	–	–	–	–	1	1	1	–	8	2	–	17	–	9	–	–	–	–	–	–	–	–	–	–	–	–	1	1	21
		–	–	–	–	–	*4*	*1*	–	–	*6*	*1*	–	*11*	–	*5*	–	*1*	*1*	–	–	–	–	–	–	*1*	–	–	–	*3*	*13*
	>15	–	–	–	–	–	3	–	–	–	5	–	–	11	–	4	–	–	–	2	–	–	–	–	–	–	–	–	–	–	12
		–	–	–	–	–	*2*	–	–	–	*9*	–	–	*8*	*1*	*6*	–	–	–	–	–	*1*	–	–	–	–	–	–	–	*1*	*10*
	>20	–	–	–	–	–	–	–	–	–	5	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	7
		–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	*2*	*1*	*3*
Lophius piscatorius	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
	>40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	6
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	–	*9*
	>50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*6*	*1*	*7*
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	6	17
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	*1*	*10*

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ.	Alpheidæ.	Crangonidæ.	Processa.	Galathea.	Upogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Atelecyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Zeus faber	>5	–	–	–	–	–	–	–	1	–	3	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	6
		–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*5*	–	*5*
	>10	–	–	–	–	–	–	–	–	1	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	3	17
		–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*	*1*	*10*
	>15	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	1	7
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*5*	–	*5*
	>20	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	10	6	18
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
Callionymus lyra	>5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
	>10	1	–	–	3	–	2	–	–	–	–	–	–	–	–	3	3	–	4	–	–	1	–	–	–	–	3	–	–	2	15
		3	–	–	*1*	–	*4*	–	–	–	–	–	–	–	–	*1*	*2*	*1*	*1*	*1*	–	–	–	–	–	–	*5*	–	–	*1*	*11*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	4	–	–	1	3	–	–	–	–	10	–	–	5	25
		1	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	*3*	*2*	*4*	–	*1*	*6*	–	–	–	–	*13*	–	–	*2*	*25*
	>20	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	5	3	6	–	–	5	–	–	–	–	9	–	–	–	15
		–	–	–	*3*	–	–	–	–	–	–	–	–	–	–	–	*1*	*5*	–	–	–	*3*	–	–	–	*1*	*10*	–	–	*1*	*18*
Cepola rubescens	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*2*
	>40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	5
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*4*	*4*
	>50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*7*	*7*
Gadus luscus	>10	–	–	–	2	–	–	–	–	–	3	1	–	1	–	8	9	4	3	–	1	7	1	–	–	–	–	4	–	–	25
		–	–	–	*1*	–	–	–	–	–	*4*	–	–	–	–	*7*	*6*	*5*	*4*	*1*	–	*9*	–	–	–	–	–	*5*	*1*	*25*
	>15	–	–	–	1	–	–	–	–	–	–	–	–	–	–	5	7	1	8	–	1	12	–	–	–	–	–	–	–	–	25
		–	–	–	*2*	–	–	*1*	–	–	–	–	–	–	–	*8*	*3*	*3*	*6*	*1*	*1*	*11*	–	–	–	*7*	–	–	*1*	–	*25*
	>20	–	–	–	–	–	–	–	–	–	5	–	–	–	–	12	1	1	2	5	–	9	–	–	–	–	–	–	9	4	25
		–	–	–	*3*	–	–	*1*	–	–	*1*	*1*	–	–	–	*13*	*14*	*4*	*4*	*1*	*2*	*5*	*2*	–	–	*3*	*1*	*1*	*1*	–	*25*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	2	3	–	–	3	1	–	–	–	–	–	3	–	5
		–	–	–	*1*	–	–	–	–	–	*1*	–	–	–	–	–	*3*	*1*	*1*	*1*	*1*	*4*	–	–	–	–	–	–	*1*	–	*8*
Gadus minutus	>5	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	>10	–	–	–	5	–	2	–	–	–	2	–	–	–	–	5	4	1	–	–	–	1	–	–	–	–	–	–	11	25	
		–	–	–	*3*	–	*1*	–	–	–	–	–	–	–	–	*3*	*2*	*4*	*1*	–	–	–	–	–	–	*21*	–	–	*2*	*2*	*25*
	>15	–	–	–	–	3	–	–	–	–	4	–	–	–	–	2	1	1	–	–	–	–	–	–	–	–	–	–	3	5	9
		–	–	–	*4*	–	*1*	–	–	–	*1*	–	–	*2*	–	–	*4*	–	–	–	–	–	–	–	–	*20*	–	–	*3*	*2*	*25*

Gadus merlangus	>5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	–	–	*17*	*1*	*19*
	>10	–	–	–	1	–	–	–	–	–	–	–	–	4	–	–	1	–	–	–	–	2	–	–	–	–	–	–	14	–	17
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*23*	–	–	–	*2*	*25*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	*3*	*1*	–	–	–	–	–	–	*25*	–	–	*3*	–	*25*
	>20	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	14	10	25
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*22*	–	–	*7*	*1*	*25*
Merluccius vulgaris	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	3	5
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	1	9
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*6*	*1*	*7*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	3	12
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*2*	*4*
Rhombus lævis	>50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
Scophthalmus norvegicus	>5	–	–	–	1	1	2	–	3	–	3	2	–	6	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	7	25
		–	–	–	–	*1*	*3*	*2*	*8*	–	*1*	–	–	*9*	*3*	*4*	*1*	*1*	–	–	*1*	–	–	–	–	–	–	–	–	*3*	*25*
Arnoglossus laterna	>5	–	–	–	–	–	7	–	1	–	6	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
		–	–	–	–	–	*4*	*1*	*1*	–	*5*	–	–	*7*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*9*
	>10	–	–	–	–	2	42	–	6	–	–	–	–	35	–	–	–	–	–	–	–	6	–	–	–	–	–	2	4	1	50
		–	–	–	–	*1*	*1*	–	*3*	–	*1*	–	–	*1*	–	*1*	–	–	*4*	–	–	*2*	–	–	–	*4*	–	–	*13*	*1*	*25*
	>15	–	–	–	–	–	4	–	1	–	–	–	–	8	–	–	–	–	2	–	–	1	–	–	–	–	–	–	1	–	8
		–	–	–	–	–	*8*	–	–	–	–	–	–	*16*	–	–	–	–	*1*	–	–	*1*	–	–	–	–	–	*1*	*1*	–	*11*
Lepidorhombus megastoma	>10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*1*
	>15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*1*	*3*
	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	*1*	*2*
Pleuronectes platessa	>20	–	–	–	2	–	–	–	–	–	–	–	–	–	–	1	5	–	–	–	–	–	–	–	–	–	1	–	–	3	10
		–	–	–	*1*	–	*1*	–	–	–	–	–	–	–	–	–	*3*	–	–	–	–	–	–	–	–	*3*	*4*	–	–	*2*	*7*
	>30	–	–	–	3	–	–	–	–	–	–	–	–	–	1	–	4	–	–	–	–	–	–	1	–	–	–	–	–	5	9
		–	–	–	*3*	*1*	*1*	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	*4*	*4*	–	–	*1*	*6*
	>40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		–	–	–	*3*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*5*	–	–	*1*	*6*
	>50	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	1	–	1	1	5
		–	–	–	*2*	–	–	–	–	–	–	–	–	–	–	–	*3*	–	–	–	–	–	–	–	–	–	*2*	–	–	*1*	*3*
Pleuronectes microcephalus	>20	–	–	–	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	25
		–	–	–	*24*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	*25*
	>30	–	–	–	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	25
		–	–	–	*25*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*25*

Name of Fish.	Length (in cm.).	Ophiuroidea.	Echinoidea.	Holothuroidea.	Polychæta.	Cumacea.	Amphipoda.	Isopoda.	Schizopoda.	Palæmonidæ.	Pandalidæ.	Hippolytidæ.	Alpheidæ.	Crangonidæ.	Processa.	Galathea.	Upogebia.	Paguridæ.	Porcellana.	Ebalia.	Inachidæ.	Portunus.	Ateleocyclus.	Gonoplax.	Corystes.	Corystes Megalopas.	Mollusca.	Polyzoa.	Pisces.	Stomach Empty.	Total number of Fishes examined.
Pleuronectes limanda	>10	*3*	–	–	–	–	–	–	–	–	–	–	–	–	–	4	4	1	1	–	–	6	–	–	–	*3*	1	–	4	16	31
					6																								*11*	*25*
	>15	*3*	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	–	–	2	–	2	2	8
					12		*3*				*1*			*1*		*1*	*1*	–	–	–	*1*	*1*				2	*1*	–	*3*	*25*
	>20	–	–	–	1	–	–	1	–	–	–	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	3	–	1	5
					9											–	*1*					*3*							*2*	*11*
Pleuronectes flesus	>20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1
		–	–	–	*2*	–	–	–	–	–	–	–	–	–	–	*1*	*1*	–	*1*	–	–	–	–	–	–	–	*2*	–	*1*	*3*
Solea vulgaris	>20	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	2
		–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	*1*
	>30	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	3
		–	–	–	*2*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	*2*
	>40	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	–	1	3
		–	–	–	*3*	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	*1*	–	*1*	*4*
Solea lutea	>5	–	–	–	–	–	3	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	–	–	*1*	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*1*	–	*1*	*5*
Solea variegata	>5	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	8	11
		–	–	–	–	–	*2*	–	–	–	–	*1*	–	–	–	–	–	–	*3*	–	–	*1*	–	–	–	–	–	–	*5*	*11*
	>10	–	–	–	–	–	11	–	–	–	3	–	–	–	–	–	–	–	9	1	–	–	–	–	–	–	1	–	5	16
		–	–	–	*10*	–	*4*	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*3*	–	*5*	*15*
	>15	–	–	–	2	–	4	–	–	–	1	–	–	–	–	–	–	–	2	–	–	1	–	–	–	–	1	–	3	7
		–	–	–	*4*	–	–	–	*1*	–	*2*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*2*	*6*
Conger conger	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*3*	–	*3*
Scyliorhinus canicula	>30	–	–	–	4	–	2	–	–	–	–	–	–	–	1	–	3	–	6	–	–	–	–	–	–	–	–	–	4	3	12
		–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	*1*	–	*3*	–	–	*2*	–	–	–	–	–	–	*4*	*2*	*10*
	>40	–	–	4	2	–	–	–	–	–	–	–	–	–	–	–	1	4	–	–	–	1	–	1	–	–	1	–	12	–	20
		–	–	–	*5*	–	–	–	–	–	–	–	–	–	–	–	*2*	*5*	*1*	–	*1*	*3*	–	*1*	*1*	–	*1*	–	*11*	*1*	*25*
	>50	–	–	–	10	–	–	–	–	1	–	–	–	–	–	–	8	7	–	–	2	1	–	–	–	–	4	–	14	–	28
		–	–	–	*7*	–	–	–	–	–	–	–	–	–	–	–	*4*	*6*	–	–	*1*	*2*	–	–	–	–	–	–	*9*	*3*	*25*
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	3	4	–	–	–	–	1	–	10	–	11
		–	–	–	*3*	–	–	–	–	–	–	–	–	–	–	–	–	*11*	–	–	*6*	*5*	–	–	–	–	–	–	*15*	*1*	*21*

Raia clavata	>10	–	–	–	1	–	2	–	–	–	2	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	3
		–	–	–	*1*	–	*3*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*3*	–	–	–	*2*	*5*
	>15	–	–	–	1	–	5	–	–	–	3	–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–	–	–	–	5
		–	–	–	–	–	*4*	*1*	*3*	–	–	–	–	*1*	–	–	–	–	–	–	–	*1*	–	–	–	*4*	–	–	–	–	*7*
	>20	–	–	–	1	–	7	–	1	–	1	–	–	1	–	1	–	–	2	–	–	–	–	–	–	–	–	–	–	–	11
		–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	–	–	–	*1*	*2*	–	–	–	–	*5*
	>30	–	–	–	1	–	14	–	–	–	10	2	–	7	–	1	10	–	–	–	–	4	–	–	–	–	–	–	1	–	19
		–	–	–	*3*	–	*12*	–	–	–	*8*	*1*	–	*4*	–	*1*	–	–	–	–	–	*6*	–	–	–	*19*	–	–	*1*	–	*23*
	>40	–	–	–	–	–	2	–	–	–	4	1	–	1	–	–	4	–	–	–	–	7	–	–	–	–	–	–	–	–	8
		–	–	–	–	–	*4*	–	–	–	*3*	–	–	*1*	–	*7*	*8*	–	–	–	–	*11*	*2*	–	–	*12*	–	–	–	–	*16*
	>50	–	–	–	–	–	1	–	–	–	6	–	–	1	–	6	9	9	–	–	–	18	2	–	1	–	–	–	–	7	25
		–	–	–	*1*	–	–	–	–	–	*3*	–	–	–	–	*8*	*10*	*7*	–	–	–	*11*	*1*	–	–	*3*	–	–	*1*	–	*25*
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	–	7	1	–	–	–	–	–	4	–	9
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	*3*	*6*	*4*	–	–	–	*1*	*1*	–	–	–	–	–	–	–	*6*
Raia maculata	>20	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2
		–	–	–	*1*	*1*	*1*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*1*	–	–	–	*1*	–	–	–	–	*1*
	>30	–	–	–	1	–	12	1	–	–	1	1	–	1	–	2	4	–	–	–	–	2	–	–	–	–	–	–	–	1	13
		–	–	–	*4*	*1*	*6*	*2*	*2*	–	–	–	–	*4*	–	–	–	–	*2*	–	–	–	–	–	–	*6*	–	–	–	–	*6*
	>40	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	1	–	–	–	–	3	–	–	–	–	–	–	3	–	5
		–	–	–	*2*	–	*3*	–	*1*	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	*2*	–	–	–	–	*3*
	>50	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	5	2	–	–	–	–	–	–	–	5
		–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	*1*	*3*	*9*	*1*	–	*1*	*7*	*2*	–	*1*	–	–	–	–	–	*11*
	>60	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	3	1	–	1	–	–	–	–	–	3
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*4*	–	–	*3*	*2*	*1*	–	–	–	–	–	*3*	–	*6*
Raia nævus	>20	–	–	–	4	–	–	–	–	–	1	–	–	4	–	–	–	–	1	–	–	3	–	–	–	–	–	–	4	–	7
		–	–	–	*3*	*1*	*3*	*1*	–	*1*	–	–	–	*1*	–	*2*	–	–	*1*	–	–	*1*	–	–	–	*3*	–	–	*1*	–	*4*
	>30	–	–	–	1	–	–	2	–	–	–	–	–	3	–	3	1	2	–	–	–	1	–	1	–	–	–	–	2	–	6
		–	–	–	*2*	–	*1*	–	–	–	–	*1*	–	*1*	–	*4*	*1*	–	–	*1*	–	–	–	–	*1*	*4*	–	–	–	–	*5*
	>40	–	–	–	1	–	–	–	–	1	–	–	–	1	–	2	2	4	–	1	–	4	–	–	–	–	–	–	–	–	5
		–	–	–	–	–	–	*3*	–	*1*	–	–	–	–	–	*3*	–	*5*	*1*	–	–	*1*	–	–	–	*2*	–	–	*1*	–	*6*
Raia brachyura	>20	–	–	–	–	–	3	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	1	4
		–	–	–	–	–	*2*	–	–	–	–	–	–	–	–	–	*1*	–	*1*	–	–	–	–	–	–	–	–	–	–	*2*	*4*
	>30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	>40	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2	–	1	–	–	1	4	–	–	–	–	–	–	–	–	5
		–	–	–	–	–	*1*	–	–	–	–	–	–	*1*	–	*3*	–	*1*	–	–	–	*2*	–	–	–	*1*	–	–	–	*1*	*6*
	>50	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	–	3
		–	–	–	–	–	–	–	*1*	–	–	–	–	–	–	–	–	–	–	–	–	?	–	–	–	–	–	–	–	–	*1*

The Seasonal Abundance and Distribution of the Pelagic Young of Teleostean Fishes Caught in the Ring-Trawl in Offshore Waters in the Plymouth Area.

By

F. S. Russell, D.S.C., B.A.,

Naturalist at the Plymouth Laboratory.

With 2 Figures in the Text.

A LARGE number of collections were made with the 2-metre stramin ring-trawl in the years 1924, 1925 and 1926, to study the vertical distribution of young fish. Seeing that all these collections were made in exactly the same way, it was considered that they would form a good basis for a study of the quantitative differences in abundance of the different species at various times of the year. Accordingly, after 1926 the collections were supplemented in 1927, 1928 and 1929 by oblique hauls with the ring-trawl fishing at the same depths as those fished in the serial hauls in the study of the vertical distribution, that is the net was fished successively at the six different depths during half-an-hour's haul for 5 minutes at each depth. The results given in this report are all based on daylight catches.

In Table 3 are brought together the average monthly catches per half-hour's haul for each year for the post-larvæ of the various species. In the case of the 1924, 1925 and 1926 observations, which were based usually on six hauls each of ten-minutes' duration at six different depths, the total number of each species caught at all depths together at any one station is taken and from it the number caught per half-hour estimated. In the later years the oblique hauls were each of one half-hour's duration. In both cases these half-hour catches have been added together for each month in the year and divided by the number of catches per month. In this way an average monthly catch for each year was obtained (Table 3). By adding the averages for any one month and dividing by the number of years in which collections were made in that month, an average monthly catch was obtained for the period of six years covered by the researches (Table 1, p. 712). In Table 2 (p. 717) are given the dates in each year when collections were made, and it can be seen that although the winter months have been very poorly represented the important period of April to September has been fairly well covered.

Figure 1 shows the average monthly catches (as given in Table 1) for

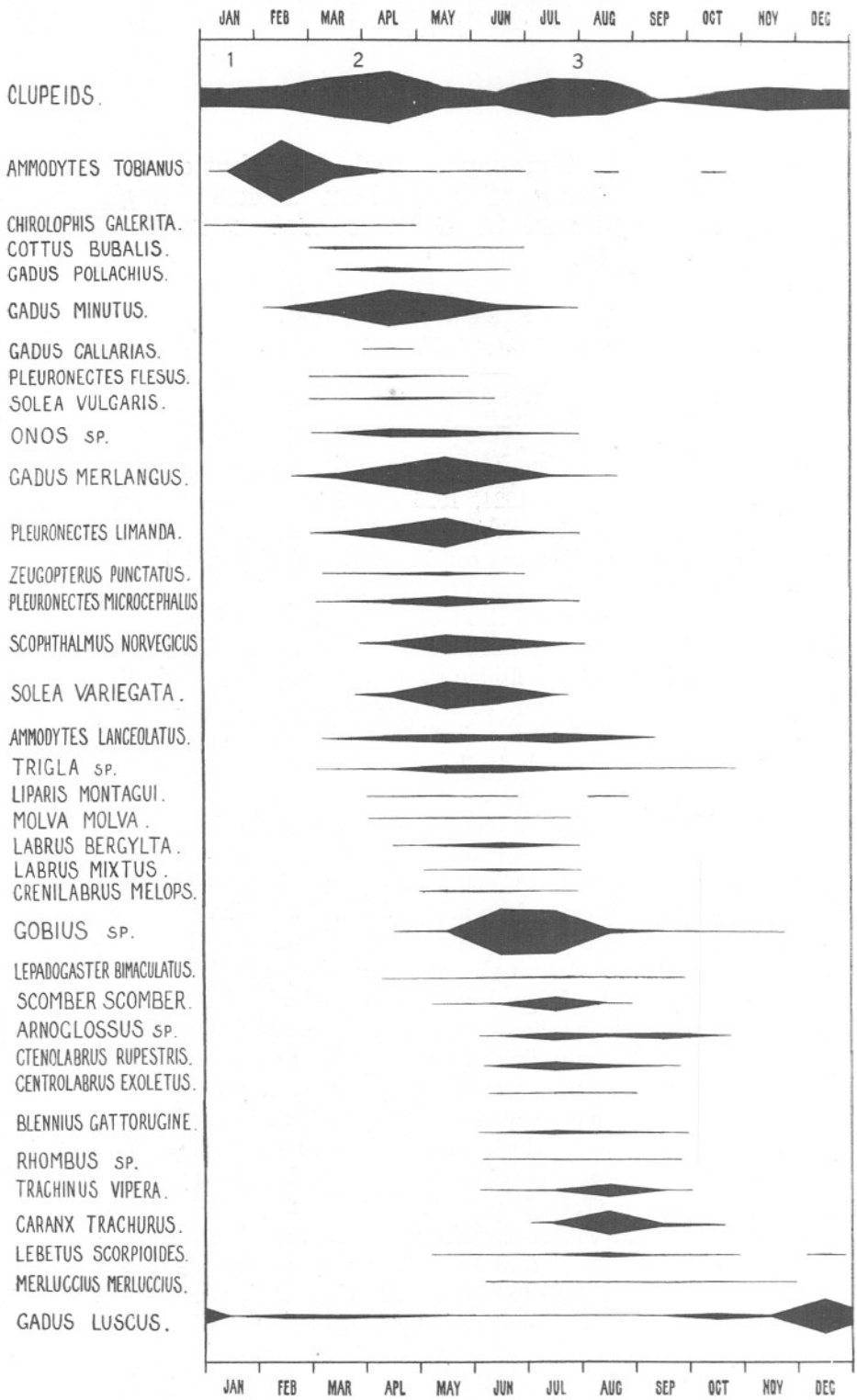


FIG. 1 (description opposite).

each species in graphic form. The abundance curves for each species are drawn to the same scale so that from this figure one can see at a glance the comparative abundance of the post-larvæ of any species of fish at

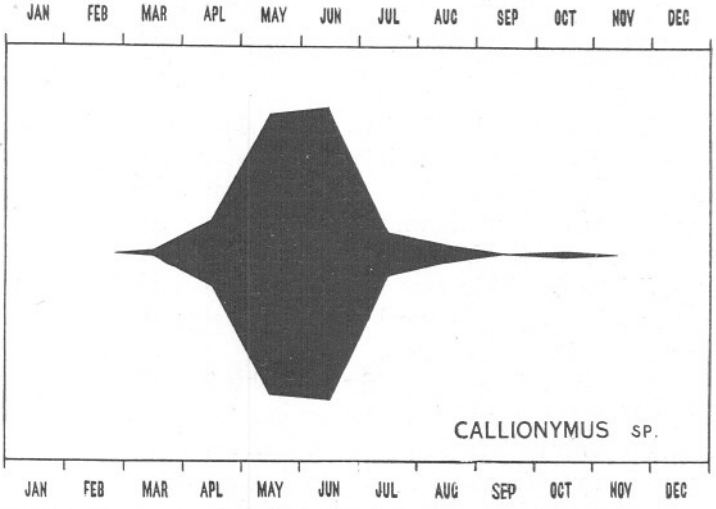


FIG. 2.—Diagram to show in graphic form the seasonal distribution and abundance of the post-larvæ of Callionymus sp., mostly *C. lyra*, in offshore waters off Plymouth. This figure is drawn to the same scale as Figure 1, and shows the marked superiority in the numbers of post-larvæ of this species over all other species, excepting perhaps the Gobies.

any time of the year. (This figure shows only those species whose average number for any month is one per half-hour's haul or more.)

In this publication only those observations made at the International Hydrographic Stations L4 and L6, or at the station two miles east of the Eddystone have been included, and from 1926 onwards practically all the collections were made from the latter position. The results are therefore indicative of the general offshore conditions. They should, if possible, be supplemented by a series of collections quite close inshore when possibly certain species, such perhaps as the wrasses, might appear more abundant.

DESCRIPTION OF FIGURE 1.

FIG. 1.—Diagram to show in a graphic form the results expressed in Table 1. The blackened areas indicate the time of year at which post-larval stages of each species may be expected in the ring-trawl catches in offshore waters off Plymouth; each area is drawn to the same scale and indicates the comparative abundance of the post-larvæ of each species as averaged over the years 1924 to 1929. Only those species whose post-larvæ appear with an average of over one specimen per half-hour's haul are shown here. In the case of the Clupeids the Figures 1, 2 and 3 indicate the periods when the catches may be expected to consist almost entirely of Herrings, Sprats, or Pilchards respectively.

N.B. The results for Gobies should probably be very much larger, these post-larvæ being generally near the bottom in the daytime and below the region sampled by the ring-trawl; the same also may hold for *Gadus minutus*.

A glance at Figure 1 shows how few species compared with the large number occurring in the area can be considered as abundant. The outstanding feature as shown in Figure 2 (drawn to the same scale as Figure 1) is the abundance of Callionymus sp. post-larvae probably mostly *C. lyra*. Ever since researches into the young stages of our fish were first systematically undertaken by Clark (1910) the abundance of this species has been noticeable.

Although the ring-trawl collections do not show the post-larval gobies to have been especially numerous it is quite possible that they are actually even more abundant than those of Callionymus. Catches with the bottom plankton net have shown that they are present in great numbers in the daytime near the bottom, and in 1927 the average catches for June and July respectively were 1354 and 3247 as against 2·1 and 2·1 in collections made by the ring-trawl fished obliquely; this is many times more numerous than Callionymus.

It is thought that these average figures will form a good basis to work on in watching for any violent fluctuations in the future. They are presented here only as data, because until such observations have covered a long period of years it will not be known how great the differences from year to year must be before they can be regarded as significant.

There is an indication that the post-larval stages of certain spring spawners were but poorly represented in the year 1929, as for example, *Gadus minutus*, *Pleuronectes microcephalus*, *Solea variegata*, and Callionymus sp. Such differences will naturally tend to lower the averages given in Table 1. Similarly the year 1926 seems to have been marked by a rather unusual abundance of young mackerel, *Scomber scomber;* never in all the past records given by Clark (1914 and 1920) and Allen (1917) have so many been caught. This may perhaps have meant an easterly extension of their normal spawning-grounds, the abundance of the copepod, *Calanus finmarchicus*, being very great in this region that summer and hence perhaps the adults moving more in this direction. At any rate there is no indication from commercial catches that 1926 was an exceptionally good survival year, as they should probably have been appearing in the catches by now (1929).

The above instances have been cited to emphasize that we do not yet know what differences to look for as being significant. The results of the research on the vertical distribution of the post-larval fishes have shown that for the majority of species oblique daytime hauls with the net fished as deep as possible should give a fair picture of the quantities of young fish present (Russell, 1928, p. 833). In the case of post-larval Clupeids, however, these results do not give a correct impression (Russell, 1930, p. 649), although if they were unusually abundant any one year their increased numbers would perhaps show up in the daytime as well as at

night. In the case of the Gobies, and also possibly *Gadus minutus* (Russell, 1930, p. 650), the hauls probably have not gone deep enough to sample the zone of their maximum abundance.

A comparison of these results with the figures given by Allen (1917) shows that there have not been any marked changes in the composition of the catches since that date, and his averages for the years up to 1914 agree well with those given here. As regards the sizes of the post-larvæ caught, there will be some slight difference for each species as the season advances. When first any species starts to appear in the catches it is natural that the majority should be very young forms, and while a few of the smallest sizes are usually to be taken throughout the season there will be a gradual increase in size of the majority as time goes on, until in the last catches in which they appear the post-larvæ will mostly be in the neighbourhood of the size at which they disappear from the ring-trawl catches either owing to their leaving the plankton or having become strong enough swimmers to evade the net. In Table 3 are given for the commoner species the sizes within which the majority of post-larvæ taken in the ring-trawl lie; larger sizes will of course be caught at times in the case of all species.

A bibliography is given here including all those papers that have been published dealing with the post-larval stages of Teleostean fishes in the Plymouth area (see pp. 720–722).

The months in which the maximum abundance of the post-larvæ of each species may be expected are given below.

MONTHS OF AVERAGE MAXIMAL ABUNDANCE OF POST-LARVÆ.

JANUARY.	FEBRUARY.	MARCH.	APRIL.
	C. harengus	*C. bubalis*	*C. sprattus*
	A. tobianus	*A. cataphractus*	*G. pollachius*
	C. galerita		*G. minutus*
			G. callarias
			P. flesus
			S. vulgaris
			Onos sp.

MAY.	JUNE.	JULY.	AUGUST.
G. merlangus	*M. molva*	*C. pilchardus*	*Zeus faber*
P. limanda	Callionymus sp.	*R. raninus*	Rhombus sp.
Z. punctatus	*L. bergylta*	*Capros aper*	*S. cabrilla*
P. microcephalus	*L. mixtus*	*S. scomber*	*T. vipera*
S. norvegicus	*C. melops*	Arnoglossus sp.	*C. trachurus*
S. variegata	Gobius sp.	*S. lascaris*	*M. surmuletus*
Trigla sp.		*S. lutea*	*C. rubescens*
L. montagui		*A. lanceolatus*	*L. scorpioides*
		C. rupestris	*B. ocellaris*
		C. exoletus	
		B. pholis	
		B. gattorugine	
		L. piscatorius	
		L. bimaculatus	

SEPTEMBER.	OCTOBER.	NOVEMBER.	DECEMBER.
—	*M. merluccus*	—	*G. luscus*

TABLE 1.

AVERAGE MONTHLY CATCHES OF POST-LARVÆ PER HALF-HOUR HAUL WITH 2-METRE RING-TRAWL FISHING AT ALL DEPTHS, 1924–1929.

	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Clupeid sp.*	23·7	30·3	51·6	70·7	25·0	15·5	48·4	42·6	1·6	16·6	30·0	22·5
Gadus pollachius	–	–	1·2	7·7	1·6	0·1	–	–	–	–	–	–
G. merlangus	–	–	7·8	32·0	55·9	32·8	2·3	0·2	–	–	–	–
G. minutus†	–	3·9	24·0	52·5	33·6	8·8	0·9	–	–	–	–	–
G. luscus	0·9	6·9	5·4	3·8	1·8	0·8	0·1	1·4	0·7	7·1	3·9	49·5
G. callarias	–	–	–	1·1	–	–	–	–	–	–	–	–
Onos sp.	–	–	0·6	14·8	10·4	3·3	0·8	–	–	–	–	–
Molva molva	–	–	–	0·1	3·5	4·6	0·1	–	–	–	–	–
Merluccius merluccius	–	–	–	–	–	0·3	0·2	0·2	0·2	1·6	0·9	–
Raniceps raninus	–	–	–	–	–	0·04	0·2	0·2	–	0·1	–	–
Capros aper	–	–	–	–	–	0·04	0·3	0·3	0·1	–	–	–
Zeus faber	–	–	–	–	–	–	–	0·1	–	–	–	–
Arnoglossus sp.	–	–	–	–	–	0·2	12·4	7·6	10·5	2·0	–	–
Rhombus sp.	–	–	–	–	–	0·2	1·8	2·4	0·6	–	–	–
Scophthalmus norvegicus	–	–	–	5·8	29·8	18·3	6·4	–	–	–	–	–
S. unimaculatus	–	–	–	–	+	+	+	–	–	–	–	–
Zeugopterus punctatus	–	–	0·6	1·2	6·2	0·8	–	–	–	–	–	–
Pleuronectes limanda	–	–	6·6	21·8	45·3	8·8	0·2	–	–	–	–	–
P. flesus	–	–	0·3	4·5	0·7	–	–	–	–	–	–	–
P. microcephalus	–	–	0·3	6·3	16·1	8·4	1·5	–	–	–	–	–
Solea vulgaris	–	–	0·3	4·9	1·0	0·04	–	–	–	–	–	–
S. variegata	–	–	–	5·8	40·5	29·1	3·4	–	–	–	–	–
S. lascaris	–	–	–	–	–	–	0·1	–	–	0·4	–	–
S. lutea	–	–	–	–	–	–	0·1	–	–	–	–	–
Serranus cabrilla	–	–	–	–	–	–	–	0·3	0·1	0·2	–	–
Caranx trachurus	–	–	–	–	–	–	3·9	34·4	3·6	2·0	–	–
Mullus surmuletus	–	–	–	–	–	–	–	0·1	–	–	–	–
Ammodytes tobianus	0·6	90·9	20·7	2·6	0·1	0·2	–	0·2	0·4	0·2	–	–
A. lanceolatus	–	–	2·4	8·6	13·9	9·1	14·8	8·1	–	–	–	–
Cepola rubescens	–	–	–	–	–	0·04	0·1	0·4	–	–	–	

Callionymus sp.	–	–	8·7	89·0	377·6	395·0	59·2	24·1	1·1	9·6	0·9	–
Labrus bergylta	–	–	–	0·1	1·3	9·1	1·2	–	–	–	–	–
L. mixtus	–	–	–	–	0·2	5·9	1·4	–	–	–	–	–
Ctenolabrus rupestris	–	–	–	–	–	2·5	12·0	4·9	0·1	–	–	–
Crenilabrus melops	–	–	–	–	–	2·9	2·5	0·7	–	–	–	–
Centrolabrus exoletus	–	–	–	–	–	1·3	1·9	0·8	–	–	–	–
Trachinus vipera	–	–	–	–	–	0·4	2·6	18·3	1·0	–	–	–
Trachinus draco	–	–	–	–	–	–	–	–	0·1	–	–	–
Scomber scomber ‡	–	–	–	–	0·1	5·8	22·8	0·2	–	–	–	–
Gobius sp.§	–	–	–	0·9	1·8	68·8	62·9	8·0	1·2	0·5	0·9	–
Lebetus scorpioides	–	–	–	–	0·2	0·7	2·7	8·7	1·5	0·3	–	2·1
Blennius ocellaris	–	–	–	–	–	0·2	0·4	0·8	–	–	–	–
B. pholis	–	–	–	–	0·1	0·8	0·8	0·2	–	–	–	–
B. gattorugine	–	–	–	–	–	2·5	6·4	5·2	0·3	–	–	–
Chirolophis galerita	0·3	3·0	2·0	0·3	–	–	–	–	–	–	–	–
Trigla sp.¶	–	–	1·5	3·0	13·4	12·5	5·5	3·5	0·7	0·9	–	–
Cottus bubalis	–	–	4·5	2·6	0·7	0·5	–	–	–	–	–	–
Agonus cataphractus	–	–	0·3	0·1	0·1	–	–	–	–	–	–	–
Liparis montagui	–	–	–	0·3	1·1	0·8	–	0·3	–	–	–	–
Lepadogaster bimaculatus	–	–	–	0·3	0·1	2·4	1·6	1·3	0·3	–	–	–
Lophius piscatorius	–	–	0·3	0·04	–	0·3	0·8	0·1	–	–	–	–
Belone vulgaris+	–	–	–	–	–	–	–	–	0·1	–	–	–

* Includes *Clupea harengus*, *Clupea sprattus*, and *Sardina pilchardus*. Post-larval herring occur mostly in January, February, and March; sprat in March, April, and May, the increase being generally due to larger numbers of recently hatched sprat: from May till end of year the catches are mostly pilchard which spawn intermittently throughout the summer.

† *Gadus minutus* post-larvæ live normally very deep in the water in the daytime, and possibly these averages should be considerably higher to give a true picture.

‡ In calculating these averages for *Scomber scomber*, the mackerel, the results for 1926 have not been included as it is thought that perhaps this may have been an abnormal year (see Table 3).

§ The post-larval gobies live very near the bottom in the daytime, and these averages should probably be very much higher.

¶ Consist of *Trigla gurnardus*, *T. cuculus*, and *T. hirundo* chiefly.

\+ Less than 0·1.

TABLE 2.

DATES ON WHICH COLLECTIONS WERE MADE.

	1924	1925	1926	1927	1928	1929	Total days.
January	—	—	—	—	9th 16th 26th 30th	—	4
February	—	—	—	—	2nd 20th 27th	—	3
March	—	—	—	—	5th 21st 30th	—	3
April	—	2nd 8th 29th	9th 13th (i) 13th (ii) 22nd 26th	4th 14th 26th	4th 11th 12th 23rd	10th 19th 23rd 29th	19
May	29th	19th (i) 19th (ii)	6th 19th	2nd 9th 16th 25th	—	6th 13th 23rd 27th	13
June	25th	4th (i) 4th (ii) 17th 18th 19th	3rd 4th 25th 30th	2nd 9th 29th	—	6th 11th 25th	16
July	1st 15th 16th	1st (i) 1st (ii) 16th 29th	6th 13th 26th	8th 12th 21st 26th	—	3rd 9th 18th 23rd 30th	19
August	—	6th	4th	4th 8th 19th 26th 31st	—	9th 15th 22nd 26th	11
September	—	—	22nd	6th 15th 19th	—	4th 6th 10th 17th 24th	9
October	—	—	—	4th 13th 18th 24th	—	3rd 10th 16th	7
November	—	—	—	1st	—	—	1
December	—	—	—	15th 21st	—	—	2

TABLE 3.

AVERAGE MONTHLY CATCH OF POST-LARVÆ PER 30-MINUTE HAUL WITH RING-TRAWL.

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Clupeid sp.	1924					42·0	28·5	67·2					
Herring }	1925				47·7	10·8	9·2	6·6	0·9				
Sprat }	1926				95·4	57·9	15·9	63·0	150·0	1·2			
Pilchard }	1927				107·4	7·8	8·1	81·3	14·1	1·2	2·4	30·0	22·5
5–20 mm.	1928	23·7	30·3	51·6	82·5								
	1929				20·7	6·3	15·9	24·0	5·4	2·4	30·7		
Gadus pollachius	1924					–	–	–					
Pollach	1925				10·5	0·3	0·1	–	–				
4·5–12 mm.	1926				3·3	5·7	0·3	–	–	–			
	1927				0·9	1·2	–	–	–	–	–	–	–
	1928	–	–	1·2	21·6								
	1929				2·4	0·6	–	–	–	–	–		
Gadus merlangus	1924					42·0	80·4	2·1					
Whiting	1925				31·2	83·1	23·7	4·5	–				
4–12 mm.	1926				52·5	55·8	36·6	0·9	0·6	–			
	1927				14·4	51·0	8·4	0·6	0·2	–	–	–	–
	1928	–	–	7·8	29·7								
	1929				32·4	47·7	15·0	3·6	–	–	–		
Gadus minutus	1924					33·9	24·9	4·2					
Poor Cod or Bib	1925				42·9	49·8	4·8	–	–				
4–12 mm.	1926				56·1	40·2	12·9	–	–	–			
	1927				17·4	43·2	–	–	–	–	–	–	–
	1928	–	3·9	24·0	135·6								
	1929				10·5	0·9	1·2	0·3	–	–	–		
Gadus luscus	1924					3·0	1·5	–					
Pouting or Pout	1925				2·1	–	0·1	0·2	–				
4–10 mm.	1926				3·9	3·6	1·8	–	2·4	–			
	1927				1·5	2·4	0·3	–	0·6	0·3	2·1	3·9	49·5
	1928	0·9	6·9	5·4	8·4								
	1929				3·0	–	0·3	0·3	2·4	1·8	12·0		
Gadus callarias	1924					–	–	–					
Cod	1925				–	–	–	–	–				
4–10 mm.	1926				2·1	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	0·3								
	1929				3·3	–	–	–	–	–	–		
Onos sp.	1924					15·0	3·0	3·0					
Rockling	1925				24·3	8·4	0·9	–	–				
4–10 mm.	1926				17·1	23·7	7·2	–	–	–			
	1927				0·3	3·9	0·9	–	–	–	–	–	–
	1928	–	–	0·6	31·8								
	1929				0·3	0·9	4·5	0·9	–	–	–		
Molva molva	1924					9·9	9·9	–					
Ling	1925				–	0·9	0·6	0·6	–				
5–14 mm.	1926				0·1	4·8	12·3	–	–	–			
	1927				–	1·5	–	–	–	–	–	–	–
	1928	–	–	–	0·3								
	1929				–	0·3	–	–	–	–	–		
Merluccius	1924					–	1·5	–					
merluccius	1925				–	–	–	–	–				
Hake	1926				–	–	0·2	0·9	–	–			
5–10 mm.	1927				–	–	–	0·2	0·6	–	1·5	0·9	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·3	0·6	1·7		
Raniceps raninus	1924					–	–	–					
Lesser Forkbeard	1925				–	–	–	0·2	0·6				
4–6 mm.	1926				–	–	0·2	0·6	–	–			
	1927				–	–	–	0·2	0·2	–	0·3	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·2	–	–	–		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Capros aper	1924					–	0·2	–					
Boar-fish	1925				–	–	–	–	–				
3–6 mm.	1926				–	–	–	–	0·5	–			
	1927				–	–	–	0·8	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·5	0·3	–		
Zeus faber	Only caught August, 1926. Average 0·5.												
John Dory													
Arnoglossus sp.	1924					–	0·9	4·2					
Scaldbacks	1925				–	–	–	4·8	4·5				
4–20 mm.	1926				–	–	0·1	18·3	9·9	16·8			
	1927				–	–	–	15·0	7·2	3·0	0·9	–	–
	1928	–	–	–	–								
	1929				–	–	–	19·5	8·7	11·7	3·0		
Rhombus sp.	1924					–	0·8	–					
Turbot and Brill	1925				–	–	–	–	–				
4–10 mm.	1926				–	–	0·1	3·2	8·6	0·6			
	1927				–	–	–	3·3	0·8	0·6	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	2·4	0·3	0·6	–		
Scophthalmus	1924					32·1	20·4	17·4					
norvegicus	1925				22·5	92·1	13·8	2·4	–				
Norway Topknot	1926				0·9	15·3	42·6	1·8	–	–			
4–10 mm.	1927				0·9	8·7	3·6	0·9	–	–	–	–	–
	1928	–	–	–	4·8								
	1929				–	0·6	11·1	9·3	–	–	–		
S. unimaculatus	Only 6 caught during the 6 years. E1 17/6/24, 2; A, 1/7/25, 1; 7/5/24, 1; 17–18/7/25, 2 (dusk and dark).												
Zeugopterus	1924					11·1	–	–					
punctatus	1925				1·8	12·6	0·2	–	–				
Topknot	1926				0·9	2·7	3·6	–	–	–			
4–10 mm.	1927				1·2	4·2	–	–	–	–	–	–	–
	1928	–	–	0·6	2·1								
	1929				–	0·6	–	–	–	–	–		
Pleuronectes	1924					24·0	15·9	0·9					
limanda	1925				26·4	69·6	3·9	0·3	–				
Dab	1926				24·3	50·1	9·3	–	–	–			
5–12 mm.	1927				6·6	68·4	2·1	–	–	–	–	–	–
	1928	–	–	6·6	37·2								
	1929				14·7	14·4	12·6	–	–	–	–		
Pleuronectes flesus	1924					–	–	–					
Flounder	1925				1·2	2·7	–	–	–				
4–9 mm.	1926				6·0	0·6	–	–	–	–			
	1927				3·9	0·2	–	–	–	–	–	–	–
	1928	–	–	0·3	10·8								
	1929				0·6	–	–	–	–	–	–		
Pleuronectes	1924					21·9	21·6	4·5					
microcephalus	1925				8·7	24·6	3·9	0·9	–				
Merrysole or	1926				3·6	27·6	13·2	1·2	–	–			
Lemon Dab	1927				1·5	6·0	0·6	–	–	–	–	–	–
4–13 mm.	1928	–	–	0·3	17·7								
	1929				–	0·6	2·7	0·9	–	–	–		
Solea vulgaris	1924					–	–	–					
Common Sole	1925				2·4	1·2	–	–	–				
4–9 mm.	1926				6·0	1·8	0·2	–	–	–			
	1927				6·3	1·2	–	–	–	–	–	–	–
	1928	–	–	0·3	3·3								
	1929				6·3	0·6	–	–	–	–	–		
Solea variegata	1924					20·1	111·0	6·1					
Thickback	1925				9·9	101·4	6·3	0·9	–				
4–11 mm.	1926				5·7	49·8	25·5	3·9	–	–			
	1927				2·1	29·4	0·3	3·6	–	–	–	–	–
	1928	–	–	–	10·2								
	1929				0·9	1·8	2·4	2·7	–	–	–		
Solea lascaris	1924					–	–	–					
Sand Sole	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	0·3	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·4	–	–	0·7		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Solea lutea	1924					–	–	–					
Solenette	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	–	–	–		
Serranus cabrilla	1924					–	–	–					
Sea Perch	1925				–	–	–	–	–				
	1926				–	–	–	–	1·0	0·3			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	0·3	–	–
Caranx trachurus	1924					–	–	6·3					
Horse Mackerel	1925				–	–	–	–	–				
or Scad	1926				–	–	–	1·8	107·1	4·8			
4–15 mm.	1927				–	–	–	9·9	9·3	0·3	0·3	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	21·3	5·7	3·7		
Mullus surmuletus	1924					–	–	–					
Red Mullet	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	0·4	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Ammodytes tobianus	1924					–	–	–					
Lesser Sandeel	1925				0·2	–	0·1	–	–				
4–20 mm.	1926				2·4	0·3	0·5	–	–	1·2			
	1927				7·8	–	0·3	–	0·6	–	–	–	–
	1928	0·6	90·9	20·7	0·9								
	1929				1·5	–	–	–	0·3	–	0·3		–
Ammodytes	1924					12·0	16·5	35·1					
lanceolatus	1925				11·1	37·5	7·5	18·9	5·1				
Greater Sandeel	1926				1·5	12·6	10·8	13·5	22·5	–			
5–20 mm.	1927				8·7	6·9	5·4	3·6	0·9	–	–	–	–
	1928	–	–	2·4	21·0								
	1929				0·9	0·6	5·1	2·7	3·9	–	–		
Cepola rubescens	1924					–	–	–					
Red Band Fish	1925				–	–	–	–	–				
	1926				–	–	–	0·2	–	–			
	1927				–	–	–	–	–	0·7	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·5	–	–		
Callionymus sp.	1924					347·1	1102·5	95·1					
Dragonets	1925				55·8	442·8	144·9	80·7	3·6				
3–8 mm.	1926				99·6	507·6	648·0	39·3	70·5	–			
	1927				24·0	533·7	24·3	11·4	7·8	1·8	18·9	0·9	–
	1928	–	–	8·7	212·1								
	1929				53·4	57·0	55·2	69·3	14·4	1·5	0·3		
Labrus bergylta	1924					0·9	24·0	4·5					
Ballan Wrasse	1925				0·2	1·8	1·2	0·3	–				
4–9 mm.	1926				0·2	3·0	12·6	0·2	–	–			
	1927				–	0·6	6·9	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	0·6	1·2	–	–	–		
Labrus mixtus	1924					–	22·5	5·4					
Cuckoo Wrasse	1925				–	0·3	0·2	–	–				
4–9 mm.	1926				–	0·6	6·0	1·2	–	–			
	1927				–	–	0·9	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	0·6	–	–	–		
Ctenolabrus rupestris	1924					–	1·5	5·7					
	1925				–	–	0·3	1·2	0·6				
4–9 mm.	1926				–	–	9·9	39·6	8·4	–			
	1927				–	–	0·6	6·0	4·5	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	7·5	6·0	0·3	–		
Crenilabrus melops	1924					–	6·6	11·7					
	1925				–	–	–	0·3	2·4				
4–7 mm.	1926				–	–	5·4	0·3	–	–			
	1927				–	–	2·4	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	0·3	–	–		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Centrolabrus exoletus 4·7 mm.	1924					–	0·9	5·7					
	1925				–	–	0·1	0·6	2·4				
	1926				–	–	1·8	2·1	–	–			
	1927				–	–	3·0	0·2	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	0·6	0·9	0·6	–	–		
Trachinus vipera Lesser Weever 3–11 mm.	1924					–	–	0·6					
	1925				–	–	–	3·3	3·6				
	1926				–	–	0·6	4·2	57·0	–			
	1927				–	–	1·2	2·4	3·9	0·3	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	2·4	8·7	2·7	–		
Trachinus draco Greater Weever	1924					–	–	–					
	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	0·2	–		
Scomber scomber Mackerel 4–12 mm.	1924					–	15·0	8·1					
	1925				–	–	6·0	2·4	–				
	1926				–	–	18·9	178·5	146·4	–			
	1927				–	0·6	1·2	23·4	0·9	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	1·2	57·3	–	–	–		
Gobius sp. Gobies 3–10 mm.	1924					6·9	278·4	170·4					
	1925				–	0·3	5·7	12·9	11·4				
	1926				2·1	–	41·4	68·1	5·4	–			
	1927				0·3	0·9	2·1	2·1	6·0	0·9	0·6	0·9	–
	1928	–	–	–	2·1								
	1929				–	–	16·2	60·9	9·3	2·7	0·3		
Lebetus scorpioides 3–6 mm.	1924					–	0·9	0·9					
	1925				–	–	0·1	0·9	5·1				
	1926				–	0·9	2·4	8·4	25·5	1·8			
	1927				–	0·2	0·3	1·2	1·5	0·3	0·3	–	2·1
	1928	–	–	–	–								
	1929				–	–	–	2·1	2·7	2·4	0·3		
Blennius ocellaris Butterfly Blenny	1924					–	0·9	0·6					
	1925				–	–	–	0·2	1·5				
	1926				–	–	–	1·2	0·9	–			
	1927				–	–	–	–	0·6	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Blennius pholis Shanny	1924					–	0·9	1·2					
	1925				–	0·3	0·2	1·2	0·6				
	1926				–	–	2·4	0·9	–	–			
	1927				–	0·2	0·3	0·9	0·2	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	–	–		
Blennius gattorugine Tompot 5–10 mm.	1924					–	3·6	6·0					
	1925				–	–	0·9	5·4	2·1				
	1926				–	–	7·2	12·6	8·4	–			
	1927				–	–	0·9	2·1	3·6	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	5·7	6·6	0·9	–		
Chirolophis galerita Yarrell's Blenny 4–7 mm.	1924					–	–	–					
	1925				0·6	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	0·3	3·0	2·0	–								
	1929				0·8	–	–	–	–	–	–		
Agonus cataphractus Pogge	1924					–	–	–					
	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	0·3	0·3								
	1929				0·3	0·3	–	–	–	–	–		
Trigla sp. Grey and Red Gurnards, and Tub 4–12 mm.	1924					9·9	45·0	9·9					
	1925				1·5	38·4	3·3	5·4	0·6				
	1926				6·0	5·7	7·8	2·4	5·1	0·6			
	1927				–	7·5	3·9	6·0	1·5	–	–	–	–
	1928	–	–	1·5	0·3								
	1929				7·2	5·7	2·7	3·6	6·6	1·5	1·7		

		Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Cottus bubalis	1924					0·9	1·5	–					
Father Lasher	1925				0·3	0·6	0·1	–	–				
5–8 mm.	1926				1·5	–	0·3	–	–	–			
	1927				1·5	0·9	–	–	–	–	–	–	–
	1928	–	–	4·5	6·0								
	1929				3·6	0·9	0·6	–	–	–	–		
Liparis montagui	1924					–	3·6	–					
Montague's Sucker	1925				0·2	1·2	–	–	1·0				
7–10 mm.	1926				0·3	–	–	–	–	–			
	1927				–	3·0	–	–	–	–	–	–	–
	1928	–	–	–	0·8								
	1929				0·3	–	0·3	–	–	–	–		
Lepadogaster	1924					–	7·5	3·6					
bimaculatus	1925				–	0·3	0·2	1·5	0·9				
Doubly Spotted	1926				–	0·3	2·4	0·6	2·1	–			
Sucker	1927				1·5	–	–	–	0·2	–	–	–	–
5–10 mm.	1928	–	–	–	–								
	1929				–	–	2·1	2·1	2·1	0·9	–		
Lophius piscatorius	1924					–	–	1·5					
Angler	1925				–	–	–	–	–				
5–9 mm.	1926				0·2	–	0·6	1·8	–	–			
	1927				–	–	0·3	0·3	0·2	–	–	–	–
	1928	–	–	0·3	–								
	1929				–	–	0·6	0·3	–	–	–		
Belone vulgaris	1924					–	–	–					
Garfish	1925				–	–	–	–	–				
	1926				–	–	–	–	–	–			
	1927				–	–	–	–	–	–	–	–	–
	1928	–	–	–	–								
	1929				–	–	–	–	–	0·2			

BIBLIOGRAPHY.

1888. Cunningham, J. T. The Spawn of the Pilchard. Journ. Mar. Biol. Assoc., Old Series, No. 2. p. 247.

1891. —— On Some Larval Stages of Fishes (with Plates III and IV). Journ. Mar. Biol. Assoc., N.S., Vol. II, No. 1, p. 68.

1891. —— The Reproduction and Growth of the Pilchard (with Plate X). *Ibid.*, Vol. II, No. 2, p. 151.

1891. —— The Egg and Larva of *Callionymus lyra* (with Plate V). *Ibid.*, Vol. II, No. 2, p. 89.

1892. —— Ichthyological Contributions. *Ibid.*, Vol. II, No. 4, p. 325.

1892. Holt, E. W. L. Note on *Scomber scomber* Linn. (The Mackerel). *Ibid.*, Vol. II, No. 4, p. 396.
Ibid., Vol. II, No. 4, p. 396.

1894. Cunningham, J. T. The Life-History of the Pilchard. *Ibid.*, Vol III, No. 2, p. 148.

1894. —— Young Stages of *Zeugopterus punctatus*. *Ibid.*, Vol. III, No. 3, p. 202.

1895. —— On a Specimen of Leptocephalus Morrisii. *Ibid.*, Vol. IV, No. 1, p. 73.

1895. —— The Larva of the Eel. *Ibid.*, Vol. III, No. 4, p. 278.

1897. Holt, E. W. L. Preliminary Notes on the Reproduction of Teleostean Fishes in the the South-Western District. *Ibid.*, Vol. V, No. 1, p. 41.

1898. —— Notes on the Reproduction of Teleostean Fishes in the South-Western District. *Ibid.*, Vol. V, No. 2, p. 107.

1898. Holt, E. W. L., and Scott, S. D. A Record of the Teleostean Eggs and Larvæ observed at Plymouth in 1897. *Ibid.*, Vol. V, No. 2, p. 156.

1898. Dunn, Matthias. On the Occurrence of Large Numbers of Larval Herrings at the Surface. *Ibid.*, Vol. V, No. 2, p. 184.

1898. Holt, E. W. L., and Byrne, L. W. Notes on the Reproduction of Teleostean Fishes in the South-Western District. *Ibid.*, Vol. V, No. 3, p. 333.

1900. Garstang, W. Preliminary Experiments on the Rearing of Sea-fish Larvæ. *Ibid.*, Vol. VI, No. 1, p. 70.

1903. Browne, F. Balfour. Report on the Eggs and Larvæ of Teleostean Fishes observed at Plymouth in the Spring of 1902. *Ibid.*, Vol. VI, No. 4, p. 598.

1909. Schmidt, J. The Distribution of the Pelagic Fry and the Spawning Regions of the Gadoids in the North Atlantic from Iceland to Spain. Conseil Perm. Internat. pour l'Explor. de la Mer. Rapp. et Proc. Verb., Vol. X, Special Part, No. 4.

1910. Hefford, A. E. Notes on Teleostean Ova and Larvæ. Journ. Mar. Biol. Assoc., N.S., Vol. IX, No. 1.

1914. Clark, R. S. General Report on the Larval and Post-Larval Teleosteans in Plymouth Waters. *Ibid.*, Vol. X, No. 2, p. 327.

1917. Allen, E. J. Post-Larval Teleosteans Collected near Plymouth during the Summer of 1914. *Ibid.*, Vol. XI, No. 2.

1918. Lebour, M. V. The Food of Post-Larval Fish. *Ibid.*, Vol. XI, No. 4, p. 433.

1919. —— The Food of Post-Larval Fish, No. II (1918). *Ibid.*, Vol. XII, No. 1, p. 22.

1919. —— The Young of the Gobiidæ from the Neighbourhood of Plymouth. *Ibid.*, Vol. XII, No. 1, p. 48.

1919. —— Feeding Habits of Some Young Fish. *Ibid.*, Vol. XII, No. 1, p. 9.

1919. —— Further Notes on the Young Gobiidæ from the Neighbourhood of Plymouth. *Ibid.*, Vol. XII, No. 1, p. 146.

1920. Clark, R. S. The Pelagic Young and Early Bottom Stages of Teleosteans. *Ibid.*, Vol. XII, No. 2, p. 159.

1920. Ford, E. The Post-Larval Stages of Ammodytes Species Captured during the Cruises of s.s. *Oithona* in Plymouth Waters in the Year 1919. *Ibid.*, Vol. XII, No. 2, p. 241.

1920. —— Note on a Leptocephalus Stage of the Conger. *Ibid.*, Vol. XII, No. 2, p. 249.

1920. Lebour, M. V. The Eggs of *Gobius minutus, pictus* and *microps*. *Ibid.*, Vol. XII, No. 2, p. 253.

1920. —— The Food of Young Fish (1919). *Ibid.*, Vol. XII, No. 2, p. 261.

1921. —— The Larval and Post-Larval Stages of the Pilchard, Sprat and Herring from Plymouth District. *Ibid.*, Vol. XII, No. 3, p. 427.

1921. —— The Food of Young Clupeoids. *Ibid.*, Vol. XII, No. 3, p. 458.

1922. FORD, E. On the Young Stages of *Blennius ocellaris* L., *Blennius pholis* L., and *Blennius gattorugine* L. *Ibid.*, Vol. XII, No. 4, p. 688.

1922. —— On the Post-Larvæ of the Wrasses occurring near Plymouth. *Ibid.*, Vol. XII, No. 4, p. 692.

1924. LEBOUR, M. V. The Food of Young Herring. *Ibid.*, Vol. XIII, No. 2, p. 325.

1925. —— Young Anglers in Captivity and Some of their Enemies. A Study in a Plunger Jar. *Ibid.*, Vol. XIII, No. 3, p. 721.

1926. RUSSELL, F. S. The Vertical Distribution of Marine Macroplankton, II. The Pelagic Young of Teleostean Fishes in the Daytime in the Plymouth Area, with a Note on the Eggs of certain Species. *Ibid.*, Vol. XIV, No. 1, p. 101.

1926. —— The Vertical Distribution of Marine Macroplankton, III. Diurnal Observations on the Pelagic Young of Teleostean Fishes in the Plymouth Area. *Ibid.*, Vol. XIV, No. 2, p. 387.

1927. LEBOUR, M. V. The Eggs and Newly Hatched Young of the Common Blennies from the Plymouth Neighbourhood. *Ibid.*, Vol. XIV, No. 3, p. 647.

1928. RUSSELL, F. S. The Vertical Distribution of Marine Macroplankton, VIII. Further Observations on the Diurnal Behaviour of the Pelagic Young of Teleostean Fishes in the Plymouth Area. *Ibid.*, Vol. XV, No. 3, p. 829.

1930. —— The Vertical Distribution of Marine Macroplankton, IX. The Pelagic Young of Teleostean Fishes in the Plymouth Area. *Ibid.*, Vol. XVI, No. 2, p. 639.

Herring Investigations at Plymouth. VIII. The Transition from Larva to Adolescent.

By

E. Ford, A.R.C.Sc.,

Fisheries Naturalist at the Plymouth Laboratory.

With 12 Figures in the Text.

CONTENTS.

Introduction.

Investigations concerning the main events in the transformation of the transparent eel-shaped larval herring into the silvery and scaled adolescent fish may proceed along two lines. In the first place, information may be sought as to the biological processes which bring about each event. For example, attention may be directed to the study of the differential growth of the body by which the form of the adult is attained; or, to the manner in which the scales are developed. But, secondly, it is of vital importance to learn how much the events of metamorphosis are affected by circumstances of time and place. Thus, at Plymouth, as elsewhere, we need to know the extent of possible differences in form and size between young fishes which have metamorphosed from larvæ born at different times.

Sufficient material has been collected from the rivers flowing into the sea at Plymouth to yield information along both the above lines of investigation. In the first section of this paper attention is given to the

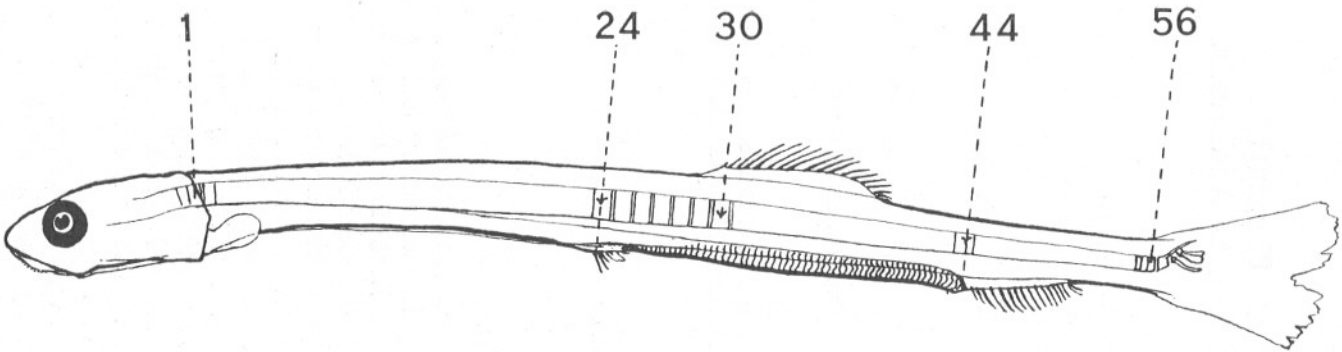


FIG. 1.—Semi-diagrammatic drawing of post-larval herring. Body-length (L_B) of 33 mm. Position of pelvics, first dorsal ray and anus with respect to vertebræ. Total number of vertebræ is 56, exclusive of compound urostyle.

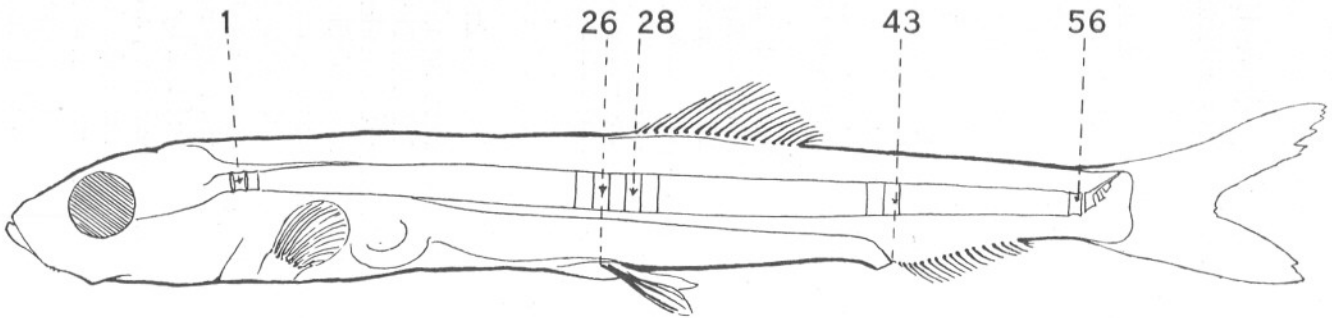


FIG. 2.—Post-larval herring; body-length (L_B) of 36 mm. Note apparent movement of pelvics, dorsal fin and anus with respect to vertebræ.

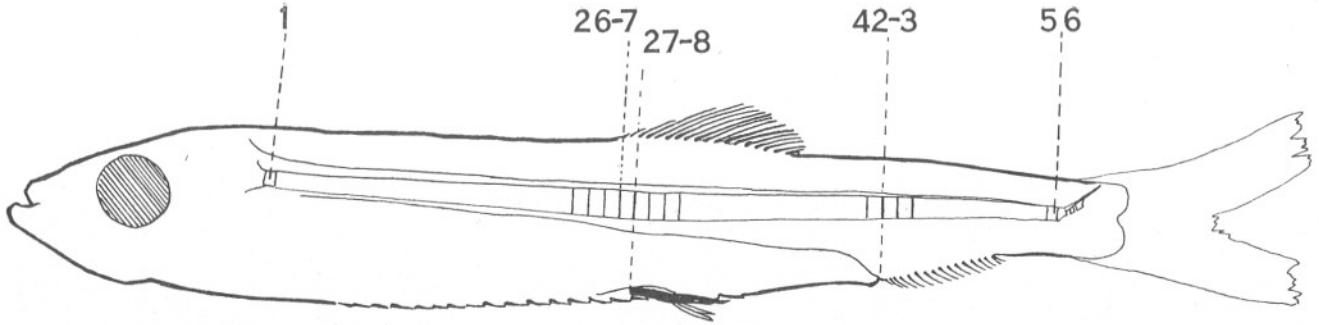


FIG. 3.—Post-larval herring; body-length (L_B) of 37 mm. Pelvics now lie slightly farther back than first dorsal ray with respect to vertebræ. Anus has moved still farther forward.

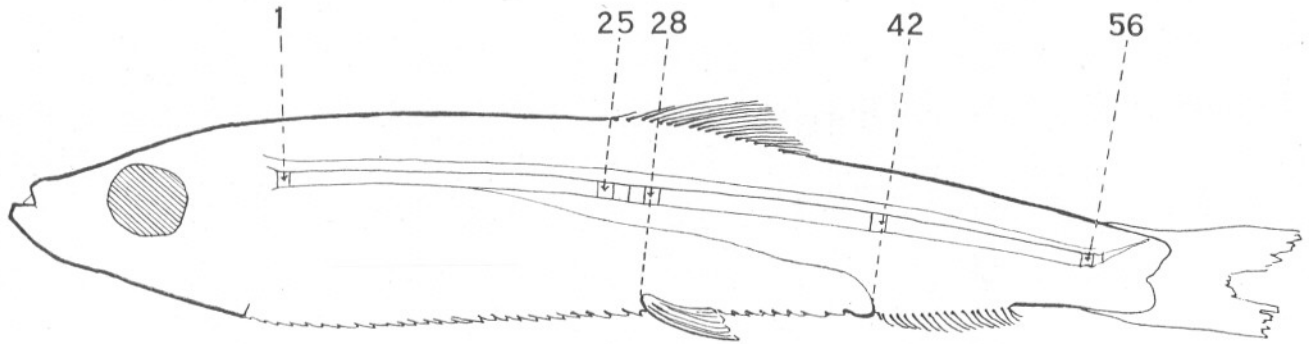


FIG. 4.—Post-larval herring; body-length (L_B) 45 mm. Pelvics well behind first dorsal ray, and anus beneath vertebra 42.

question of the differential growth of the body, while in the second, problems arising out of observed differences between samples of metamorphosing fishes are discussed.

Collection of Data.

The fishes studied were caught in a small-meshed Saltash tuck-seine in the Rivers Tamar and Lynher [charts of the district are given by Ford (**3**) and Percival (**6**)]. As a measure of length, the body-length L_B from the tip of the snout to the end of the caudal peduncle, was used in preference to the more familiar total-length L_T, for reasons previously stated in Ford (**3**, p. 307). The value of L_T is approximately equal to 7/6 L_B. The method of statistical "grouping" was also the same as that hitherto used; e.g. fishes from 30 to 34 mm. would be grouped in the 30 mm. group, and those from 35 to 39 mm. in the 35 mm. group, when grouping was by intervals of 5 mm. For the first part of the work, fifty specimens of each of the four body-length groups 30 mm., 35 mm., 40 mm., and 45 mm. from any one day's sample were utilised. These were stained in alizarin either whole, or after the excision of one side by means of a safety-razor blade, and then cleared in xylol. A count of the total number of vertebræ in each specimen was made, and the position, either immediately above or below a particular vertebra, of the first dorsal fin-ray, the pelvics and the anus noted. The count of the total number of vertebræ stopped at the vertebra immediately preceding the compound urostyle (*vide* Ford, **2**, p. 253). In determining the relative position of the fins and anus, it frequently happened that the structure concerned occupied a position opposite the interval between two adjacent vertebræ. In such cases an entry of $\frac{1}{2}$ was made to each of the appropriate vertebræ classes. At a later stage in the work, actual measurements along the body to determine well-defined body intervals were made on specimens prior to staining.

CHANGE OF FORM.

Alteration in Position of Fins and Anus Relative to Vertebræ.

Fage (**1**) and Lebour (**5**) have shown that in the gradual adjustment of the fins and anus of the larva to the positions they occupy in the adult, these structures alter their place with respect to the vertebræ.* Thus

* Since this paper has been in the hands of the printer, the important work by Dr. Schnakenbeck on the development of the herring has appeared. (*Entwicklungsgeschichtliche und morphologische Untersuchungen am Hering.* Berichte d. Deutsch. wissenschaftl. Komm. f. Meeresforschung, Neue Folge, Band V Heft 2, Berlin, 1929.) Dr. Schnakenbeck has studied the process of metamorphosis in relation to the growth of the myotomes. Excellent illustrations are given.

there is a relative movement forward of the dorsal fin and anus, but a backward one of the pelvics. In order to assist those readers who may not be familiar with these facts, Figures 1, 2, 3, and 4 have been inserted. But as individual fishes differ in their total number of vertebræ from 53 to 58, it is clearly of importance to study the effect of this difference in total with regard to the relative movements of fins and anus. For example, the 25th vertebra, under which the pelvics may lie in a fish having a total of 55 vertebræ, is not in the same relative position along the vertebral column as the 25th vertebra of a second fish having 57 vertebræ. Hence, in analysing the progress of development over a range of time or size, it is necessary to take into account the total number of vertebræ of the individuals concerned.

Fishes with 56 Vertebræ.

It is convenient to commence with those fishes which form the greater proportion of each sample taken, namely, those with a total of 56 vertebræ. Data are available for a total of 746 such fishes caught during the months of April, May and June, and varying in body-length from 30 to 49 mm. The position of the pelvics in these specimens varies from beneath the 24th vertebra to beneath the 29th. The variation in position of the first dorsal ray (D^1) when the pelvics lie under the 24th, 25th to the 29th vertebra respectively is given in the following table :—

TABLE I.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Position of 1st Dorsal Ray (D^1). No. of Specimens in which D^1 lies above vertebra as under								Totals.	Position of D^1 Working means.
	24	25	26	27	28	29	30	31		
24	–	–	–	–	–	–	2	–	2	29·5*
24–25	–	–	–	–	½	3	6½	3	13	29·42
25	–	–	–	1	3½	23½	33	9	70	29·15
25–26	–	–	–	1½	2	13½	6	5	28	28·89
26	–	–	8½	16½	37½	46	29	2½	140	28·06
26–27	–	1	8	10	16½	8	½	–	44	27·05
27	2½	26	60½	57½	20	3½	1	–	171	25·97
27–28	1	25½	19½	5½	3½	–	–	–	55	25·23
28	3½	75	90	4½	–	–	–	–	173	25·05
28–29	–	8	23	1	–	–	–	–	32	25·28
29	–	6½	10	½	–	–	–	–	17	25·15
Totals	7	142	219½	98	83½	97½	78	19½	745	

* For statistical purposes, the middle of the 30th vertebra is regarded as point 29·5, and similarly from each of the other means, 0·5 is subtracted.

In Figure 5, below, the mean positions of D^1 given in the right-hand column of Table I are plotted against the successive positions of the pelvics (curve AB), while the straight line CD is simply the result of plotting the positions of the pelvics both as ordinates and abscissæ. It will be seen that AB and CD cross at point 26·35; that is to say, the first dorsal ray is vertically above the pelvics at this point

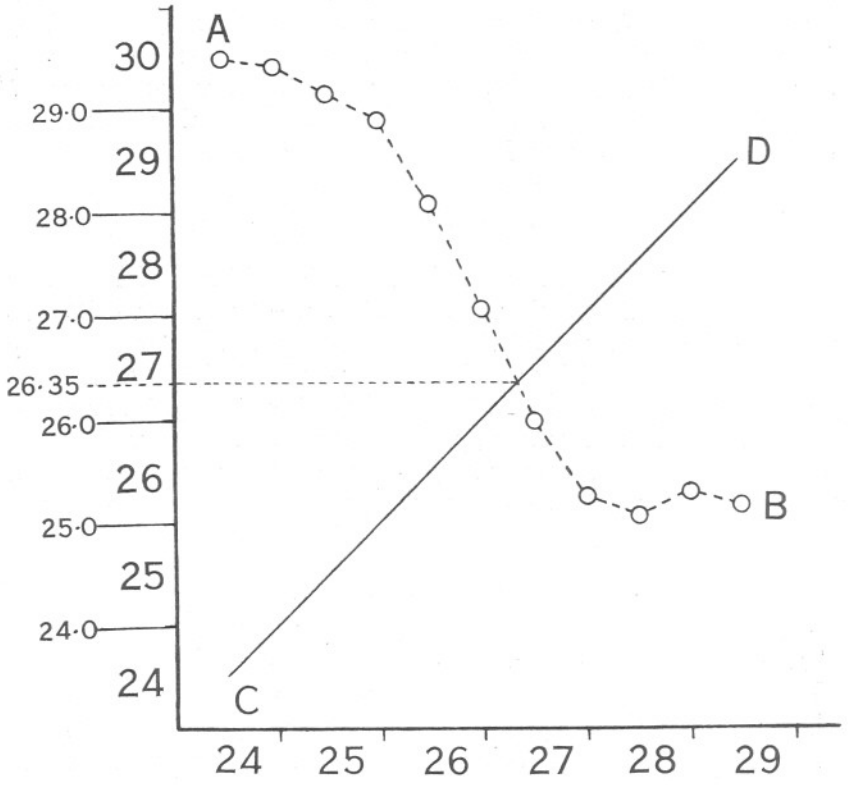


Fig. 5.—The positions of first dorsal ray (ordinates) for observed positions of pelvics (abscissæ) with respect to vertebræ, in fishes with a total of 56 vertebræ, are shown in the graph AB. The successive positions of the pelvics are represented by the straight line CD. The pelvics lie immediately beneath the first dorsal ray at point 26·35 along the vertebral column; i.e. at the level of the anterior part of the 27th vertebra (see text above).

which is approximately the middle of the 27th vertebra. It is also apparent that the dorsal fin and the pelvics continue their movement beyond this stage, so that finally the first dorsal ray comes to lie several vertebræ in front of the pelvics, in contrast with its original position well behind the latter.

Corresponding data for fishes with 56 vertebræ on the position of

the anus with respect to pelvics and vertebræ are given in Table II below :—

TABLE II.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Position of Anus. No. of Specimens in which Anus lies beneath vertebræ as under. 41	42	43	44	45	46	Totals.	Position of Anus. Working means.
24	–	–	–	1	½	½	2	44·25*
24–25	–	–	4	6	2½	½	13	43·46
25	–	1	30½	26½	11½	½	70	43·21
25–26	–	1	14½	7½	5	–	28	43·09
26	2½	46½	63	22½	5½	–	140	42·37
26–27	1	18½	19½	4½	½	–	44	42·14
27	4½	87½	73½	4½	–	–	170	41·96
27–28	1	31½	22½	1½	½	–	57	41·96
28	2½	68½	97½	4½	–	–	173	42·10
28–29	–	10	22	–	–	–	32	42·19
29	–	5	11	1	–	–	17	42·26
Totals	11½	269½	358	79½	26	1½	746	

* For statistical purposes, the middle point of the 45th vertebra is regarded as point 44·5, and similarly from each of the other means, 0·5 is subtracted.

The mean positions of the anus are plotted against the successive positions of the pelvics in Figure 6 on page 730. By erecting a perpendicular at point 26·35 along the horizontal axis, and noting the ordinate of the point E at which the perpendicular intersects the curve, we can determine the mean position of the anus when the first dorsal ray is immediately above the pelvics. This occurs when the anus is at point 42·0 or, in other words, when the anus is midway between the 42nd and the 43rd vertebræ. By this time, unlike the dorsal fin, the anus has practically completed its forward movement.

It may not have escaped notice that the curves for both the dorsal fin and anus tend to rise slightly at the right-hand end. This suggests that a slight reversal of the direction of movement relative to vertebræ may take place towards the end of metamorphosis.

Effect of Change in Total Number of Vertebræ.

Data on the position of the first dorsal ray and anus with respect to the pelvics, for fishes with 55 or 57 vertebræ, are given in Tables VII and VIII at the end of this paper. These are summarised graphically in Figure 7, in which the effects of a change in the total number of vertebræ are clearly demonstrated. It is seen that the higher the total number of vertebræ the higher are the mean values for the position of both D^1 and anus for any given position of the pelvics. Thus, the mean position along

the vertebral column at which D^1 is vertically over the pelvics, and the position of the anus at that time, in the three cases is as follows :—

Total No. of vertebræ.	D^1 and Pelvics.	Anus.
55	26·05	41·5
56	26·35	42·0
57	26·60	42·6

Differential Growth as an Explanation of Movements of Fins and Anus.

No proof is here needed of the elementary fact that during the greater part of the relative changes in position of fins and anus, the fish as a whole increases in length. Furthermore, mere inspection first of a larva and then of a newly-metamorphosed fish suffices to verify the fact that

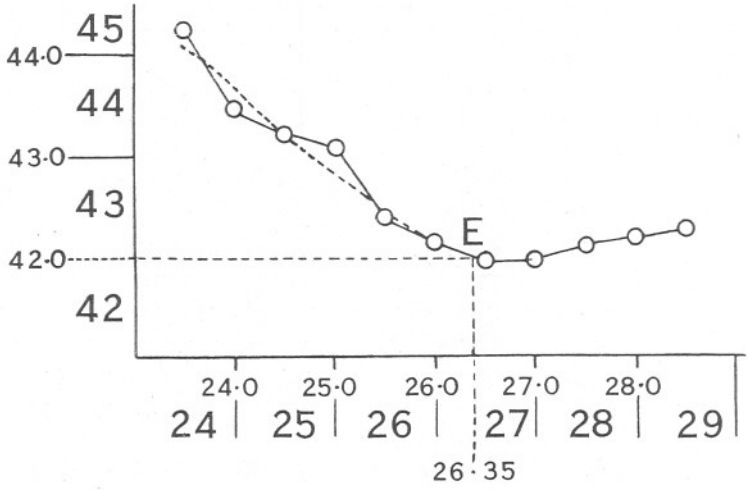


FIG. 6.—The positions of the anus (ordinates) for observed positions of pelvics (abscissæ) with respect to vertebræ, in specimens with a total of 56 vertebræ. The position of the anus when the first dorsal ray is vertically above the pelvics is given by the ordinate of point E, namely, point 42·0 along the vertical column (i.e. beneath the junction of the 42nd and 43rd vertebræ), see text, page 729.

the various body-intervals such as the distance from the pelvics to the anus, or from the anus to the end of the caudal peduncle, form a markedly different proportion of the whole length in the two cases. It would seem a simple additional step to measure selected body-intervals for successive stages in position of fins and anus, and thus to determine in absolute units of length, the growth of each body-interval throughout metamorphosis. The data of the present time-series of samples, however, do not lend themselves to so simple statistical treatment, since the length at which any

given phase of metamorphosis is reached varies over a wide range, and there is much overlap in length among the different phases. The extent and significance of these differences in length form a study of their own and are discussed in a later section of this paper. Despite the fact that

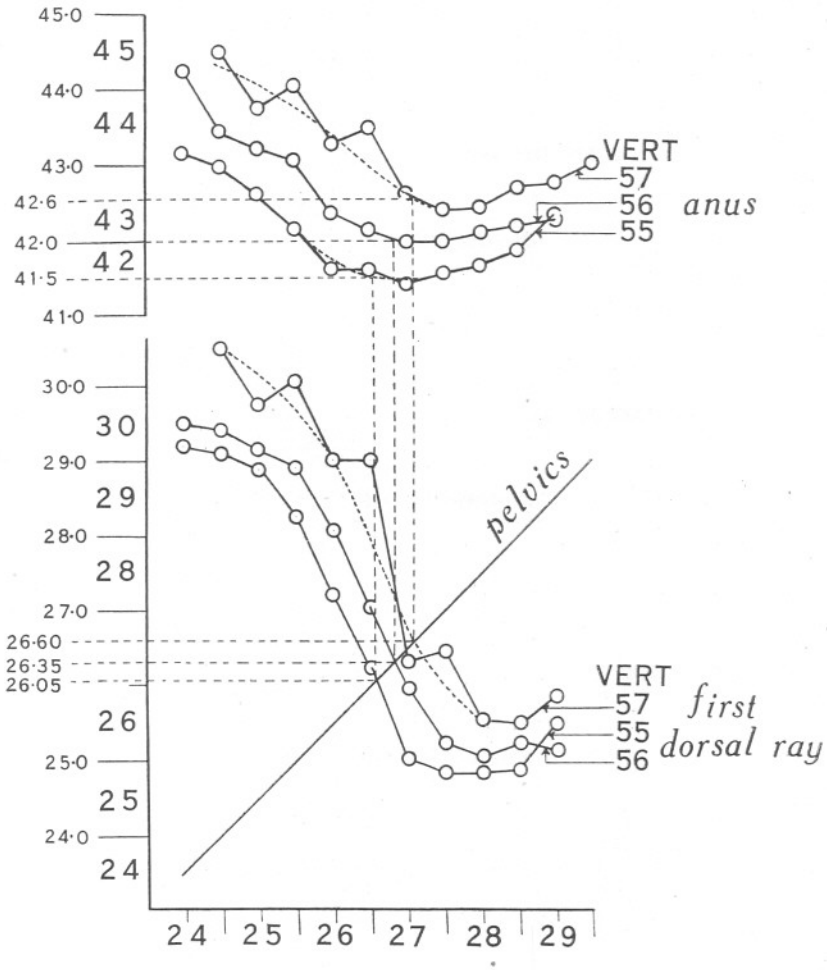


FIG. 7.—Positions of the first dorsal ray and anus (ordinates) for observed positions of the pelvics (abscissæ) with respect to vertebræ in fishes having 55, 56, and 57 vertebræ respectively. The diagram is merely a composite one, combining the results of figures corresponding with those shown in Figs. 5 and 6.

individuals at the same phase of metamorphosis vary in absolute length, it is still possible to watch the change in *proportionate* length shown by given body-intervals from phase to phase. It is found that while some intervals increase in proportion, others decrease. Now a decreasing

proportion as metamorphosis proceeds may indicate one of three things. In the first place, the body-interval may be actually decreasing in length ; secondly, it may be remaining quite stationary throughout ; or thirdly, it may be increasing in absolute length but at a slower rate than the fish as a whole. A study of the available data has shown that the distance from the pelvics to the anus, and from the back of the brain to the insertion of the first dorsal ray, both undergo a marked reduction in

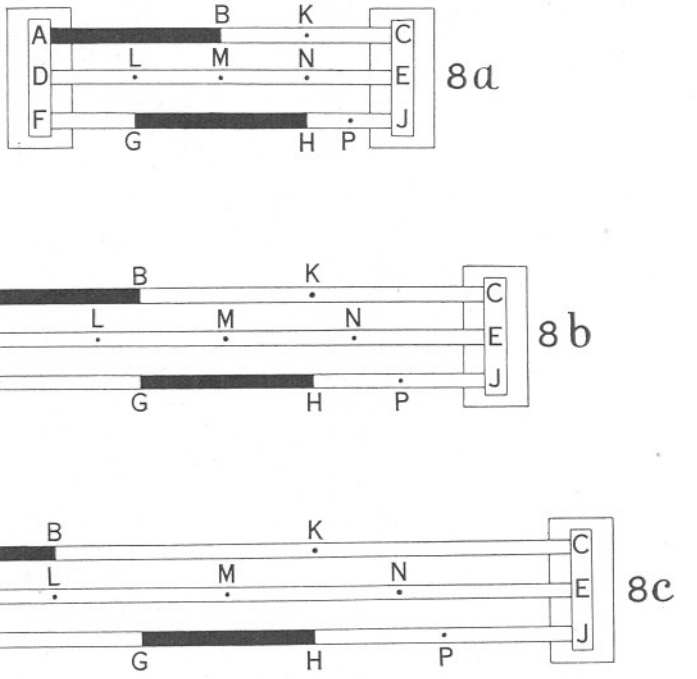


FIG. 8.—Diagrams illustrating the results of stretching the model composed of tape and elastic described in the text below.
8A.—Unstretched model. Portions AB and GH are constructed of rigid tape : the remaining parts of the three horizontal components are elastic. Total length is 4 units.
8B.—Model stretched to a total length of 6 units.
8C.—Model stretched to a total length of 8 units.

proportion as development proceeds. This observation, as will be realised later, is of great significance as an aid to the understanding of the mechanism of growth during metamorphosis, and in order to demonstrate this point the more clearly, the reader is asked to devote patient attention to the action of some simple models constructed of tape and elastic. The first model is rectangular in form as shown in Figure 8a. It consists essentially of three parallel components AC, DE and FJ, each four units in length, connected at their ends by wooden stays AF and CJ.

The uppermost component AC consists of a tape portion AB of two units in length, and an elastic portion BC, also two units in length. The middle component DE is entirely elastic, being merely marked off into four equal sections at points L, M and N. The third component FJ consists of a portion of tape GH two units long, inserted between single units of elastic FG and HJ. The positions of different points along AC and FJ may be expressed either in units of length from the wooden end AF, or with respect to their position above or below points in any one of the three components. Thus, with the model in its unstretched condition, the following positions may be noted :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point M
G	1	,, below ,, L
H	3	,, ,, ,, N

By holding the wooden ends AF and CJ and pulling outwards, the three components may be stretched equally to a new length. As an initial stretching, let the total length be increased from four units to six. Figure 8b represents the new situation. The positions of the three points B, G and H are now seen to be :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point G; above but to the left of point M.
G	2	Directly below point B; above but to the right of point L.
H	4	Below but to the left of point N.

A further stretching is now applied so that the total length becomes eight units. Figure 8c reproduces the model at this stage, and the final positions of points B, G and H are :—

Point.	Distance from AF in units.	Position with reference to points in other components.
B	2	Directly above point L; above but to the left of point G.
G	3	Below mid-point between points L and M.
H	5	Below mid-point between points M and N.

Thus, as the result of these two stretchings, the appearance of the model has been greatly changed, and points B, G and H have altered their positions relative to one another and to points along the middle component DE. In addition, the proportions of various parts of the three

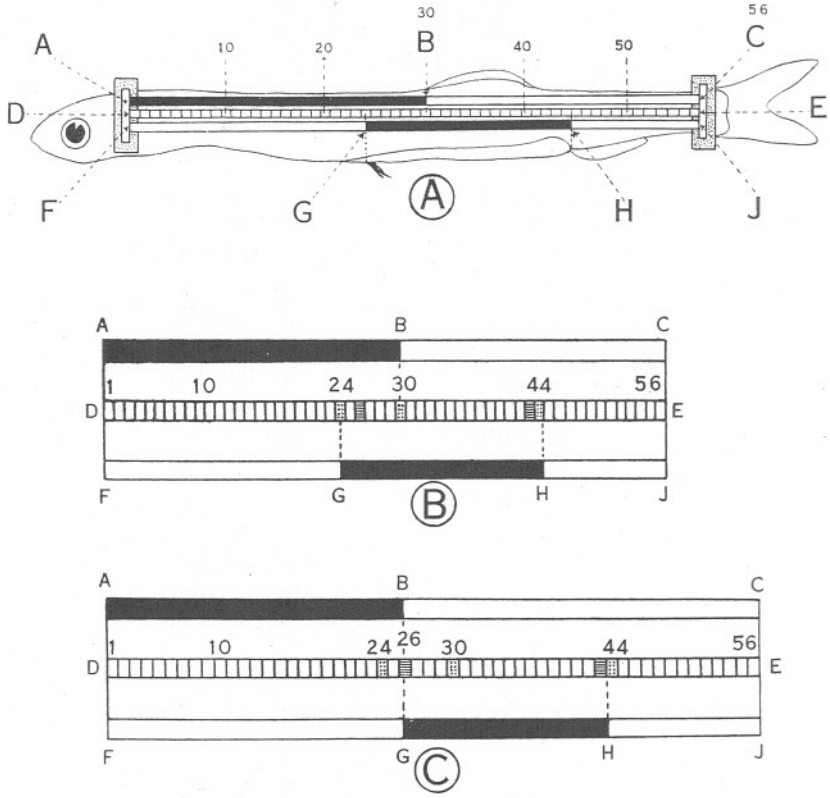


FIG. 9A.—A tape and elastic model, similar in character to that shown in Fig. 8A, is here superimposed on a diagrammatic representation of a post-larval herring, so that points B, G, and H coincide with the pelvics, first dorsal ray and anus respectively with respect to the vertebræ.

FIG. 9B.—Diagram of the model thus created. The middle component is divided into 56 equal parts to represent 56 vertebræ; point B lies above the middle of the 30th vertebra, point G beneath the middle of the 24th vertebra and point H beneath the junction of the 44th and 45th vertebræ.

FIG. 9C.—Diagram representing the model when stretched to a length of 65·1 units as compared with its original length of 56 units. Note how the positions of points B, G and H with respect to vertebræ have changed as the result of stretching.

components have also changed. Dealing first with component AC, it is seen that point B has moved to the left from above point M to above point L, while the distance AB has become reduced in proportion from one-half the total length to one-quarter. Simultaneously, BC has increased in proportion from one-half to three-quarters. The component

DE being entirely elastic extends uniformly throughout its length, so that points L, M and N remain unaltered in relative position along DE. The composite component FJ, on the other hand, has undergone alteration; the elastic portions FG and HJ have each increased from one-fourth of the total length to three-eights, while the rigid tape portion GH has become reduced in proportion from one-half to one-quarter. As the result, point G has moved to the right from its original position beneath point L to a new one between points L and M; and point H to the left from beneath point N to between points N and M.

In Figure 9A a three-component rectangular model is shown superimposed over a diagrammatic outline of a larval herring, so that the different portions of the model roughly represent the body-intervals of the fish over which they fall. In this way we may experiment with a model approximating to the correct proportions of the fish itself. It is seen that this model is only an elaborated counterpart of the simple model just considered, in which point B now represents the position of the first dorsal ray, G coincides with the insertion of the pelvics, and H with the anus. The component DE is here divided into as many blocks as there are vertebræ in the fish—and it may be taken in this instance that there are 56 vertebræ. As before, portions AB and GH in the model can be regarded as rigid and represented by tape, while the remainder is of elastic. For the sake of simplicity, also, all the vertebræ may be considered equal in size (length). Referring back to the data in Tables I and II (pp. 727 and 729) it is noted that with the pelvics situated beneath the middle of the 24th vertebra, the first dorsal ray (represented by point B in the model) lies opposite the middle of the 30th vertebra, and the anus (point H in the model) below the junction of the 44th and 45th vertebræ.

As there are 56 vertebræ in the fish, it will be convenient to regard the total length, AC, of the model as 56 units, so that the dimensions of the model can at once be stated :—

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	26·5	23·5	20·5	12·0

It is obvious that by stretching the model, points B and H, as in the simple model, will move to the left, relative to points along the centre component DE, and point G to the right. That is to say that the first dorsal ray and the anus will make a forward movement over the vertebræ while the pelvics shift backwards. This is in accordance with fact (p. 727). If stretching is carried sufficiently far, point B (representing the first dorsal ray) can be brought immediately over point G (representing the pelvics). It is possible to calculate the new total length to which the model must be stretched to reproduce this phase, and also the points

along the vertebral column over which the first dorsal ray, the pelvics, and the anus lie :—

Let the new length of the model be x.

Since AB and GH are non-elastic, their lengths remain unaltered throughout the stretching.

With the model in its stretched condition, its dimensions are :

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	(x—29·5)	$\frac{(x-20\cdot5)\ (23\cdot5)}{(23\cdot5+12\cdot0)}$	20·5	$\frac{(x-20\cdot5)\ (12\cdot0)}{(23\cdot5+12\cdot0)}$

In this condition AB=FG, or $29\cdot5=\frac{(x-20\cdot5)\ (23\cdot5)}{(23\cdot5+12\cdot0)}$

$$\therefore\ x=65\cdot1$$

Substituting the value 65·1 for x in the above table of dimension :—

Intervals	AB	BC	FG	GH	HJ
Units of length	29·5	35·6	29·5	20·5	15·1

The positions with respect to the vertebræ of points B, G and H are given by :—

Position of B and G $\frac{29\cdot5\times56}{65\cdot1}=25\cdot4$ (i.e. practically opposite the middle of the 26th vertebra.)

Position of H $\frac{(29\cdot5+20\cdot5)\ (56)}{65\cdot1}=43\cdot0$ (i.e. opposite the junction of 43rd and 44th vertebræ.)

Referring back to the data given on page 728 it is seen that the first dorsal ray passes the pelvics at the level of the 27th vertebra, the anus being then at the level of the 43rd vertebra. The model then (see Figs. 9b and c), has brought point B (representing the first dorsal ray) forward at rather too quick a rate, and point H (representing the anus) too slowly, although it has rightly made the total shift greatest in the case of point B (the first dorsal ray).

It was shown on page 730 that the position along the vertebral column at which the first dorsal ray is vertically above the pelvics, and the position of the anus at that time is dependent upon the total number of vertebræ (*vide* Table on p. 730 and Fig. 7 on p. 731). It is easy to see from the model how this could arise, for an alteration in the number of vertebræ means a changing of the number of subdivisions of the middle component DE. With the model stretched to a length of 65·1 units, the intervals along the components AC and FJ will be precisely the same whatever the number of parts into which the centre component DE is divided. Thus, point B will lie immediately above point G at a

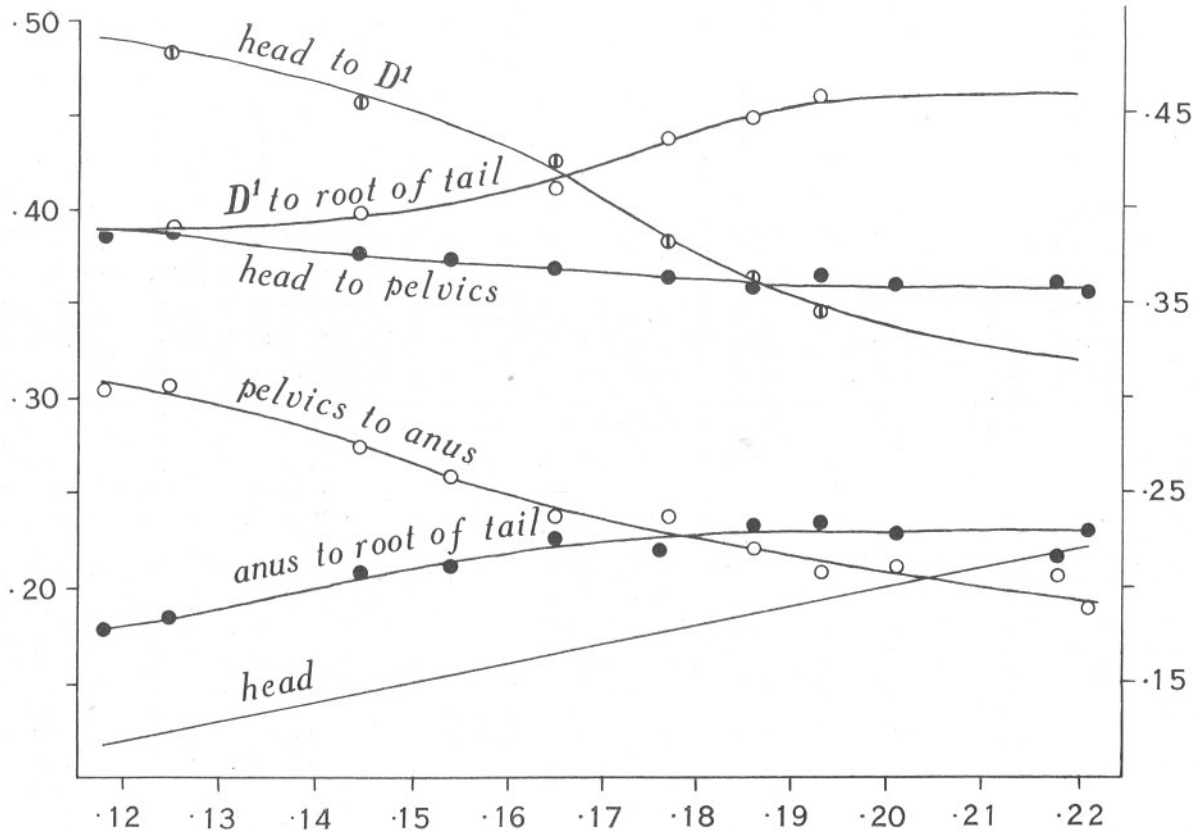


FIG. 10.—Curves showing the proportions of various body-intervals for successive values of the proportion of the head (abscissæ). See Table III on page 739.

distance of 29·5 units from the origin regardless of the division of DE into 55, 56, or 57 parts. But the position along DE to which B and G are opposite will *not* be the same in the three cases :—

1. When DE is divided into 55 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5 \times 55}{65{\cdot}1} = 24{\cdot}9$ along DE
2. When DE is divided into 56 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5 \times 56}{65{\cdot}1} = 25{\cdot}4$ along DE
3. When DE is divided into 57 parts, points B and G will lie opposite point . . . $\frac{29{\cdot}5 \times 57}{65{\cdot}1} = 25{\cdot}8$ along DE

Hence the model, like the direct observations on the fish themselves, shows that the higher the number of vertebræ, the higher are the values for the positions of the first dorsal ray, the pelvics and the anus at the same phase of development.

The model is also useful in the study of the change in position relative to vertebræ of the dorsal and anal fins in their entirety. Referring to Figure 8a, the base of the dorsal fin is represented by the anterior portion BK of the component BC. During stretching, point B moves forward with respect to the vertebræ while point C obviously does not. Clearly then, any point between B and C will make some forward movement, the amount depending upon the relative distance of the point from B. Thus point K, representing the hinder end of the base of the dorsal fin, will move forward relative to the vertebræ, but not so quickly as point B. As the result of stretching, the dorsal fin as a whole will appear to move forward and will also tend to cover more and more vertebræ as stretching continues. Similarly with the anal fin. Point H at the anterior end of component HJ moves forward, while point J remains at rest relative to the vertebræ ; point P representing the posterior end of the anal fin will move forward, but at a slower rate than H. Thus the anal fin will tend to move forward and to cover more vertebræ as stretching is applied.

Summarising, it may be said that an elementary model incorporating three distinct systems of differential growth, viz., along the dorsal surface, along the vertebral column and along the ventral surface, respectively, will broadly speaking reproduce the salient features of the relative movements of fins and anus during metamorphosis.

The Changing Proportions of the Body during Metamorphosis.

In the foregoing considerations, attention has been centred mainly on the alteration in relative position of definite points along the dorsal and ventral surfaces of the body and along the vertebral column. It is now necessary to consider the changing proportions of the body-intervals between the moving points. The curves shown in Figure 10 on page 737 are based on data derived from actual measurements of approximately 500 fishes in different phases of metamorphosis, so selected that the whole sequence of transition from the nude post-larva to the scaled and silvery adolescent was represented. The lengths of the different intervals along each fish were determined by direct measurement on a squared rule under magnification, and the absolute measurements then converted into proportions of the body-length L_B of the fish. The resulting data were finally summarised according to the proportionate length of the head, which increases as metamorphosis proceeds, and the mean results were plotted as shown in Figure 10. From these curves the following Table of Values has been prepared :—

TABLE III

Length of Certain Body-intervals Expressed as Proportions of Body-length (L_B).

Head (tip of snout to back of brain).	Head to D^1.	D^1 to end of caudal peduncle.	Head to pelvics.	Pelvics to anus.	Anus to end of caudal peduncle.
·12	·490	·390	·390	·305	·185
·13	·479	·391	·384	·295	·190
·14	·466	·394	·378	·284	·199
·15	·450	·400	·374	·265	·210
·16	·430	·410	·370	·248	·218
·17	·405	·425	·366	·237	·225
·18	·378	·442	·362	·230	·228
·187	**·361**	**·452**	**·361**	**·223**	**·229**
·19	·355	·455	·360	·217	·230
·20	·340	·460	·359	·210	·230
·21	·330	·460	·358	·202	·230
·22	·320	·460	·357	·193	·230

Attention is first directed to the phase of metamorphosis when the first dorsal ray (D^1) lies immediately above the pelvics, i.e. when the distance from the head to the pelvics is equal to that from the head to D^1. It is seen from the above Table that when this occurs the head constitutes ·187 of the body-length. At this stage, also, the length from

the anus to the end of the caudal peduncle has reached a proportionate length slightly exceeding that from the pelvics to anus.

It is of particular interest here to go back to the use of models similar to those employed in previous discussions. The first model, represented in Figure 11a, is similar to that shown in Figure 8a, save that the central component DE need not be used in the present instance, and its dimensions are in accordance with the data in the above Table when the head comprises ·12 of the body-length :—

Intervals.	AB	BC	FG	GH	HJ	Total length of model.
Units of length . .	49	39	39	30·5	18·5	88·0

As before, AB and GH are assumed to be non-elastic and therefore represented by tape, while the remaining intervals are represented by the correct lengths of elastic of uniform grade. The calculated dimensions of this model when it is stretched until AB is equal to FG, as in Figure 11c (representing the phase when the first dorsal ray is vertically over the pelvics) are :—

Intervals.	AB	BC	FG	GH	HJ	Total length of model.
Units of length . .	49	53·8	49	30·5	23·3	102·8

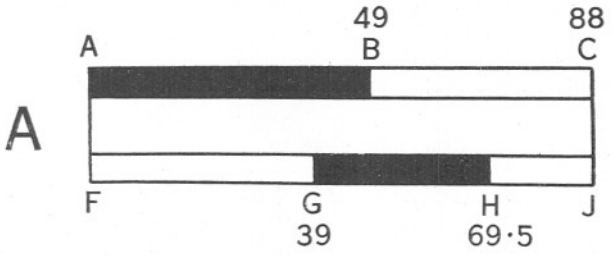
The head of the fish at this phase comprises ·187 of the body-length L_B. The total length of the model (102·8 units) thus represents ·813 L_B, so that $L_B = \frac{102·8}{·813} = 126·4$ units.

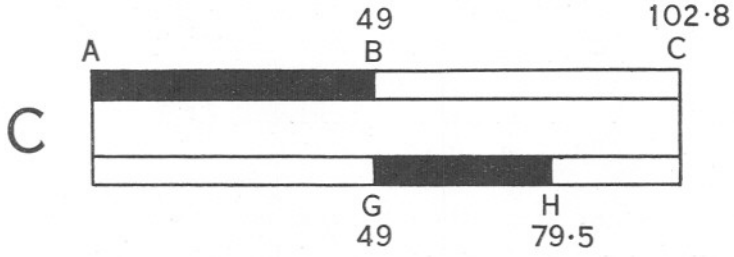
The proportions of the body-intervals as actually determined from measurements of fish, and as represented by the model are, thus, as follows :—

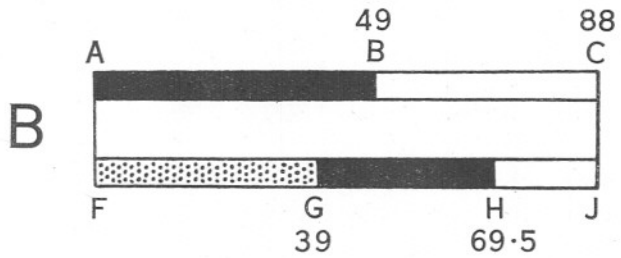
Head.	Head to D^1 (AB)	D^1 to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)
Actual ·187 . . .	·361	·452	·361	·223	·229
Model — . . .	·388	·426	·388	·241	·184

It is evident that the model has not reproduced the results from measurements ; AB, FG, and GH are too large, while BC and HJ are too small.

A little experimenting with the model will show that the insertion of a stiffer elastic for the interval FG has an important effect. The model will now have to be stretched to a greater length in order to bring point B over G, and as the result, intervals AB, FG and GH will be







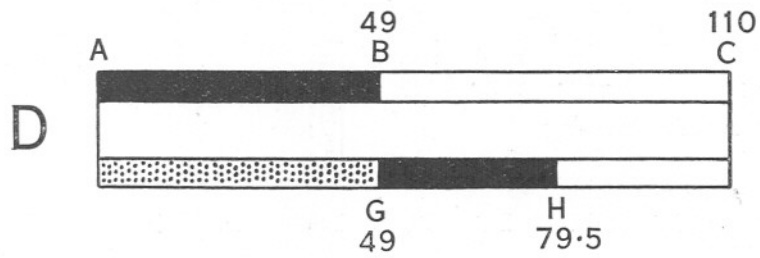


FIG. 11A.—Tape and elastic model described in text on page 740. In this case the interval FG is constructed of elastic similar in stretching quality to the elastic used in the other parts of the model.

FIG. 11B.—A second tape and elastic model, similar in dimensions to that shown in Fig. 11A but differing in that the interval FG is constructed of an elastic $\frac{1}{10}$ times as resistant as the elastic used in other components. This difference is indicated by stippling.

FIG. 11C.—The model shown in Fig. 11A is here stretched until point G lies immediately beneath point B. The total length of the model is 102·8 units.

FIG. 11D.—The model shown in Fig. 11B is here stretched until point G lies immediately beneath point B. The total length of the model is 110 units.

proportionally reduced, while BC and HJ will be increased. Now this is just what is required if the model is to reproduce an exact picture of actual measurements. Imagine then, that BC is constructed of a stiffer elastic of such stretching capacity that it is $\frac{11}{10}$ as resistant to strain as the elastic of which BC and HJ are constructed (Fig. 11b). With this new model stretched until point B is above G (Fig. 11d) the calculated dimensions are :—

AB	BC	FG	GH	HJ	Total length of model.
49	61	49	30·5	30·5	110·0

The new length of the model, 110·0, represents ·813 L_B, and therefore L_B is $\frac{110}{\cdot 813}$=135·3 units.

The proportions of the different intervals of the body as represented by the new model, as compared with actual fish measurements may now be given :—

Head.	Head to D¹. (AB)	D¹ to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)
Actual ·187 . . .	·361	·452	·361	·223	·229
New model — . . .	·362	·451	·362	·225	·225

Hence, by the mere substitution of stiffer elastic for the interval BC, the model has been made to reproduce a very satisfactory picture of actual measurements.

By dividing the absolute length of an interval after stretching by its original length, an idea may be obtained of the relative increase made :—

Head.	Head to D¹. (AB)	D¹ to end of caudal peduncle. (BC)	Head to pelvics. (FG)	Pelvics to anus. (GH)	Anus to end of caudal peduncle. (HJ)	L_B
Before stretching						
1·0	1·0	1·0	1·0	1·0	1·0	1·0
After stretching						
2·11	1·0	1·56	1·26	1·0	1·65	1·54

These figures are instructive as showing that with the exception of the two intervals AB and GH which were not allowed to stretch at all, each of the other intervals has enlarged at a rate of its own. The head and the interval HJ have grown at a rate considerably faster than that

of the fish as a whole, whereas BC has grown at approximately the same rate as the fish as a whole, while FG has increased at a much slower rate than these others.

So far, however, growth has only been carried far enough to bring the first dorsal ray above the pelvics, but it has already been shown at an earlier stage that the first dorsal ray travels still farther forward and the pelvics backward, before metamorphosis is complete. Let the model, therefore, be further stretched until its total length is 119·5 units. The lengths of the body-intervals will then be :—

AB	BC	FG	GH	HJ	Total length of model.
49	70·5	54·9	30·5	34·1	119·5

Now, for the reason which will presently become clear, the above intervals will be expressed as proportions, not of 119·5 but of $\frac{119{\cdot}5}{1{\cdot}0-0{\cdot}22}$ or 153·5 :—

AB	BC	FG	GH	HJ
·32	·46	·358	·199	·223

Referring back to Table III on page 739, it is seen that when the head comprises ·22 of the body-length L_B, the proportions of the body-intervals vary but little from those given. Thus, by stretching the model to a length of 119·5 units, approximately correct results for a fish whose head comprises ·22 L_B are arrived at. The proportions of GH and HJ are admittedly not entirely accurate, but this is not surprising when it is remembered that by this time the broader features of metamorphosis are practically completed, and the fish is settling down to growth as an adolescent.

It must now be emphasised that the whole of the above considerations have been made possible by arranging that two parts of the model, viz., AB and GH, shall remain at a constant absolute length under all circumstances of stretching. This postulates that in the process of metamorphosis, *the distance from the back of the brain to the first dorsal ray, and the interval between the pelvics and the anus, remain unaltered in absolute length.* Certain it is that if this hypothesis is used in the manner indicated above, reasonably accurate representations of successive phases of metamorphosis can be produced by a simple model. Conceivably these intervals may actually alter slightly in length as the fish grows and differentiates, but the increases cannot be anything approaching those made by other intervals, so that the assumption that there is no change in length is sufficiently accurate for practical purposes.

This conclusion may serve to dispel a possible inclination on the part of the reader to criticise the foregoing paragraphs as a laborious consideration of highly theoretical models composed of tape and elastic, rather than as the presentation of precise data concerning the condition of actual fishes during their transition from larva to adolescent. It is easily realised that if the models lead to a correct understanding of the growth processes during metamorphosis, then it at once becomes possible for workers to foresee the effects of a change of circumstances upon the progress of transition. *Any circumstance which will affect the relative proportions of the initial body-intervals of the larva, or the number of vertebræ, or which at any subsequent stage of metamorphosis will influence the rate of growth of the body-intervals, must inevitably be reflected in the morphological character of the end-result, which in this case is the adolescent fish.* The next section of this paper has to deal with this highly important side of herring investigations, and it will then become apparent how helpful the observations described above can be.

Changes with Time of Sampling.

It has already been pointed out that in a time-series of samples of metamorphosing herrings taken at Plymouth, the length of the fish at which any given phase of transition is reached varies over a wide range, and that there is much overlap in length-range from phase to phase. It is of the greatest practical importance to discover the significance of these differences. Only when this is properly appreciated can we hope correctly to use available biometric data in identifying local forms and races of herrings.

In an endeavour to present an orderly account on this important section of the work, I have found it convenient first to deal with the actual changes in length with time ; next with coincident changes in the average number of vertebræ ; and, finally, to discuss the results in general.

Changes in Length.

As the process of transformation from larva to adolescent herring is one of continuous alteration rather than of abrupt transformation, it is necessary to decide arbitrarily upon convenient criteria of stage of metamorphosis. In the present instance the method is to define the stages according to the positions of the fins and anus with respect to vertebræ. One might equally well adopt as a criterion the degree of development of other characters such as the keeled scales, the general body-scales, or the scheme of pigmentation, or even a combination of such characters. But as data on the relative positions of fins and anus have already been used in the study of the normal process of meta-

morphosis, they may be made to serve here. There is one possible disadvantage in so doing, however, and that is, one must take into account the total number of vertebræ, for, as has already been shown, the relative positions of the fins and anus are dependent upon this factor. This necessitates the statistical treatment of data under separate vertebræ-classes.

On a number of occasions during the months of April and May, 1928, fifty specimens of each of four body-length groups were stained in alizarin, and the position of the fins and anus with respect to vertebræ noted. In Table IV the data on the position of the pelvics in the fishes with a total of 56 vertebræ are summarised :—

TABLE IV

Position of Pelvics with Respect to Vertebræ in Fishes with 56 Vertebræ.

Date 1928	Body-length group (mm.).	Serial No. of vertebra under which pelvics lie.						Total No. of specimens.
		24	25	26	27	28	29	
April 5	30	3·5*	15·5	2·0	–	–	–	21
,, 19	,,	2·5	19·0	10·0	0·5	–	–	32
May 1	,,	1·0	17·0	9·0	–	–	–	27
,, 8	,,	–	10·0	20·5	0·5	–	–	31
,, 18	,,	–	2·5	23·5	7·0	–	–	33
,, 30	,,	–	–	9·5	19·5	2·0	–	31
April 5	35	1·0	14·0	9·5	0·5	–	–	25
,, 19	,,	0·5	1·5	14·5	9·5	–	–	26
May 1	,,	–	6·5	20·0	4·5	–	–	31
,, 8	,,	–	1·5	24·0	10·0	0·5	–	36
,, 18	,,	–	–	11·5	23·5	2·0	–	37
,, 30	,,	–	–	0·5	23·0	10·0	0·5	34
April 19	40	–	–	3·0	8·0	–	–	11
May 1	,,	–	–	8·0	23·5	1·5	–	33
,, 8	,,	–	–	1·5	16·5	10·0	1·0	29
,, 18	,,	–	–	–	15·0	14·5	0·5	34
,, 30	,,	–	–	–	5·5	19·0	2·5	27
May 8	45	–	–	–	3·0	23·5	3·5	30
,, 18	,,	–	–	–	2·0	23·5	1·5	27
,, 30	,,	–	–	–	1·5	21·0	7·5	30

The data of the above table are shown graphically in Figure 12. It will be noticed that in each body-length group, the position of the pelvics tends to fall under a later vertebra in the series as date of sampling gets later. Thus in the 30 mm. body-length group the pelvics on average lie beneath the 25th vertebra on April 5th, but under the 26th and even

* An entry of 0·5 was made when pelvics were below junction of two adjacent vertebræ.

TABLE V. NUMBER OF FISH AT FOLLOWING STAGES OF DEVELOPMENT.

Date 1928.	Body-length group. (mm.)	Total No. of Fish in sample.	Pelvics in front of First Dorsal Ray (D^1) by :—							Pelvics beneath (D^1) O	Pelvics behind First Dorsal Ray (D^1) by :—			
			$6\frac{1}{2}$ vert.	6 or $5\frac{1}{2}$ vert.	5 or $4\frac{1}{2}$ vert.	4 or $3\frac{1}{2}$ vert.	3 or $2\frac{1}{2}$ vert.	2 or $1\frac{1}{2}$ vert.	1 or $\frac{1}{2}$ vert.		$\frac{1}{2}$ or 1 vert.	$1\frac{1}{2}$ or 2 vert.	$2\frac{1}{2}$ or 3 vert.	$3\frac{1}{2}$ or 4 vert.
April 5		50	6	28	16	–	–	–	–	–	–	–	–	
April 19		51	–	8	20	15	7	1	–	–	–	–	–	–
May 1	30	52	–	7	14	22	6	1	2	–	–	–	–	–
May 8		50	–	4	14	20	12	–	–	–	–	–	–	–
May 18		46	–	–	3	2	15	21	4	1	–	–	–	–
May 30		50	–	–	1	1	–	7	7	16	13	5	1	–
April 5		50	–	3	18	26	3	–	–	–	–	–	–	–
April 19		51	–	1	2	10	13	10	10	4	1	–	–	–
May 1	35	51	–	–	1	13	17	12	4	4	–	–	–	–
May 8		49	–	–	–	7	19	15	2	4	2	–	–	–
May 18		50	–	–	–	–	–	5	19	13	12	1	–	
May 30		51	–	–	–	–	–	–	–	5	16	19	11	–
April 19		15	–	–	–	–	–	1	3	7	4	–	–	–
May 1		51	–	–	–	–	–	4	6	18	16	7	–	–
May 8	40	50	–	–	–	–	–	–	1	9	17	21	2	–
May 18		51	–	–	–	–	–	–	–	–	9	28	14	–
May 30		54	–	–	–	–	–	–	–	–	–	19	29	6
May 8		51	–	–	–	–	–	–	–	–	1	25	25	–
May 18	45	50	–	–	–	–	–	–	–	–	–	21	28	1
May 30		52	–	–	–	–	–	–	–	–	–	12	35	5

the 27th towards the end of May. It is also seen that the fishes of the 30 mm. body-length group taken on May 30th are, so far as the position of the pelvics is concerned, practically as far advanced as those of the 40-mm. group on April 19th.

This change in position of the pelvics with time is accompanied by corresponding changes in position of the dorsal fin and anus, as well as by changes in pigmentation and degree of development of the scales. Furthermore, similar results are obtained when the data for fishes having a total of 55 or 57 vertebræ are used instead of those of fishes with 56 vertebræ. Clearly, then, it may be said that the later the sample is taken the more advanced in metamorphosis are the individuals of any given body-length group, and in order further to impress this fact, Table V has been prepared showing the number of fishes in each of a series of classes according to the position of the first dorsal ray (D^1) relative to the pelvics.

Using the 30 mm. body-length group as an example, it is seen that the specimens taken on April 5th are all relatively early transition stages in which the pelvics are at least $4\frac{1}{2}$ vertebræ in front of the first dorsal ray (D^1), whereas those of May

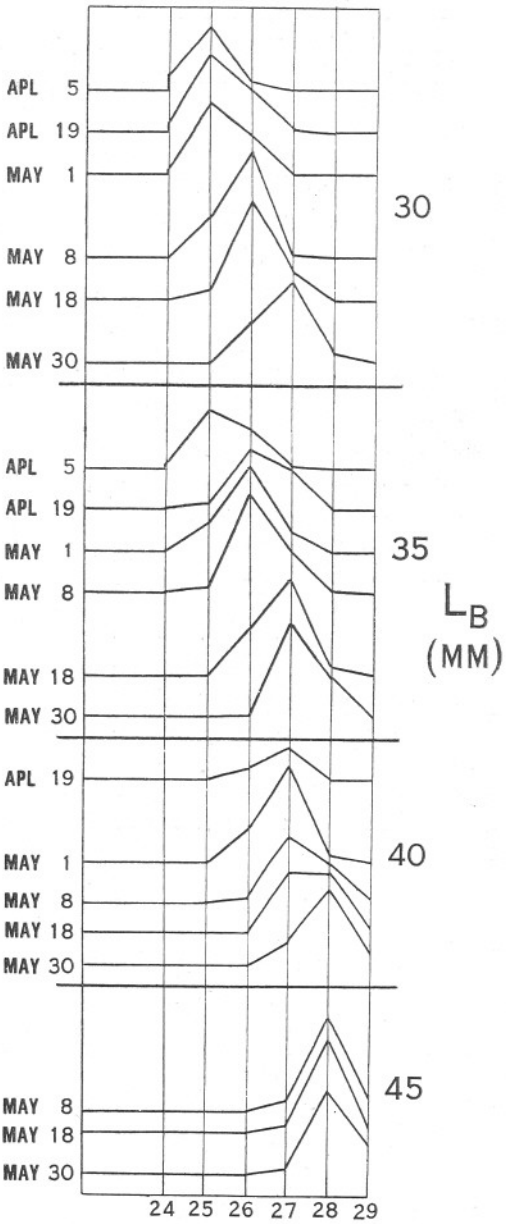


FIG. 12.—Graphic representation of data given in Table IV on page 745.

30th are much more advanced stages in which the pelvics are on average immediately beneath D[1].

Stating the matter in another way, it may be said that for any stage of metamorphosis the length in later samples is shorter than that in earlier ones. This may be illustrated by extracting the data from Table V relative to the stage when the pelvics lie beneath the first dorsal ray :—

Date 1928.	Body-length Groups (mm.). 30	35	40
April 19	–	4	7
May 1	–	4	18
,, 8	–	4	9
,, 18	1	13	–
,, 30	16	5	–

Thus, on April 19th and May 1st, this stage of development was not reached until a length of 40 mm. had been attained ; on May 18th specimens of 35 mm. were at this stage, and on May 30th, those of the 30 mm. group. Similar data could, if necessary, be produced to show that during the months of May and June of the year 1929, this phenomenon was again apparent, so that it may be regarded as a frequent and probably normal occurrence.

Change in the Average Number of Vertebræ.

It has been shown above that the individuals of a given length-group are more advanced in metamorphosis in later samples than in earlier ones. It is instructive next to consider the value of the average number of vertebræ in the same fishes. In Table VI relevant data are shown for individuals of the 30-mm. and 35-mm. groups :—

TABLE VI.

Body-length group (mm.).	No. of Vertebræ	Date of Sample (1928) April 5	April 19	May 1	May 8	May 18	May 30
30	54	–	1	1	–	–	–
	55	26	15	17	13	7	14
	56	21	32	27	31	33	30
	57	3	3	5	6	5	2
	Average	*55·54*	*55·73*	*55·72*	*55·86*	*55·95*	*55·74*
35	54	2	1	–	–	–	–
	55	15	17	16	9	7	14
	56	25	26	31	36	37	34
	57	7	4	3	3	6	1
	58	–	1	–	–	–	–
	Average	*55·73*	*55·735*	*55·74*	*55·86*	*55·98*	*55·735*

The data show that the average number of vertebræ does not remain constant throughout the series of samples; on the contrary, there is a definite tendency for it to rise as the sampling is later.

A number of instances might be given which would show that within the same day's sampling, the average number of vertebræ changes with the body-length group. The following two cases are worthy of mention because they demonstrate to a marked degree how the average may change :—

Date of Sample.	No. of Vertebræ	Body-length Group (mm.). 30	35	40	45	50	55	60	65
	55	1	2	10	17	–	–	–	–
May 26th,	56	28	30	31	28	–	–	–	–
1927	57	21	17	8	5	–	–	–	–
	58	1	1	1	–	–	–	–	–
	Average	*56·44*	*56·34*	*56·00*	*55·76*				
	54	–	–	–	–	–	–	1	1
June 25th,	55	–	–	–	–	7	9	18	16
1928	56	–	–	–	–	40	35	27	28
	57	–	–	–	–	3	6	4	5
	Average					*55·92*	*55·94*	*55·68*	*55·74*

One particular point of interest is plainly demonstrated by the data for May 26th, 1927. It will be noticed that the average number of vertebræ for the individuals of the 30-mm. group is the highest and that for the 45-mm. group the lowest. It should also be noted that the fishes of the 30-mm. group are the least advanced in development, and those of the 45-mm. group almost completely metamorphosed. Thus, *within the same sample*, a lower average number of vertebræ coincides with a more advanced stage of metamorphosis.

Significance of Results in "Racial Investigations."

It is hardly necessary to point out that the observations described above raise questions of great significance to herring biologists engaged in what have come to be known as "racial investigations." Why should the length at any given phase of metamorphosis tend to decrease as the time of sampling gets later? Why, simultaneously, should the average number of vertebræ tend to rise? To what extent are these facts due to differences between the adult fishes which produced the larvæ, and how much is due to the variation in physical conditions under which the eggs were incubated and the larvæ developed? On his answers to these questions will depend an investigator's interpretation of those significant differences which he frequently observes between random samples of herrings. In the opinion of the present writer we cannot confidently assess the significance of these differences until we know from actual

experiment the extent to which the biometric characters of a new generation may differ from those of their parents as the result of the physical conditions under which development takes place. Thus, in the present instance, who can say whether the diminishing length of a given phase of metamorphosis and the simultaneous increase in average number of vertebræ was due more to the fact that the larvæ had sprung from different parent-stocks, than, say, to the effects of contemporary changes of temperature over the area during the season of incubation and development of the larvæ ? Past work has certainly shown that the spawning shoals visiting Plymouth waters are by no means uniform in morphological character ; but it is equally true that the temperature undergoes marked change, falling first to a minimum and then gradually rising again. Larvæ incubated and developed at a relatively low temperature might be expected to require a longer time than those reared at a higher temperature to reach a certain stage ; the size at which this stage is reached would probably be larger.*

In addition, there is some reason for supposing that at the lower temperature, the number of vertebræ would tend to be higher. Such expectations, if applied to the particular local circumstances, will produce results which fit the observed facts quite as reasonably as the hypothesis of purely hereditary influences. But in the absence of relevant knowledge, it is impossible to say how much either has played in producing the end-result. In general, therefore, although quite real biometric differences are observable between random samples of herrings, their interpretation is still open to question and will remain so until experimental work has yielded that fundamental knowledge which alone can render interpretation possible.

LITERATURE CITED.

1. FAGE, L. Engraulidæ, Clupeidæ. Report on the Danish Oceanographical Expeditions, 1908–10, to the Mediterranean and adjacent Seas. Vol. II, Biology, A.9, 1920.

2. FORD, E. Herring Investigations at Plymouth. I. Methods of Collection and Treatment of Data. Journ. Mar. Biol, Assoc., N.S., Vol. XV, No. 1, 1928.

* Gray (**4**, p. 129), for example, has shown experimentally that when trout eggs are incubated at low temperatures the embryos at the moment of hatching are significantly larger than those hatching from eggs which have been incubated at higher temperatures. Increasing the temperature of incubation increases the growth-rate of the embryo, but, at the end of larval life, the full-time embryo is smaller than after slower development at a lower temperature. At higher temperatures, a larger proportion of the available yolk is required for the maintenance of the embryo, leaving a smaller proportion available for the formation of new tissue.

3. Ford, E. Herring Investigations at Plymouth. IV. The Growth of Young Herrings in the Neighbourhood of Plymouth. Journ. Mar. Biol. Assoc., N.S., Vol. XV, No. 1, 1928.

4. Gray, J. The Growth of Fish. III. The Effect of Temperature on the Development of the Eggs of *Salmo fario*. British Journ. Exp. Biol., Vol. VI, No. 2, 1928.

5. Lebour, M. V. The Larval and Post-Larval Stages of the Pilchard, Sprat and Herring from Plymouth District. Journ. Mar. Biol. Assoc., N.S., Vol. XII, No. 3, 1921.

6. Percival, E. A Report on the Fauna of the Estuaries of the River Tamar and the River Lynher. Journ. Mar. Biol. Assoc., N.S., Vol. XVI, No. 1, 1929.

TABLE VII.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Total No. of verte-bræ.	Position of 1st Dorsal Ray (D^1). No. of Specimens in which D^1 lies above vertebræ as under. 24	25	26	27	28	29	30	31	Totals.	Position of D^1. Working means.*
24		–	–	–	–	1	3	9	1	14	29·21*
24–25		–	–	–	–	–	4½	9	1½	15	29·10
25		–	–	–	–	7	20	17	4	48	28·87
25–26		–	–	–	1	4½	8	2½	–	16	28·25
26		–	1½	6	13	17	12½	1	–	51	27·21
26–27	55	–	1½	7½	5½	3½	1	–	–	19	26·24
27		1	33½	16	7½	–	–	–	–	58	25·02
27–28		1½	12	8	½	–	–	–	–	22	24·84
28		3½	37	24½	–	–	–	–	–	65	24·82
28–29		–	5	3	–	–	–	–	–	8	24·87
29		–	–	3	–	–	–	–	–	3	25·5
Totals		6	90½	68	27½	33	49	38½	6½	319	
24–25		–	–	–	–	–	–	–	1	1	30·5
25		–	–	–	–	–	3	4	4	11	29·75
25–26		–	–	–	–	–	–	3½	4½	8	30·06
26		–	–	–	–	2½	5	8	1½	17	29·0
26–27		–	–	–	–	½	½	2	–	3	29·0
27	57	½	1½	11½	14½	3	2	1	–	34	26·32
27–28		–	½	4½	5	3	1	–	–	14	26·46
28		–	9½	23	9½	½	½	–	–	43	25·56
28–29		–	–	6	–	–	–	–	–	6	25·5
29		–	½	3	2½	–	–	–	–	6	25·83
29–30		–	1	–	–	–	–	–	–	1	24·5
Totals		½	13	48	31½	9½	12	18½	11	144	

* For statistical purposes, the middle point of the 30th vertebra is regarded as point 29·5.

TABLE VIII.

Position of Pelvics. No. of specimens in which pelvics lie beneath vertebræ as under.	Total No. of vertebræ.	Position of Anus. No. of Specimens in which Anus lies beneath vertebræ as under. 41	42	43	44	45	46	Totals.	Position of Anus. Working means.*
24		–	1	2½	8½	1	–	13	43·23*
24–25		–	1	6	6	1	–	14	43·0
25		–	11	21½	12	2½	–	47	42·63
25–26		–	7½	6½	2	–	–	16	42·16
26		8	30	11	2	–	–	51	41·64
26–27	55	4½	8½	5½	½	–	–	19	41·61
27		10½	44	5½	–	–		60	41·42
27–28		2½	15½	4	–	–	–	22	41·57
28		3½	46½	14	–	–	–	64	41·66
28–29		–	5	3	–	–	–	8	41·87
29		–	½	2½	–	–	–	3	42·33
Totals		29	170½	82	31	4½		317	
24–25		–	–	–	–	1	–	1	44·5
25		–	–	½	7	2	½	10	43·75
25–26		–	–	–	5	4½	½	10	44·05
26		–	½	4	11	1½	–	17	43·29
26–27	57	–	–	1	1	1	–	3	43·5
27		–	4½	22½	5½	1½	–	34	42·62
27–28		–	4	9½	2½	–	–	16	42·41
28		–	6½	32½	4	–	–	43	42·44
28–29		–	–	5	1	–	–	6	42·67
29		–	–	4½	1½	–	–	6	42·75
29–30		–	–	½	½	–	–	1	43·0
Totals		–	15½	80	39	11½	1	147	

* For statistical purposes, the middle point of the 44th vertebra is regarded as point 43·5.

On the Occurrence and Habits of the Siphonophore, *Stephanomia bijuga* (Delle Chiaje).

By

N. J. Berrill,

Department of Zoology, M'Gill University, Montreal.

With One Figure in the Text.

According to E. T. Browne, 1899, *Stephanomia bijuga* (Delle Chiaje) (syn. *Cupulita sarsii* Haeckel and *Agalmopsis elegans* Sars, partim) belongs to the surface Atlantic fauna. It has been recorded at Valencia from March to November, and while suffering badly from the destructive power of gales it must occur at times in enormous numbers, for in November, 1898, tow-nets were taken that were full of isolated pneumatophores. Into the more confined waters of the English Channel, however, it penetrates apparently very rarely, the only record being that of a single specimen taken a mile or two out from Plymouth Sound in March, 1902.

It is of some interest, therefore, to record its occurrence in great numbers in the main and secondary channels of the Salcombe Estuary, even to the heads of the tidal creeks, on May 17–19, 1929. This profusion coincided with a similar abundance of the three Ctenophores commonly occurring in these waters, namely, *Beroe cucumis* Fabricius, *Bolina infundibulum* Fabricius, and *Pleurobrachia pileus* Fabricius, and not only were these abundant, but they also had reached what is possibly their maximum size. Individuals of Beroe frequently were seen of at least six inches in length. Ten days later all trace of Siphonophores and Ctenophores had vanished, with the exception of some small individuals of Beroe, and these last were not seen to approach the large size already mentioned until after two months.

Stephanomia was noticed floating and swimming a few inches below the surface of very calm water, though all that was visible was the red pigment of the gastrozoids, but as several individuals were obtained in perfect condition and were kept alive in glass vessels for some days, a description of its form and behaviour may be of some interest. Unfortunately no microscope or lens was available, so that only the coarser details were observed.

The general form is seen in Figure 1 A, which is typical of the great

majority of the individuals encountered, i.e. two to three inches in length and with three or four sets of nectophores ; but apart from the details shown in the figure, the observations more concerned the habits than the anatomy.

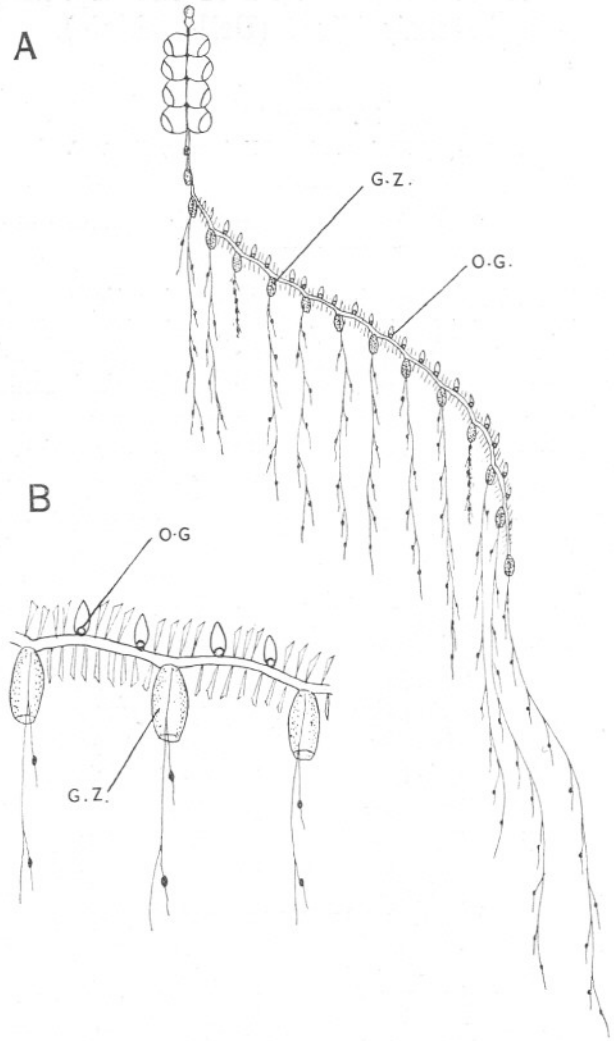


FIG. 1.

Unless disturbed, Stephanomia apparently remains perfectly quiescent, and in an inclined position. The pneumatophore causes the whole organism to float to the top of still water, and that part of the stem bearing the nectophores hangs vertically below it, but the rest of the

stem falls away from the basal nectophores at an angle of about forty-five degrees. The reason for this seems obvious, for in this position the long contractile filaments hang separately, vertically, and evenly spaced, whereas if the whole organism assumed a vertical position in the quiescent state the filaments would hang down together as one cluster, with a relatively small volume of water with its contained organisms exposed to their influence.

The result, therefore, of the inclined position is to form, in effect, a very efficient trap for small actively moving organisms such as copepods. Undisturbed, the Stephanomia drifts placidly with the current and consequently small active forms are in constant danger of swimming into the grating of filaments as herring are into a drift-net. Contact of any small particle with a single filament or tentacle causes the instantaneous contraction of the latter towards its associated gastrozoid. Stronger stimulation of one or more filaments not only results in their contraction, but also that of the stem itself up to the base of the nectophores. Usually such stimulation also affects the nectophores so that the organism moves actively away. Sometimes, however, the swimming movements seem to start spontaneously, and an individual suddenly swims through the water at about 8 cm. per second, setting into motion also any with which it may collide. At 16° C., to produce the above movement, the nectophores contract simultaneously about four times per second.

The characteristic inclined position when quiescent is apparently due to the presence of an oil-globule in two persons, that may be modified bracts, occurring between every pair of gastrozoids, as is shown in Figure 1 B. Typical bracts are numerous on all sides of the stem between the gastrozoids, but the forms containing an oil-globule are to be found only on its upper side, opposite to that bearing the gastrozoids themselves.

REFERENCES.

ALLEN, E. J., and TODD, R. A. 1903. Fauna of the Salcombe Estuary. Jour. Mar. Biol. Assoc., N.S., Vol. 6.

BROWNE, E. T. 1899. Fauna and Flora of Valencia Harbour, Ireland. Proc. R. Irish Acad., Vol. 21 (Ser. 3, Vol. 5), p. 667.

HAECKEL, E. 1888. Report on the Siphonophora. Rep. Voy. Challenger Zool., Vol. 28, p. 234.

SARS, O. 1846. Fauna Littoralis Norvegiæ. Vol. 5, Pt. 1, p. 32.

An Apparatus for Keeping Marine Organisms Under Circulation in Narrow Observational Tanks.

By
A. J. Grove, M.A., D.Sc.

With 1 Figure in the Text.

THIS apparatus was elaborated during some preliminary observations on the biology of the polychæte worm *Melinna adriatica*, and in view of its possibilities for facilitating observations on other small marine organisms, an account of it seems desirable.

Tanks sufficiently narrow to enable the worms in their long slender tubes to remain in position near to the sides in order that the organism might be observed with a hand lens or binocular microscope, were made from two sheets of glass separated by a piece of rubber tubing bent into an arc, and the whole clipped tightly together by means of six spring washing pegs. By the use of tubing of different thicknesses, tanks of different widths can be made according to the material used and type of observation desired. A simple support for the tank was made from a block of wood in which were bored two holes to hold the lower clips. In practice, such tanks were found to be practically water-tight, but to protect the bench it was found convenient to place the block in a shallow tray.

Such tanks enabled the worms to be kept under close observation, but owing to their narrowness the quantity of water contained in them was small, and for extended observational work it was desirable that a circulation of freshly aerated water should be established. This was effected by a modification of the circulating system for aquaria previously described (Cannon and Grove, 1927), and the arrangement is seen in Figure 1.

The tank A is connected by siphons to a jar B on one side, and a shallow vessel C on the other. The ends of the siphons dipping into the tank have to be drawn out because of the narrowness of the tank. One should dip lower into the tank than the other. Jar B* is connected by a wide siphon with the circulating jar in which is suspended the air-blast tube, the drawn-out, turned-up end of which enters the circulating tube which passes

* Jar B is not absolutely essential. The siphon from the tank could pass directly into the circulating jar, but the insertion of the jar between the tank and the circulating jar was found convenient during manipulation, and, as mentioned later, if other tanks are inserted in the circulation.

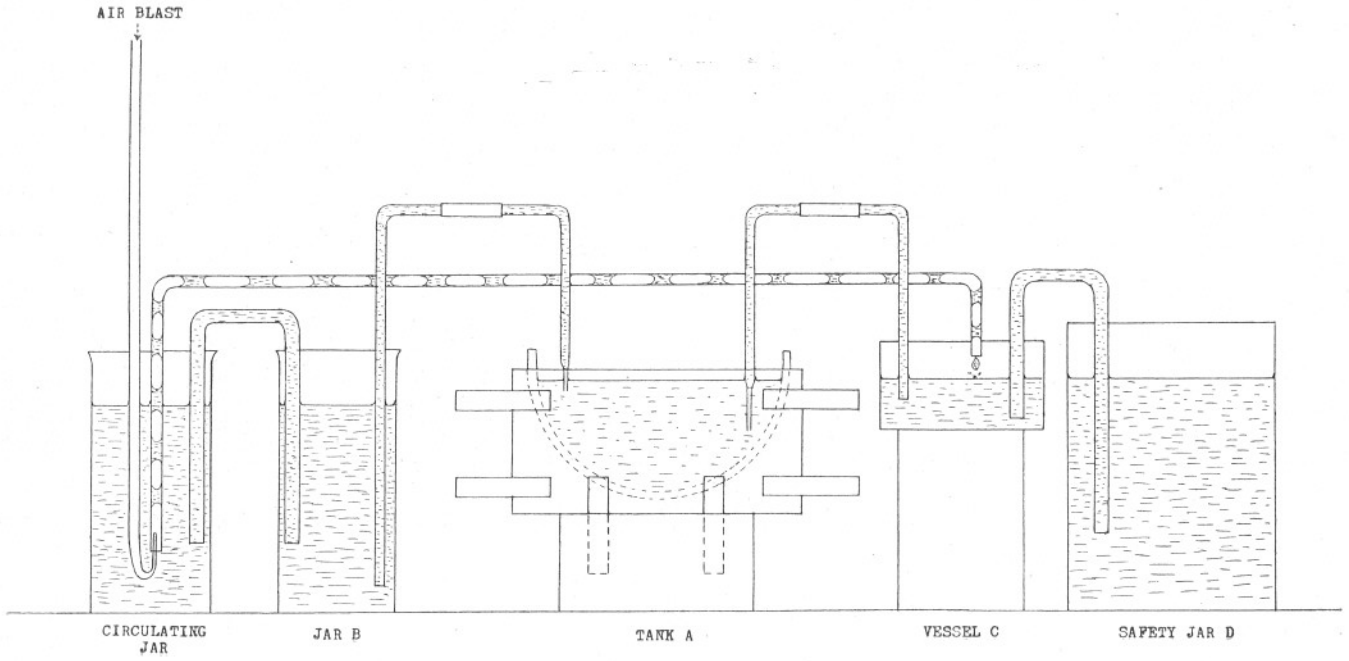


FIG. 1.

thence to vessel C. When the air blast is turned on, a stream of bubbles of air and water pass along from the circulating jar to the vessel C. This tends to lower the level of the water in the circulating jar, to compensate for which water is drawn from jar B through the tank A from vessel C, establishing a circulation. Because, however, of the fineness of the drawn-out ends of the siphons dipping into the tank, the flow of water through the tank to the circulating jar is slower than that from the circulating jar to vessel C by way of the circulating tube. There is therefore a tendency for vessel C to overflow and a big difference of level of water to be established between vessel C and the circulating jar. This difficulty was overcome by connecting vessel C by means of a siphon with a wide jar D. Then, a considerable quantity of water would have to be carried over by the circulating tube before the level in C and D would be raised sufficiently for flooding to occur.

With the apparatus arranged in this way, after the circulation has been running for a short time, an equilibrium is set up so that a difference of level (depending on the rate of flow in the circulating tube and the size of the narrow ends of the tank siphons) is maintained between the vessel C and jar B, giving an indication of the rate of flow of water through the tank.

The following points were found to require attention in order that the apparatus may work efficiently. The drawn-out ends of the tank siphons should be made carefully to fit into the tank, and it is essential that the inflow siphon should be wider than the outflow, otherwise the tank is apt to be emptied to the level of the outflow siphon because water cannot enter from the inflow sufficiently rapidly. In the apparatus used, the inflow siphon was the lower one, because a flow of water along the surface of the mud in the tank without it being stirred up was desired. The reverse arrangement would work equally well. It will be found convenient for manipulation if the tank siphons are made in two pieces joined together by rubber tubing. This is a convenience when placing them in position, for after filling, a siphon can be maintained full of water by pinching the rubber tubing and the two ends are free to be inserted into the tank or jar as the case may be.

The vessel C should be of convenient size (a finger bowl was actually used) so that there is as much surface as possible while the shallowness will ensure that only freshly aerated water passes into the tank. If a deeper jar is used there is some danger of stagnation in the lower part of the jar.

In the first trials the tank was made of ordinary glass, but from various observations it was found that the worms were in all probability negatively phototropic and the simplicity of construction of the tanks enabled a number of tentative experiments to be carried out on the use of coloured

lights, for, by using glass of different colours for the sides of the tank, the activities of the animals under these varying conditions could be tested until the most suitable was found.

The figure gives the arrangement for one tank, but if it is so desired (as in parallel phototropic experiments with different coloured glasses), other tanks can be inserted into the circulation. It is essential, of course, that for each tank the inflow siphon should come direct from vessel C, the outflow passing into a convenient jar which is in siphonal connection with B.

The air blast for the circulation was taken in the original experiments from the Laboratory system, but where such is not available, the simply made pump described previously (Cannon and Grove, 1927) can be substituted.

If the observations are to extend over a lengthy period, it may be necessary to change the water in the safety jar D occasionally, for it is obvious that when the apparatus is running continuously and the equilibrium has become established, the water in this jar does not enter into the circulation, and is consequently likely to become foul.

REFERENCE.

CANNON, H. G., and GROVE, A. J. (1927). An Aerating and Circulating Apparatus for Aquaria and General Use. Journ. Roy. Micro. Soc., Vol. XLVII, pp. 319–322.

Preliminary Notes on the Bionomics of the Amphipod, *Corophium volutator* Pallas.

By

T. J. Hart, B.Sc.

With 4 Figures in the Text.

Introduction and Previous Work.

The Amphipod *Corophium volutator* Pallas has been described, mainly from a purely systematic standpoint, under the synonyms *C. grossipes* Linnæus, *C. longicorne* Latreille, and *C. bicaudatum* Linneo (Della Valle). Stebbing in his standard work (**19**) on the Gammaridea, accepts *volutator* as the earliest, and modern French and Danish authors follow him.

Corophium volutator is found in the greatest abundance on certain mudflats in estuarine areas round the coasts of N.W. Europe, but by no means everywhere. It appears that the nature of the substratum and the salinity of the water are two of the main factors leading to its localized distribution, and accordingly an investigation of the conditions which define its habitat is likely to throw light on some very interesting problems. These notes record the first stages of such an investigation, together with a study of the intimately related problems of the feeding habits and life-cycle of the animal.

It seems that no detailed account of the feeding mechanism of any Amphipod has yet been published; though Hunt (**11**) gives a short and pithy description of a "filter-feeding" mechanism in Ampelisca. This author classes most of the Amphipoda he deals with as selective deposit feeders, but states that though this is true in so far as they are bottom-living forms, the actual mechanism is probably more often of a type such as would lead to their being classed under his scheme as suspension-feeders. However, it seems obvious from a study of their appendages that some Amphipoda do not possess a filtering mechanism, while it is highly probable that many more combine the habit of feeding on larger particles with filter feeding, as Cannon has found in several of the lower Malacostraca.

Corophium volutator approaches this last type, though, as would be expected from its peculiar habitat, the feeding methods are somewhat specialised and probably differ in detail from those of Amphipoda generally.

As regards the life-cycle, Blegvad (**3**) in his exhaustive study of *Gammarus locusta* from this standpoint has summarised the scanty observations of previous workers. He gives good reasons for supposing that a life-cycle of a certain type is common to a number of littoral Amphipoda of widely different genera. Several broods are hatched each year, the last brood maturing slowly through the winter and commencing to breed in the following spring. Most of the adult individuals of the previous year die off during the winter, but a few breed again in the late winter and early spring. These species are thus annual or nearly so.

While my material has so far been insufficient for the results to be conclusive, they seem to show a life-cycle of an essentially similar type for *Corophium volutator*.

Sexton's wonderful work on the moulting and growth stages of Gammarus (**16**) furnishes the only exact information on these points in the whole of Amphipod literature. Her method is to isolate the just hatched young and collect all the moults from that stage onwards *from one individual*. Thus this method applies only to animals reared under aquarium conditions. *Corophium volutator* does not, like *Gammarus chevreuxi* Sexton, breed all the year round (not, at any rate, in the North), and, as most of my work was done perforce during the winter, I could not, most unfortunately, follow it up on these lines. Enough has been gathered from detailed observations of material obtained at different times of the year, to anticipate most interesting and important results from an investigation of Corophium by this method.

The bulk of this work having been presented as a degree thesis at the University of Leeds, I have to thank Prof. Garstang for permission to publish, also for suggesting the work in the first instance, and for help and encouragement throughout. Through the kindness of Dr. Allen, I was able to carry on the work at the Marine Biological Laboratory at Plymouth for three weeks during April, 1929, and so was able to study Corophium from a widely different locality. I have to thank several members of the staff, in particular Mrs. Sexton, Dr. Orton, and Mr. Ford, for much valuable advice and encouragement, and would like in conclusion to pay tribute to the entire working staff for the great kindness with which I was received.

Material and Methods.

The bulk of the material on which these observations are based was obtained from Whitby harbour. In April, when working at the Plymouth Laboratory, a few Corophium were obtained from the mud-flat between Ditchend and Southpool lake in the Salcombe estuary, and a fairly abundant material from the Cornish bank of the River Tamar, ½ mile below Calstock, where the dilution is considerable.

In August, 1929, a rich material of Corophium was found in some of the tidal creeks around Blakeney Point, Norfolk, one batch in distinctly brackish water. Unfortunately I have not yet been able to work up this material in detail, but some information gained has been incorporated in this note.

At Whitby, on the W. side of the low-water channel above the bridge, opposite the L. & N.E.R. goods yard, there is a wide expanse of moderately soft, uniform, grey mud, traversed by but few small runnels, and uncovered at about half-tide. In this mud *Corophium volutator* forms the dominant species of the animal community. In bright sunny weather Corophium could be found crawling freely over the surface, and could easily be collected in large numbers. It soon became apparent that only the larger individuals were being captured in this way, and accordingly an attempt was made to devise a simple method of collecting fairly large numbers which, if not giving a really true index of the density of population, at any rate seemed to ensure a fair proportion of the smaller individuals being caught. The procedure was as follows :—

The mud over an area of 1 sq. metre was scooped up to a depth of about 5 in. (about the maximum depth of Corophium burrows) and passed through a wire sieve of 1 sq. mm. mesh. The Corophium left amongst the larger detritus were then picked out with forceps. Even so it was found that comparatively few of the smaller free-living young were caught, but it was impossible to use a smaller mesh, as the work was thereby rendered so slow that even 1 sq. m. of mud could not be worked in one intertidal period. Accordingly 500 c.c. samples of mud were taken and sieved out at leisure in the laboratory, thus affording a rough indication of the numbers of young present.

In attempting further to elucidate the nature of the life-cycle, living Corophium, caught in October, were successfully kept in an aerated tank, supplied with mud, sea-water, and a circulating apparatus in the laboratory at Leeds for a considerable period, but the animal does not seem to breed in winter, not, at any rate, in the North, and unfortunately during the great frost of February, 1929, the heating was kept on day and night and the animals incontinently perished.

I was therefore forced to rely largely upon measurement investigations of the type evolved by Blegvad (**3**) in his great work on the Biology of *Gammarus locusta*. As I was only able to make four quantitative collections from Whitby : in July, October, and December, 1928, and March, 1929, these measurements can hardly be considered really critical. A further sample, very kindly sent to me by Mr. George Duke of Robin Hood's Bay on April 13th, helped to strengthen the argument considerably, and in conjunction with a careful examination of each specimen as it was measured, a life-cycle of a type essentially similar to that postulated

by Blegvad (*loc. cit.*) for a number of littoral Amphipoda, seemed to be disclosed. I therefore considered it worth while tabulating the results, in the hope of vindicating them by a more thorough investigation in the future.

The method of measuring employed was the same as that described by Blegvad: the animals were extended on a millimetre scale under a dissecting microscope and the length taken from telson to rostrum.

To gain an accurate idea of the nature of the substratum in which *Corophium volutator* lives, samples of mud from the different localities worked were graded and analysed for organic content by the method used by Allen (**1**) for classifying bottom-deposits.

The salinity range of the water in the natural habitat of this species must be considerable, and constantly varying. Some estimations by silver nitrate titration were made, however, with a view to comparing the probable range in the different localities. To determine the change in salinity which the animals could actually endure, small numbers were isolated under different conditions, with a small amount of mud from their natural habitat.

To ascertain the nature of the food, small numbers of living Corophium were kept under various conditions in finger bowls and small dishes, aerated with a pipette at definite intervals. Strips of Ulva, Enteromorpha, and decaying deciduous leaves were tried as food, but without success, as it appears that the animals feed on smaller particles of organic detritus. When mud from the natural habitat was supplied, small winter-caught Corophium could be kept almost indefinitely under these conditions.

The actual feeding process was observed partly by fixing the animal on its back in a capsule of sea-water with plasticine, and using a dissecting microscope, and partly by enclosing living individuals against the side of a rectangular slide-trough and observing them with binocular mounted horizontally.

To observe swimming currents, etc., suspensions of carmine and starch stained with iodine were employed.

In examining the structure of the appendages various methods were tried. Staining with acetic-alum-carmine, Bethe's old stain for chitin, and picro-nigrosin, showed the musculature and general features very beautifully, but the two last-named are difficult to control. Finally, it was found that the arrangement of spines and setæ could best be made out by comparing glycerine mounts of (*a*) fresh material; (*b*) material fixed in formalin-sea-water; and (*c*) similar material subsequently treated with alcoholic potash, a method which Hansen has recommended.

The arrangement of the mouth-parts was in part made out by dissection, and also by cutting thick sections of material embedded in

clove-oil-celloidin. This modification of Cannon's method was evolved by Mr. Dennell.

GENERAL BIOLOGY.

1. Habitat, Substratum and Salinity.

Though often occurring in great numbers, *C. volutator* has an exceedingly localised distribution. The unfortunate naturalist who is in need of specimens, and simply goes to the nearest estuarine mud-flat to find them, is likely to have a day's arduous search for nothing. With foul black mud, or Zostera, they will have nothing to do, but are to be found in certain areas of fairly soft greyish mud, when the other conditions are suitable.

A good description of a typical habitat for *C. volutator* has been given by Delage (**8**) in his work on the circulation of the Edriophthalma; he says, "Corophium is found at Roscoff, in the mud of the harbour. They are not really very abundant except in an easily defined zone a little below the level of high-water neaps. At places where the mud is rendered black by abundance of decaying organic detritus, one never finds them." Stephensen (**20**) quotes Th. Mortensen to the effect that in company with the Spionid *Pygospio elegans* Claparède, Corophium is very numerous in certain areas of sandy mud in some of the Danish Fjords where the salinity is fairly low (*ca.* 6–16°/$_{oo}$). Finally, Gurney (**10**) has described *Corophium volutator* living in colonies of the hydroid Cordylophora, when ascending far up the East Anglian rivers into regions where the salinity is very slight.

Descriptions such as sandy mud, and mud not blackened by decaying organic matter, do not give sufficient information as to composition, and Dr. Orton suggested that it would be useful to give an accurate description of the mud which *C. volutator* normally inhabits. This I have attempted to do by the methods Allen (**1**) employed for grading bottom deposits.

The mud was passed through sieves with perforated zinc bottoms, the perforations being 5, 2·5, 1, and 0·5 mm. in diameter.

The portions retained by each sieve were dried on a filter paper, and later by gentle heat. Most of the mud passed through these sieves. Of the remainder, that which settled in the washing water in one minute was collected and dried, being equivalent to the "fine-sand" grade, and the residue in the water was left for 24 hours to settle, representing Allen's "Silt." The various fractions were carefully dried and weighed, and their percentage of the total sample calculated. Only in Whitby mud were the portions retained by the sieves an appreciable fraction of the total dry weight, and there they formed barely 9%. Accordingly in describing the different muds I have termed them collectively the "coarse grades," fine sand, and silt being spoken of as "fine grades."

Having obtained the dry weight of the various grades, the organic content was found by loss in weight on bunsen ignition (R. H. Worth, in **1**). I have not yet been able to carry out investigations of the carbonate content, for which blow-pipe ignition was needed. This is unfortunate as the pH of the muds is definitely on the alkaline side, *ca.* 8·2, which is surprising in view of the high organic content. In the course of this part of the work, it became very evident that an investigation of the physical factors of muddy foreshores, as influencing the organisms living on them, of the type recently worked out by J. R. Bruce (Journ. Mar. Biol. Assoc., XV, No. 2) for sandy beaches, would prove a very interesting and probably valuable study in itself.

Samples of mud from three different localities worked, Whitby, Salcombe and Calstock, have been analysed by the above methods, and the results, together with rough values for the salinity and frequency of Corophium in the different localities, are given in Tables I, II, and III.

Corophium is most abundant at Whitby (Table I), and is, moreover, the dominant species of the animal community of the mud there. In this mud there is a certain amount of shelly gravel, small stones and coarse sand, to the extent of nearly 9% of the dry weight, though some of this is due to large organic, mainly deciduous detritus, of the remaining 91%, 56% represents fine sand and 35% silt. The total organic content is 6·32% by weight. The coarse grades contain relatively twice as much organic matter as the fine grades. The salinity range appeared to be 21·8–35‰.

At Salcombe (Table II) Corophium is very scarce and this is probably due to the fact that the mud dries off almost completely at low tide, which is never the case where Corophium is plentiful. A titration gave 35·2‰ at half-flood (Corophium level in this Estuary). The mud on the whole is very similar to the Calstock sample, though the total organic content is not so high—only 7·08% by weight. The whole character of the mud is finer than the Whitby sample, as silt exceeds fine sand here by 12%.

At Calstock (Table III) the mud is finer still, and the organic content is higher, 10·41% by weight. It is therefore improbable that the texture of the mud is responsible for the scarcity of Corophium at Salcombe, as at Calstock it is fairly plentiful, *ca.* 40 individuals per sq. m. The cause of the disparity between the populations of these two localities is to be sought for in the almost complete drying-off of the mud at Salcombe. In the case of the relative frequency at Whitby (*ca.* 150 per m. sq.) and Calstock, I have no doubt that the difference is due to the texture and general character of the mud of the two localities. The coarser Whitby mud would allow of more rapid diffusion of oxygenated water by capillarity between its particles, and the Calstock mud, with its high organic content, is verging on the blackened condition in which, as Delage long ago pointed out, one never finds Corophium. It is true that the salinity at Calstock

must be appreciably lower than at Whitby. At Calstock a titration of flood-time water indicated 22·8°/$_{oo}$ as the upper limit of the range. But Corophium from any of the three localities would withstand great dilution under laboratory conditions, and it seems probable that only the extreme limit of tidal influence would prove to be the limit of their riverward extension in nature. A factor which must also be taken into account is the rate of evaporation during the intertidal period. Some of Bruce's results

Table I.

Analyses of Mud Inhabited by *Corophium volutator*.

Whitby.—W. side Harbour, opposite L. & N.E.R. Goods Yard.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	5·39	0·49	7·75
,, 2·5 mm. ,,	0·97	0·19	3·01
,, 1 mm. ,,	1·34	0·14	2·12
,, 0·5 mm. ,,	1·11	0·07	1·12
Settled in 1 min.	56·17	1·94	30·62
,, 24 hrs.	35·04	3·49	55·38

Total organic content % by wt. *6·32*

Coarse grades, gravel, shell fragments, large vegetable detritus, 8·788%.
Fine sand and silt, 91·312%.
Organic content of coarse grades, 10·13% by wt.
Organic content of fine grades, 5·08% by wt.
Corophium dominant, over 150 per sq. m., few small.
Nereis diversicolor etc., salinity 21·8–35 (?) °/$_{oo}$.

Table II.

Salcombe. Mud-flat between Ditchend and Southpool Lake.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	0·32	0·11	1·55
,, 2·5 mm. ,,	1·10	0·29	4·09
,, 1 mm. ,,	1·10	0·37	5·32
,, 0·5 mm. ,,	0·78	0·11	1·55
Settled in 1 min.	42·15	2·44	34·46
,, 24 hrs.	54·55	3·76	53·12

Total organic content % by wt., *7·08*

Coarse grades (mainly shell fragments and vegetable detritus), 3·40%.
Fine sand and silt, 96·60% by wt.
Organic content % by wt. of coarse grades, 25·88.
Organic content % by wt. of fine grades, 6·35.
Corophium scarce, less than 1 per sq. m. *Polychæta* (*Melinna adriatica* and Nereids) apparently dominant.
Salinity ebb-tide water 35·2°/$_{oo}$—conclude no dilution.

TABLE III.

CALSTOCK. CORNISH BANK OF THE R. TAMAR, HALF A MILE BELOW VILLAGE.

Grade.	Dry wt. % of total sample. grm.	Org. cont. % by wt. of total sample. grm.	Org. cont. % of total organic wt. grm.
Retained by 5 mm. sieve	0·22	0·16	1·73
,, 2·5 mm. ,,	0·57	0·14	1·34
,, 1·0 mm. ,,	0·66	0·09	0·87
,, 0·5 mm. ,,	1·03	0·44	4·23
Settled in 1 min.	41·39	2·83	27·19
,, 24 hrs.	56·13	6·75	64·64

Total organic content % by wt., *10·41*

Coarse grades (vegetable detritus and gravel), 2·48% by wt.
Fine sand and silt, 97·52% by wt.
Organic content % by wt. of coarse grades, 33·46.
Organic content % by wt. of fine grades, 9·82.
Corophium fairly plentiful, *ca.* 40 per sq. m. *Nereis diversicolor* (large) dominant.
Salinity range must be great, *ca.* 0·8–16°/$_{oo}$ opposite Calstock itself (Percival, Jour. Mar. Biol. Assoc., Vol. XVI, 1929) on titration of flood-tide water gave 22·8°/$_{oo}$.

indicate that in the coarser mud evaporation would be less rapid. As before stated, Corophium is most plentiful where small puddles cover most of the mud at low water, and where the mud is relatively coarse. The most productive locality I have yet found for Corophium is in a certain tidal creek in the Salicornia marsh at Blakeney Point, Norfolk. Here the mud is very coarse, the salinity never less than 34°/$_{oo}$ and Corophium reaches a density of *ca.* 1000 per m. sq. Here also the organic content is very low (0·8% by weight). The inference is that the nature of the substratum, and not the salinity of the water, is the chief factor defining the habitat of this species of Corophium.

In this connection it is interesting to compare the remarks of Ussing (**22**) in a brief account of the biology of *Corophium Bonelli* M. Edw. in Mariagerfjord, E. Denmark. He found this animal to be the dominant species of a definite Epifauna (" Paa-fauna ") on the Mytilus clumps, and that it attains its optimum opposite Aamölle where the salinity is 14–15°/$_{oo}$ " just like its companion *C. grossipes* (=*C. volutator*) in Randers Fjord." From the above I can only conclude that the substratum was more suited to Corophium than that found higher up the estuaries I have worked. Only once I have found Corophium really abundant in a region of really low salinity—in the mouth of a small river in N. Norfolk connecting by faulty sluice-gates with a tidal creek, known locally as " Stukey Freshes." Here in July Corophium was as plentiful as at Whitby, though the salinity was only 0·7–3·6°/$_{oo}$. The mud was of about the same consistency as at Whitby, and organic content low. In September there was a heavy

accumulation of vegetable detritus, and the stream had to be cleared, but not before Corophium had rapidly diminished in numbers.

In addition to those I have worked myself, I have found records of *C. volutator* from the following British localities :—East Norfolk rivers, ascending to regions of very slight salinity living amongst Cordylophora (Gurney) ; very abundant in the Dee estuary (Spence Bate) ; Exmouth (Allen and Todd) ; tide pools near high water, Lytham–St. Anne's, Ribble estuary (Prof. Garstang).

An idea of the extent of its geographical range may be gathered from the following scattered references : in Christiana Fjord at Moss, G. O. Sars ; at Hangesand on the W. coast of Norway, Boeck ; Danish coasts, Stephensen ; Bohnslaa, Bruzelius ; Baltic, Lindstrom ; Kattegat, Meinert ; Dutch coast, Hoek ; coasts of France, Roscoff, Caen, Bernieres-sur-Mer, etc., Mercier and others ; Adriatic, Meller ; besides the various British localities.

G. O. Sars (**15**) dredged *C. volutator* in 2–5 fathoms of water in Christiana Fjord, whereas round our coasts it is always found in the intertidal zone. This is possibly an example of the general fact that species with a wide geographical distribution tend to be found in deeper water towards the polar limit of their range.

As regards the actual change in salinity which *C. volutator* can endure, it was found that starting with 40 c.c. of sea-water and adding 15 c.c. distilled water daily two Salcombe caught males showed no signs of inconvenience at the end of three weeks. In another experiment specimens from Salcombe were put straight into fresh water and specimens from Calstock straight into laboratory tank water (*ca.* 36°/$_{oo}$). The experiment was set up on April 13th and had to be discontinued on the 29th. Almost all the individuals (two females and one male were used in each experiment) were still flourishing, but such young as were hatched apparently died at the first moult, and one of the Calstock females died after the eggs had hatched. If the salinity were changed gradually therefore, it seems reasonable to suppose that Corophium could be kept and bred in fresh water, and possibly even in hypertonic sea-water.

2. Burrowing and Locomotion.

C. volutator normally burrows vertically into the mud to a depth of not more than five inches. Frequently the burrows are U-shaped, having two openings. When kept in a dish with a shallow layer of mud, shallow burrows, perforce nearly horizontal, are formed. If the mud is insufficient even for this, they agglutinate it together in clumsy tubes, reminiscent of the more workmanlike structures of the regular tube-building species, *C. crassicorne*, with the aid of the secretion from the glands of the second

pereiopods, which is normally used merely to keep the walls of the burrows intact.

In burrowing, the large pediform second antennæ are first brought into play, and when these are immersed the gnathopods, and more particularly the first and second pairs of pereiopods, continue to enlarge the hole and haul the animal head-first into it, purchase being obtained by the elongated specialised fifth pereiopods. Additional drive is given by the continual beating of the abdominal pleopods and the bending of the abdomen under the body so that the uropod spines become embedded and propel the animal forward when the abdomen is straightened again. When crawling freely in the film of water on the surface of the mud *C. volutator* may progress slowly by scrambling action of the thoracic appendages and the beating of the pleopods, the first two pairs of pereiopods doing most of the work. A much more common method of progression, and one which is always used if the mud has dried off completely, might well be described as "looping." The second antennæ are lifted, thrust forward, and the first joint hooked into the mud. The animal hauls itself up to them like a ship kedging off a shoal, what time the abdomen is flexed ventrally so that when the animal straightens out for the next heave with the antennæ, it is thrust forward a further half of its length by the straightening of the abdomen. This mode of locomotion gives an effect very similar to that of a looper caterpillar, and the animal can progress quite fast by it. The structures concerned obviously lend themselves very efficiently to the process, the uropods with their short strong spines forming an ideal fulcrum.

When swimming clear of the bottom, the animal nearly always lies on its back, though capable of performing complicated evolutions on occasions, to which its specific name is possibly due. The two great second antennæ are laid back like the arms of a man about to dive, so serving as an admirable cut-water. All the other limbs are held stiff, with the exception, of course, of the pleopods. These beat rhythmically, but exactly out of phase with each other, i.e. with a metachronial rhythm. The basal joints of the fourth and fifth pereiopods are provided with a dense fringe of plumose setæ, which apparently helps to confine the current produced by the pleopod and direct it backwards, so propelling the animal forward. This mode of progression might be aptly compared to that of the early stern-wheel paddle-steamers.

3. Relations with Other Animals.

In the section on feeding habits, it is shown that *C. volutator* feeds mainly in vegetable detritus, and is *not* actively carnivorous preying upon small worms and gasteropods, as was formerly supposed.

In the Whitby mud it was the dominant species in the animal community. In addition to Corophium I found fair numbers of small *Nereis*

diversicolor and the small gasteropod *Paludestrina stagnalis*. Both these forms, in muds of a slightly different character, where Corophium is absent, may be present in countless thousands. In the Whitby mud were also a few small Lamellibranchs, probably *Tellina balthica*. Besides these, in the runnels there were a few small specimens of *Crangon vulgaris*, and in March I found some berried individuals of *Hippolyte varians*. Small shore crabs were occasionally present, also flounders, which come up on to the flats when the tide is up to feed on Corophium, and sometimes get stranded in small runnels. In the stomach of one small flounder I found 32 Corophium, and no doubt other fish take them on occasions. *C. salmonis*, one of the two large species described by Bradley (**5**) from the Pacific coast of North America, is found in large numbers in some of the salmon there.

At Salcombe the mud, though stiffer, was also stickier, and Corophium was scarce. Nereis and *Melinna adriatica*, which builds vertical tubes coming just above the surface of the mud, appeared to be dominant.

The Calstock mud was softer and darker than that at Whitby. Large *Nereis diversicolor* were dominant, and Corophium was fairly plentiful. I saw no signs of any other animals.

In the two localities worked at Blakeney Point, the salt-water "Yankee Creek" and the brackish "Stukey Freshes," Corophium was in both cases dominant though infinitely more abundant in the former. In "Yankee Creek" there were besides Corophium a large number of small *Nereis diversicolor*, but these were outnumbered five to one. A few *Tellina fragilis*, Carcinus, and *Crangon vulgaris* were also present. At "Stukey Freshes" other animals inhabiting the mud were *Nereis diversicolor* and the Isopods *Cyathura carinata* and *Sphæroma rugicauda*.

Besides fish, Corophium is preyed upon by wading birds and gulls. I have an original sketch by Mr. A. H. Patterson of Yarmouth of a wader with a Corophium struggling in its bill.

I have not as yet noted any parasites, apart from the fact that several of the Whitby Corophium had small individuals of Mytilus growing upon them. Presumably the spat, falling upon soft and unsuitable ground, finds in Corophium the best apology available for a hard substratum.

4. Feeding Habits.

Bate and Westwood (**2**) state that *C. volutator* attacks Annelids and Molluscs, the only other animals commonly occurring in the same mud. They give a "charming vignette" of the animal engaged in a mighty struggle with a Nereid, and state that combined assaults of such a nature are more common. However, they admit in their introduction that it is doubtful whether Corophium really does feed thus, and also admit the

improbability of the supposed migration of Corophium to deeper water in winter. Their accounts of these two phenomena are based on a letter from an early and obscure French naturalist to Latreille.

It seemed much more probable that like the majority of littoral Amphipoda, Corophium would feed on the organic detritus, mainly vegetable, present in its natural habitat. Before any attempt to study the actual feeding process was made, an experiment was set up with a view to determining this.

Small numbers of winter-caught Corophium were isolated in equal volumes of sea-water under various conditions. In the control, only the freshly filtered sea-water was present ; in another bowl mud was placed in which the organic matter had been destroyed by ignition ; another

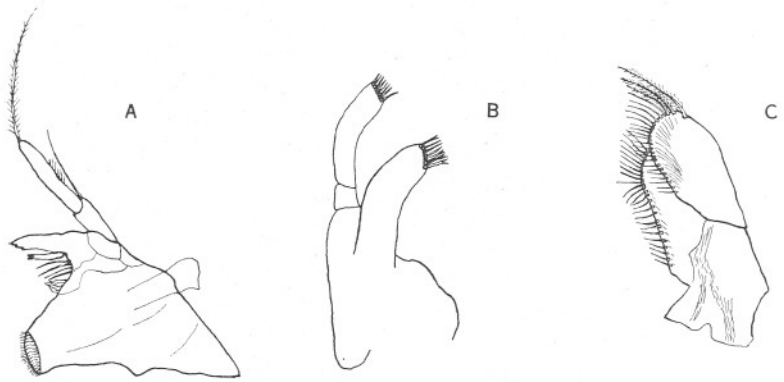


FIG. 1.—A, mandible ; B, 1st maxilla ; C, 2nd maxilla. × 120.

contained mud from which all large particles had been removed by passage through a 0·5 mm. sieve ; and in the last was mud direct from the natural habitat. By the end of a fortnight, the animals in the control experiment and with the sterilised mud were dead. Those with the sieved mud lived nearly 6 weeks, and those with natural mud were still flourishing nearly 7 weeks after the experiment had been set up, and made no attempt to molest the small molluscs present. It was thus obvious that *C. volutator* feeds on the organic detritus in the mud, together with the attendant micro-organisms, and investigations of the feeding mechanism were begun.

So far from being an active carnivorous feeder, then, *Corophium volutator* seems to feed almost entirely by selecting particles from the mud in which it lives. For this purpose the mouth-parts and gnathopods, particularly the first pair, are very well adapted. It would seem to be a true selective deposit feeder in Hunt's sense, though when in its burrow the current produced by the beating of the pleopod brings small particles

in suspension over the setæ fringing the gnathopod, so that in addition there is a filter-feeding mechanism. This last, however, is not the most important method of feeding, as nearly all the individuals examined had particles in the foregut, and adhering to the mouth-parts, of a size that are not moved by the current produced by the pleopods, even when this

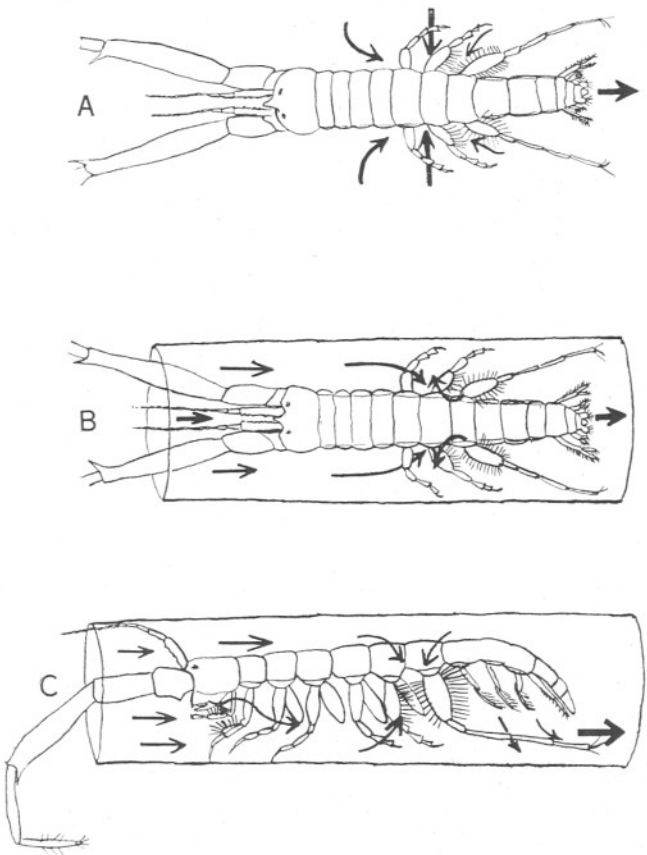


FIG. 2.—Diagrams showing the currents formed by Corophium. A, when crawling freely over the bottom; B and C, when enclosed in a tube.

current is concentrated by the walls of a tube. This can be proved by observing Corophium in a glass tube in a dish of water and adding mud from the natural habitat. Only the finest particles are carried in by the current. The confining influence of a tube is necessary for the filter-feeding mechanism to be operative at all. Otherwise the strong inflowing current is entirely lateral, as indicated in Figure 2.

By observation with a binocular microscope, of vigorous fresh-caught Corophium introduced into a glass tube as described above, the course of the currents, and the method of passing the particles caught to the inner mouth-parts can be followed (Fig. 2).

Before the feeding mechanism can be clearly explained it is necessary to give some account of the topography of the mouth-parts.

The labrum descends vertically from the extreme end of the head, and is provided with a row of small inwardly directed close set teeth near its inferior margin. On either side of the mouth-opening and immediately behind the labrum lie the mandibles. The incisor processes meet ventrally in close juxtaposition to the free edge of the labrum. The large molar processes are visible in sections at this level, lying deeper, i.e. nearer the mouth-opening proper, but their broad grinding surfaces are much wider than the incisors, and extend some distance further back in the plane of the long axis of the animal. The spinose ends of the plates of the first maxillæ overlap this backward extension of the mandibles. Overlying these ventrally come the setose plates of the second maxillæ, and outside these again are the maxillipeds, with the palps reaching as far forward as the labrum, to complete a sort of basket under the head of the animal opening forwards and inwards at the mouth (Figs. 1 and 4).

The mouth-opening itself is somewhat indefinite, lying buried beneath the molar processes of the mandibles. The paragnaths are scarcely developed at all, just two slightly raised blunt lobes with a fringe of fine short setæ, at the posterior end of the mouth-opening. Sections show the region of the mouth-opening and œsophagus to be richly supplied with glandular tissue.

When behaving as a selective deposit feeder, *C. volutator* crawls slowly about over the surface of the mud, or occasionally, on finding a patch rich in organic detritus, remains stationary while the feeding goes on. With the first gnathopods it scoops up and sifts small quantities of mud—when viewed laterally with the binocular the rain of rejected particles could clearly be seen. Larger fragments of algal detritus, etc., appeared to be conveyed to the incisor processes direct by the two terminal joints of the gnathopods. The smaller particles are retained in the fringe of the setæ on the fifth joint of the first gnathapods.

The larger food masses are not cut up by the incisor processes, which are manifestly unfitted for such a purpose, but are, as it were, tucked in between the molar processes by their action. The mandibles move laterally outwards and inwards as indicated in Figure 3, A. The particles are thrust in between the molars largely by the action of the laciniæ, and the spines that lie between them and the molars.

A considerable amount of secretion from the glands in the œsophageal wall is poured out into the cavity formed by the mouth-parts. Pear-

shaped masses of smaller food particles agglutinated together, are frequently found on the spines of the mandibles and first maxillæ.

When acting as a suspension feeder, the particles are drawn into the net formed by the fringing setæ of both first and second gnathopods, by the currents set up in the burrow (or glass tube) by the beating of the pleopods. The particles are combed out of the fringe of the second gnathopods on to the first gnathopod fringe, and their further course to the mouth is the same as that taken by the smaller particles obtained when deposit-feeding.

The transference of the smaller food particles from the setæ fringing the fifth joint of the first gnathopods to the mouth is not easy to follow, owing to the small size of the mouth-parts and the rapidity of their movements. Repeated observations of the animal fastened down upon its back with plasticine enabled the main part of the process to be made out.

The gnathopods are moved up and down against each other in the manner indicated in Figure 3, B, until the sifting of the useless particles appears to be completed to the animal's satisfaction. Even so, a large part of the gut contents can only be described as mud. One of the gnathopods is then inclined inwards so that by the rapid champing action of the maxillipeds the food particles are combed out of the setæ fringe on the gnathopod. The movement of the maxillipeds appears to be purely lateral, and the fringe of fine spines on the outer plate, together with those on the palp, appear to be the chief agents in collecting the food particles. The spines on the outer plate are so set in a sort of ball-and-socket joint that when the maxillipeds are closed, the joint admits of their being projected forwards at an angle, but not back. When the maxillipeds are opened laterally these spines are pointing inwards at right angles to the margin of the plate (Fig. 3, C), but when they close the spines bend forwards so that the food particles combed from the gnathopod fringe are thrust forward until they come within the radius of action of the incisor processes and first maxillæ (Fig. 3, C 2). It is possible that the armature of the second maxillæ functions in the same way as that of the maxillipeds, but the organs in question do not seem to play any important part in the feeding process.

The ends of the outer plates and palps of the first maxillæ move downwards and outwards, then upwards and inwards, and with the help of the secretion from the salivary glands, appear to do the bulk of the work of passing food particles on from the maxillipeds to the mandibles. Some of the larger particles, however, seemed to be passed direct to the inner side of the incisor processes by the palps of the maxillipeds.

Most of the food seems to be ground up into a pasty mass by the molar processes, but some particles, particularly fragments of algal filaments, appear to reach the fore-gut without undergoing this trituration.

The actual process of swallowing is not at all clear, but it seems probable

that suction set up by contraction of the diagonal muscles of the foregut wall may be the chief factor. The dilated horizontal part of the foregut or crop contains an exceedingly complicated arrangement of spines,

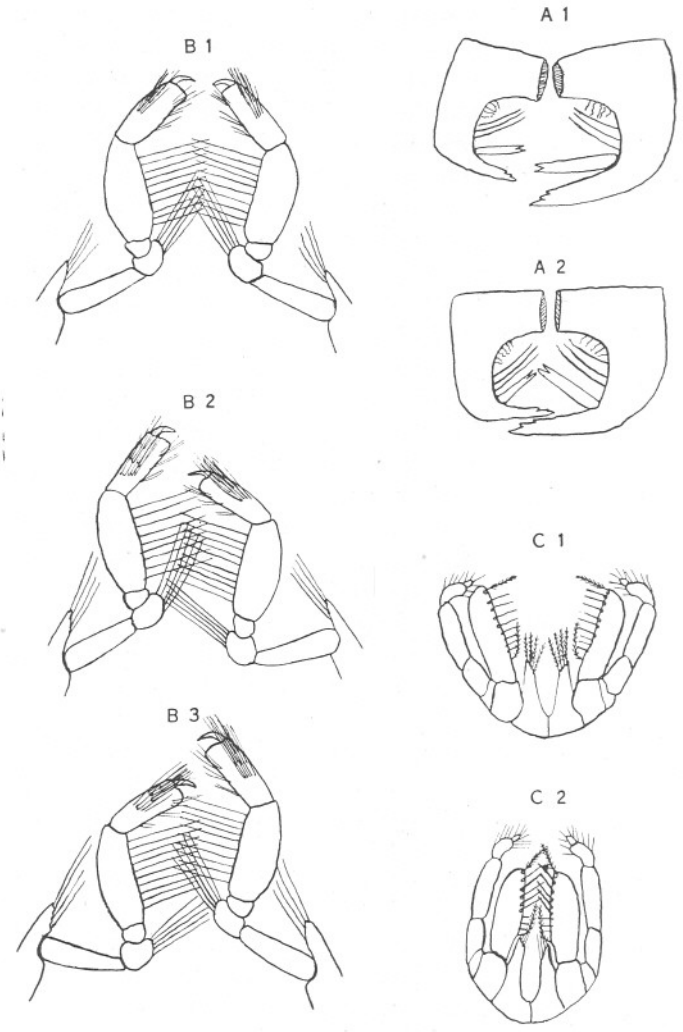


FIG. 3.—Diagrams illustrating the feeding mechanism. A, action of the mandibles; B, sifting action of the first gnathopods; C, action of the spines on the maxillipeds.

denticles and setæ, by means of which the undigested food is still further triturated. Obviously this can only take place by the action of the muscles in the wall of the crop, and it seems quite probable that this same action

sets up a suction by means of which further food particles are drawn up the œsophagus.

The œsophagus ascends almost vertically into the wide triturating stomach or crop (also sometimes termed the proventriculus) which projects anteriorly in front of the level of the mouth-opening. The forward end of the crop contains a circular ring of chitin set with strong backwardly directed triangular teeth, the "triturationsapparat" of German authors, at the level of the œsophageal opening. Just behind this is a ring set with numerous fine setæ, also directed backwards.

Further back a large ridge rises from the floor of the fore-gut and almost divides it longitudinally into two halves. This ridge is set with a fur of very fine short setæ round the crest, and on the sides with parallel rows

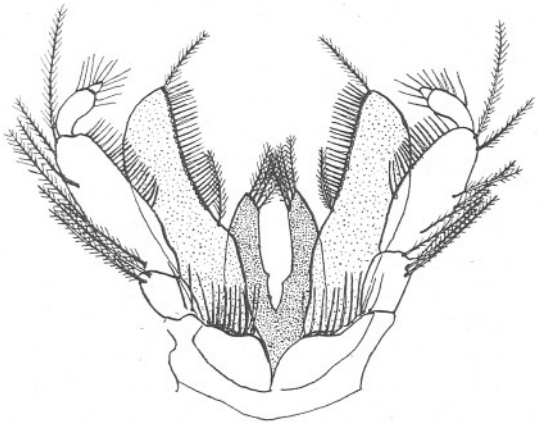


FIG. 4.—Maxillipeds, as seen from below. × 120.

of low chitinous denticles. At the extreme postero-dorsal end, the ridge also bears a tuft of longer setæ directed backwards. The armature of the ridge in general closely resembles that of the molar processes of the mandibles. On either side, where the lateral walls of the fore-gut join the floor, a low ridge is to be found directed obliquely inwards, crowned with fine short setæ. The whole apparatus will obviously furnish a very efficient triturating apparatus when the gut walls are violently contracted. These walls contain many strong diagonally interlacing muscle-bands, giving an appearance reminiscent of the network of a balloon. Behind the proventriculus the gut narrows abruptly, but the fore-gut is prolonged as a sort of funnel for some distance into the mid-gut lumen.

Little could be seen of the actual mastication of food within the proventriculus in the adult, for obvious reasons, but in young transparent individuals a violent periodic lateral contraction, followed by peristaltic

movement of food down the mid-gut, could clearly be seen. These spasmodic contractions were always followed by the appearance of a fresh supply of food particles in the proventriculus. Hence, I incline to the view that the swallowing process is to be attributed to the sucking action of the crop.

5. Life-Cycle and Breeding Habits.

Results of Measurement Investigations.

Samples from 1 sq. m. of the Whitby mud were taken at the four seasons of the year, by the methods described earlier in this paper. All the measurements were made by Blegvad's method—taking the length in millimetres from telson to rostrum : and in the case of the females, the condition of the oostegites, and eggs or young if present, was carefully examined in each individual as it was measured.

The smallest individuals in which the sexes could be distinguished with any degree of certainty without dissecting off the antennæ were about 3 mm. long. In some of these, though the oostegites were not developed, the two spines on the inferior margin of the first joint of the first antennæ, so characteristic of the females, could clearly be seen. This is a most constant secondary sexual character in all the material I have examined. All specimens below this size are lumped together as "young" in the following tables. As many of them doubtless escaped the mesh their numbers have little significance, apart from their relative frequency at midsummer, when the animals are breeding, and through autumn and winter when breeding has ceased but development is very slow : and scarcity in the spring, when the last hatched broods of the previous summer are just reaching maturity, and the animals are about to begin breeding again.

Table IV deals with the sample of *Corophium volutator* obtained from 1 sq. m. of Whitby mud on July 20th, 1928. In addition to the tabulated specimens, this sample contained 53 young under 3 mm. in length. It will be seen that immature specimens of both sexes are almost entirely lacking, from which it would seem that the first brood of the year had just reached maturity. From the measurements given it also appears that maturity is reached at a length of *ca.* 5·5 mm. in the case of the summer stock. In the great majority of the larger females the eggs were in the same advanced stage of development. I take it that this shows the free-living young of the July sample to be representative of the second or third brood of the year, as information gathered during the following April points to three weeks as the maximum period of incubation, and breeding commenced in the second week of that month.

From the figures given in Table IV it will be seen that quite a large proportion of the 7 mm. females were without eggs, but had the brood

pouch fully formed. It would seem that these represent the last of the winter stock to reach maturity, and they had probably only produced one brood when taken. The validity of this supposition is greatly enhanced when the March measurements (shortly to be described) are taken into account.

Table IV.

Results of Measurement Investigations.

Whitby sample. July 20th, 1928.

Total number of individuals examined, 196, of which 55 were young under 3 mm. in length, 73 females ranging from 5–9·5 mm., 35 males varying between 6–9·5 mm. in length, and 33 females not so fully examined of length 5–8 mm. The first series shows the information gathered from the females examined in detail.

Length mm. telson to rostrum.	No. of individuals.	No. with eggs.	No. without eggs, but brood pouch present.	No. having eggs with curled embryos.	Max. no. of eggs per brood.	Min. eggs per brood.	Average no. of eggs per brood.
5	1	–	–	–	–	–	–
5·5	3	2	–	2	8	4	6
6	3	2	1	2	12	9	10·5
6·5	10	8	2	6	35	11	25
7	22	13	9	12	39	24	28·7
7·5	15	11	4	10	48	25	33
8	13	11	2	11	45	21	34·5
8·5	3	2	1	2	39	32	35·5
9	1	–	1	–	–	–	–
9·5	1	–	1	–	–	–	–
Particulars from 33 more females, not so closely examined.							
5	2	–	–				
5·5	1	–	–				
6	3	2	1				
6·5	4	4	–				
7	14	10	4				
7·5	4	4	–				
8	2	1	1				

Table V.

Size and Frequency of the July Males.

Length in mm. telson to rostrum	6	6·5	7	7·5	8	8·5	9	9·5
No. of individuals	1	2	10	8	7	5	–	1

Table VI shows the measurements of the sample taken on October 10th, 1928. The scarcity of adults, particularly males, and larger immature stages, together with the increased proportion of free-living young was very marked. None of the larger females had eggs ; indeed, it was found that the hairs were missing from the oostegites, which showed notches where the hairs are present during the breeding season. This was borne out by examination of some forty individuals apart from those in the mature sample. My opinion is that the apparent scarcity of *C. volutator* during the autumn and winter months is not due to any migration into

deeper water as was suggested by Bate and Westwood (2), but to two main factors: firstly, that the adults, in particular the males, are dying off rapidly; secondly, that small free-living young, which do not become mature until the following spring, are exceedingly numerous, but defy ordinary methods of capture.

Table VI.

Results of Measurement Investigations.

Size and frequency of the Whitby sample obtained on October 10th, 1928. *N.B.* A 500 c.c. sample put through a finer sieve yielded 33 young. The females were not breeding.

Length in mm. telson to rostrum.	Nos. of Females.	Nos. of Males.	Young.
Under 3	–	–	21
3	12	–	–
4	6	–	–
5	4	–	–
6	3	–	
7	12	1	
8	1	1	

The total number of individuals examined was 64, of which 41 were females, 2 males and 21 young.

Table VII.

Measurements of a sample obtained at Whitby on December 29th, 1928. Only 60 individuals were found, of which 51 were females, mostly immature, 3 were males, and 6 young. A 500 c.c. sample put through a fine sieve again indicated that many young had escaped the larger mesh, as 14 young were found in it.

Length in mm. telson to rostrum.	Nos. of Females.	Nos. of Males.	Nos. of Young.
Under 3	–	–	6
3	12	–	–
4	18	1	–
5	7	–	–
6	6	–	
7	4	1	
8	4	1	

In order to prove that Corophium is not so scarce in October as the metre sample indicated, a sample of 500 c.c. of mud was put through a fine sieve in the laboratory, when 33 young were discovered. As this volume only represents about 1/20th of the metre sample, it will be seen that the scarcity of Corophium in the autumn is confined to the adults and larger immature stages. The occurrence of a fair number of individuals 7 mm. long or over shows that the adults of the previous summer had not completely died off, as one would expect thus early in the "off-season."

In the sample obtained on December 29th, 1928, the number of adults was still smaller, and the number of free-living young in 500 c.c. of mud had decreased to 14; but the number of small immature stages was considerably greater, as shown in Table VII. No breeding animals were

observed, though 21 large females apart from the sample were examined. Their oostegites were hairless, with notches where the hairs are found in the breeding season.

The last sample I have so far been able to take at Whitby was collected on March 28th, 1929 (Tables VIII and IX). The wintered females were obviously almost ready to breed, but though 107 in all were subjected to the closest scrutiny, not one was discovered actually breeding. Indeed, their oostegites were still hairless, even in the larger individuals, but were not notched as are those of the mature females of the previous summer which live on into the winter. All the latter seemed to have died off.

The following Tables VIII and IX show the results obtained from the metre sample taken at Whitby on March 28th, 1929. The males which are dealt with were more numerous than at any other time of the year. In all, this sample contained 184 specimens, of which 5 only were young under 3 mm. long, 70 were males ranging from 4–8·5 mm. in length, and 107 females of length 3–8 mm., none of which were breeding. A 500 c.c. sample put through a fine sieve did not yield any young, but 20 immature specimens of both sexes, from 4–6 mm. in length.

TABLE VIII.

Length in mm. telson to rostrum	4	4·5	5	5·5	6	6·5	7	7·5	8	8·5
Nos. of males	2	4	9	10	24	7	9	1	3	1

TABLE IX.

The females showed all stages of development of the oostegites, but in general, the larger the individuals the more advanced was this development, as shown below :—

Length in mm. telson to rostrum.	Nos. of Females.	Nos. without oostegites.	Oostegites small or vestigeal.	Oostegites well developed but hairless.
3	10	10	–	–
3·5	9	9	–	–
4	11	10	1	–
4·5	14	3	11	–
5	15	3	11	–
5·5	9	–	3	6
6	9	–	–	9
7	11	–	–	11
7·5	7	–	–	7
8	1	–	–	1

The first vestiges of oostegites were observed on females 4·5 mm. long. Larger females, of a size commonly found breeding in the summer, had well-developed oostegites, but these were hairless. It would seem, therefore, that not only is the growth of the winter stock slower than that of the summer stock, but that they also reach maturity at a greater size.

An additional small supply of Whitby material, captured on April 10th,

and very kindly sent to me by Mr. George Duke of Robin Hood's Bay, showed that all the females were then developing hairy oostegites, and some had early eggs. The early eggs of *C. volutator* are easily distinguished from those at a later stage of development, as they are smaller, of a bright golden yellow colour, and held together by a viscid secretion.

On April 13th at Calstock, I found all the female Corophium breeding, mostly with eggs in this early stage.

Free-living young were scarce, so that it seems that even on the South coast they do not start breeding until April.

A few specimens of *C. crassicorne* dredged from Plymouth Sound about this time had advanced eggs, but it is quite possible that this species, like the closely similar *C. Bonelli*, breeds all the year round, as living below low water it will not have to cope with such great fluctuations of temperature as *C. volutator*.

Isolations of females with early eggs showed the probable time of incubation to be slightly over a fortnight, and this was borne out by a further sample from Whitby very kindly obtained for me by Mr. Wight on April 19th. This sample contained females nearly all of which had eggs at an advanced stage, whereas it was known that breeding had only just commenced at Whitby on April 10th. The first young were hatched on April 23rd, and by the 29th some were being extruded from the brood pouches. I have not yet been able to observe the mating of the *C. volutator* in captivity, so I am forced to rely on this indirect evidence, and can therefore only give an approximation of the incubation period at present.

The young remain at least five days in the brood pouch. They feed in it, for their guts can plainly be seen full of food, and at least the first moult must normally take place there.

The relative number of males was much higher in the spring sample than in the summer and, as before stated, adult males had become exceedingly scarce by October. From this it would seem that the earlier broods must contain many more males than those hatched in spring and early summer.

The conclusion arrived at from the above evidence concerning the life-cycle of *Corophium volutator* at Whitby were as follows :—

The breeding period lasts from April to September : several broods are hatched each year.

The last hatched broods mature slowly through the autumn and winter, and commence breeding in the following April. During autumn and winter the individuals which had reached maturity in the previous summer die off.

The species is thus annual or semi-annual.

The Young.

The young of *C. volutator* are hatched with the full complement of adult appendages, as is the rule amongst the Gammaridea. The primary flagellum of the first antennæ consists of but three joints, instead of four, as Sexton (**17**) found in several species of Gammarus. The proportions of both pairs of antennæ to the rest of the body are very different from that of the adult. In the young the second antennæ are never more than one-third of the body-length, and the minute terminal flagellar joint of the adult is wanting. The armature of spines and setæ of several of the appendages is poorly developed or wanting in the young. Thus only a few of the large plumose setæ on the gnathopods are represented, and these appear as long spines of totally disproportionate size to the limb bearing them, and on which I have not been able to discern any accessory hairs. The fringe of plumose setæ on the basipodite of the 5th pereiopod is entirely wanting.

The form and proportions of the regions of the body in the young also differ from the adult. The general form is shorter and squatter, and the ventral flexure of the abdomen is more marked. The abdomen is also much larger in proportion to the rest of the body.

The epipodites are already present, as would be expected, for though remaining in the brood pouch for at least five days, during which time the first ecdysis takes place, the young are quite active, and feed within the pouch. This has also been observed in the young of Gammarus by Sexton (**16**). If dislodged they appear to be quite able to fend for themselves, but the first moult is a critical period, and in experiments in varying the salinity it was frequently found that under conditions which did not affect the adults adversely, all the young died at the first moult.

In some of the young taken from the brood pouch, probably after the first moult, a single large spine was present, directed obliquely forward from the basal joint of the fourth antennæ ventrally. Further study may show this to be the forerunner of the two spines characteristic of the immature and adult females. If this is so, *Corophium volutator* will be the only Amphipod so far studied in which the sexes can be distinguished at such an early stage.

DISCUSSION AND SUMMARY

The investigation of the habitat shows that the nature of the substratum is the chief factor influencing the distribution of *Corophium volutator* in this country. The accounts of Danish workers state that it reaches its optimum in regions of fairly low salinity. This is probably due to the fact that the mud is of suitable character higher up the vast estuarine areas of Denmark than it is in England. It has been shown that while Corophium

can penetrate into regions of very slight salinity, it occurred in by far the greatest numbers at the "Yankee Creek" station, at Blakeney Point, Norfolk, where the mud is very coarse, the organic content low, and the salinity rarely falls below that of the North Sea outside. At "Stukey Freshes," also at Blakeney Point, Corophium was found in considerable abundance in July, although the salinity was very low (3·6°/$_{oo}$). At this time the organic content of the mud was 6·3% and the pH 8·3. In early September there was a vast accumulation of organic detritus at this station, and the pH was found to be 7·7. The numbers of Corophium present dwindled rapidly.

The conclusion reached is that while *Corophium volutator* is capable of withstanding great salinity change, its abundant occurrence is strictly limited by the chemical and physical character of the substratum.

The peculiar features of the structure of this Amphipod and its appendages, and the methods of feeding and locomotion to which these lead, are obviously of great advantage to an animal of its peculiar way of life.

C. volutator is a characteristic member of a definite type of animal community of which the other important forms are Nereid worms and the Gasteropod *Paludestrina stagnalis*. Where the conditions approach its optimum, *C. volutator* forms the dominant species in this community, but it is also found in fair numbers in regions where Nereids become dominant. Danish writers also speak of it as occurring in immense numbers co-dominant with the Spionid *Pygospio elegans*.

In describing the Biology of the allied species, *C. Bonelli*, Ussing (**22**) mentions that this form also is a characterising species of a definite animal community. This is the well-marked Epifauna of the Mytilus clusters in certain Danish Fjords. Salinity would appear to be the chief factor influencing the distribution of this species, and where the conditions depart from its optimum, other members of the Epifauna become correspondingly more numerous.

As regards the feeding habits of *C. volutator*, the method of selective deposit feeding appeared to me much more important than suspension feeding. The method of dealing with the larger food masses recalls that described by Cannon and Manton (**7**) in *Hemimysis lamornæ*, where large food masses are conveyed to the maxillules and incisor processes by the endites of the anterior thoracic limbs. In the Decapod, *Leander serratus*, large particles are dealt with by the chelipeds according to Borradaile (**4**), but the scooping up and sifting of the ooze by the gnathapods of Corophium finds a still closer parallel in the almost identical performance of the third maxillipeds of Hermit crabs (Orton, **13**).

The suspension feeding when the animal is in its burrow, by means of the current set up by the pleopods, agrees almost exactly with the description given by Hunt (**11**) in the case of another Amphipod, Ampelisca.

The actual swallowing action I could not definitely make out, but the reasons given for the suggestion that suction from the crop is the prime factor seem fairly sound. Parker and Mocquard have suggested a similar cause in Decapoda, but Borradaile (**4**) considers this doubtful, and suggests that the constrictor muscles of the œsophagus may conduct the process. The shortness of the latter organ in Corophium would seem to render such an explanation inapplicable in this case.

The life-cycle of *Corophium volutator*, as deduced from the measurement-investigations of Whitby material, would seem to be essentially similar to that postulated by Blegvad (**3**) for several littoral Amphipoda of widely different genera : but the wintering period, when the animals are not breeding, is much longer. Most of the animals discussed by Blegvad stopped breeding in October, but began again in the following January. Further, it seemed that none of the wintering adult individuals lived long enough to start breeding again in the following spring, though the numbers so far studied are not sufficient to permit of so much stress being laid on this point at present. It has been clearly shown, however, that wintering adult females lose the hairs on their oostegites, and it would be extremely interesting to observe the re-development of these, if they did breed again. Mrs. Sexton drew my attention to the very interesting work of Unwin (**21**) on the isopod Asellus in this connection. In this animal it seems that the oostegites remain inconspicuous until the ecdysis accompanying fertilisation, when they expand to form large brood-plates. Soon after the escape of the young, the female goes through another ecdysis, and the large oostegites are replaced by smaller processes. However, I do not think any similar phenomenon occurs in Corophium, as the lamellæ of the oostegites develop gradually as in other Amphipoda —the March sample showed females with the oostegites in all stages of development, becoming more advanced with increased size of the female (Table VIII). It is only the hairs that develop suddenly. Once present these hairs seem to remain until the end of the breeding season, as many females of the summer stock had fully developed brood pouches long after all the young had been extruded.

The fact that the breeding period of *Corophium volutator* is comparatively short for an amphipod is rather surprising in view of Ussing's observation that *C. Bonelli* breeds all the year round in certain Danish Fjords (**22**). The explanation is probably to be found in the fact that *C. Bonelli* lives on the Mytilus clusters just below low-tide mark and is therefore subject to much more uniform temperature conditions than *C. volutator*, dwelling on exposed flats which dry off every tide.

The fact that females are more numerous than males was known to Delage (**8**), and he gives the sex ratio as 3 : 1. This was precisely what I found at midsummer, but in March males were much more frequent,

though still outnumbered by the females. I am at a loss to account for this, unless the last hatched broods each year contain a much greater proportion of males than the others. If this were the case, it might be that a detailed study of the development of *C. volutator* would throw light on problems of sex determination.

The extremely slow growth of the young during the winter is also exhibited in a lesser degree by *Gammarus chevreuxi*, a species which, under aquarium conditions at any rate, breeds all the year round. Of this species Sexton (Journ. Mar. Biol. Assoc., XV, 1928, p. 40) says : " The rate of development is affected to a large degree by temperature and to a lesser degree by the seasonal rhythm. Young hatched in the winter months take longer to reach maturity, even though the temperature be raised to summer conditions, than those hatched in the spring and summer." Bearing in mind what happens in *C. volutator*, it seems at least possible that this " seasonal rhythm " may be due simply to the cumulative temperature effect on thousands of generations of these brackish-water amphipods, under natural conditions.

Note on the Morphology of the Gut Diverticula.

In the course of this study of *Corophium volutator* it was discovered that the anterior dorsal gut diverticulum was bifid, but that small posterior diverticula of typical Gammaridean character were present. The dorsal diverticulum should be single in all Gammaridea, but paired in Hyperiidea and Caprellidea, according to all authorities whose works I have been able to consult. Thus Calman (**6**), Della Valle (**9**) and others.

This is interesting in view of the fact that Delage (**8**) advances the hypothesis that Corophium represents the common ancestral stock of the Caprellidea on the one hand, and the Gammaridea on the other. His view is based on a minute examination of the circulatory system of most of the main types of the old group Edriophthalma, including this particular species of Corophium. Stebbing, however, disposes of this view very effectively (**18**), arguing on general lines. But the bifid nature of the " Nackendrüse," unique among the Gammaridea so far as I have been able to ascertain, seems at first sight to lend support to Delage's view.

While Stebbing's arguments would seem to preclude the possibility of Corophium being the direct ancestor of the Caprellidea, the singly ostiate heart of Corophium, and the bifid nature of the " Nackendrüse " certainly seem to point to some sort of affinity. In this connection the evidence furnished by this disposition of the other gut diverticula in Corophium may be considered.

In the first place, Corophium is provided with a pair of posterior gut diverticula. Baldwin Spencer (**17**) has pointed out the extraordinarily

limited occurrence of these organs among higher Crustacea, though Claus has described somewhat similar organs in Copepoda. They are almost entirely confined to the Amphipoda Gammaridea, being only exceptionally present (Calman, **6**) in Caprellidea and Hyperiidea. As Della Valle has pointed out, these organs are small in Corophium, but they are quite well developed, and agree with those of the more typical Gammaridea, as described by Wrzesniowski (**23**) in structure. The presence of these organs in Corophium is a serious objection to the hypothesis that the animal represents the common ancestral stock of the Gammaridea and Caprellidea by different lines of descent, as if this were the case one would have to postulate their gradual suppression in the latter group, whereas typical Gammaridean forms (e.g. Melita) are known in which the posterior gut diverticula are partially suppressed.

Corophium is not alone among the Gammaridea in having only one pair of hepato-pancreatic diverticula, though two pairs are more usual. In Caprellidea there is one pair only, but according to Calman (**6**) it is the ventrally situated pair which is rudimentary or absent, while in Corophium the well-developed hepato-pancreatic diverticula can clearly be seen to open into the mid-gut ventrally, and indeed are rather ventrally inclined to it throughout their length. Again, the evidence furnished by these organs in Corophium is in contradiction to Delage's hypothesis.

Taking all these facts into consideration, together with Stebbing's strong argument for regarding the Gammarus type as primitive, I suggest the substitution of the following for Delage's hypothesis : that Corophium is a secondarily modified amphipod, probably derived as an early independent offshoot from the evolutional series which started from Gammaridean stock, and culminated in the degraded Caprellids. On this view it is only necessary to suppose that the two anterior pairs of ostia, poorly developed in Caprellids, have disappeared altogether in the side line which gave rise to Corophium, while the balance of evidence gained from the disposition of the various gut diverticula is also maintained.

Note on a Variation of *Corophium volutator*.

In the female of this species, the first peduncular joint of the first antenna bears ventrally typically two stout spines direct obliquely forwards. Occasionally there are three or more of these spines either on one or both of the antennæ, as has been pointed out by Mercier (**12**), though I have never come across any similar spines in the male such as he also describes as varying in number. It is perhaps significant that Poisson and Legueux (**14**), in describing a variety of another Corophium species from the same locality, make no reference to any male spines in an otherwise rather full summary of Mercier's work. In the female, however, his

account of the variation is certainly correct, though the further conclusions are somewhat doubtful. The number of individuals with more than the normal number of spines is said to be higher in brackish than in salt water, and it is claimed that this phenomenon "doivent rentrer dans la cadre de variation de place."

The numbers upon which Mercier's observations are based are very small, and he makes no mention of the time of year at which collections were made. As far as I can say at present, it appears that this variation is not due to differing salinity, but rather to some factor correlated with the much higher rate of metabolism of the summer stock. These may take no more than two months to reach maturity while the winter stock take six. Of 103 females of the summer stock, 25 showed the variation in a more or less marked degree, while 109 of the winter stock contained only 3 variants. Further, these samples, from the sample locality at Whitby, came from a place where it appears that salinity rarely falls below *ca.* 20°/$_{oo}$.

LITERATURE.

1. Allen, E. J. On the Fauna and Bottom Deposits near the thirty-fathom line from the Eddystone grounds to Start Point. Journ. Mar. Biol. Assoc., N.S., Vol. V, 1897–99, p. 365.
2. Bate, C. Spence, and Westwood, J. O. A History of the British Sessile-eyed Crustacea. Vol. II. London, 1868.
3. Blegvad, H. On the Biology of some Danish Gammarids and Mysids. Repts. Danish Biol. Stn., Copenhagen, Vol. XXVIII. 1922.
4. Borradaile, L. A. On the Structure and Function of the Mouth-Parts of Palæmonid Prawns. Proc. Zool. Soc. London, 1917, p. 37.
5. Bradley, J. Chester. Notes on two Amphipods of the genus Corophium from the Pacific Coast. Univ. of California. Publications in Zoology, Vol. 4, No. 4. 1908.
6. Calman, W. T. A Treatise on Zoology. Edited by Sir Ray Lankester, Part VII. Appendiculata. Third Fascicle. Crustacea. London, 1909.
7. Cannon, H. G., and Manton, Miss S. M. On the Feeding Mechanism of a Mysid Crustacean, *Hemimysis Lamornæ*. Trans. Roy. Soc. Edin., Vol. LV, Pt. 1, No. 10. 1926–27.
8. Delage, Yves. Contribution à l'Étude de l'appareil circulatoire des Crustaces Edriophthalmes Marins. Archives de Zoologie Exp. et Gen., Tome IX, p. 1. 1881.

9. Della Valle, A. Gammarini del Golfo di Napoli. Fauna und Flora das Golfes von Neapel Mongr., XX, 1, Vol. & Atlas. 1899.

10. Gurney, Robert. Crustacean Fauna of the East Norfolk Rivers. Trans. Norfolk & Norwich Nats. 1907.

11. Hunt, O. D. The Food of the Bottom Fauna of the Plymouth Fishing Grounds. Journ. Mar. Biol. Assoc., N.S., Vol. XIII, No. 3, p. 560. 1925.

12. Mercier, L. Variation de Place chez *Corophium volutator* (Pallas). Paris, C.R. Acad. Sci., Vol. 170, p. 410. 1920.

13. Orton, J. H. On the mode of feeding of the Hermit Crab *Eupagurus Bernhardus* and some other Decapoda. Journ. Mar. Biol. Assoc., N.S., Vol. XIV. 1926–27.

14. Poisson and Legueux. *Corophium acutum* Chevreuxi, var. n. Bull. Soc. Zool. Paris, **51**, p. 520. 1926.

15. Sars, G. O. An Account of the Crustacea of Norway. Vol. I. Amphipoda. Christiana and Copenhagen, 1895.

16. Sexton, E. W. Moulting and Growth-stages of Gammarus, with descriptions of the Normals and Intersexes of *G. chevreuxi*. Journ. Mar. Biol. Assoc., N.S., Vol. XIII, No. 2, p. 340. 1924.

17. Spencer, W. Baldwin. On the Urinary organs of the Amphipoda. Quart. Journ. Micr. Sci., Vol. XXV, p. 183.

18. Stebbing, T. R. R. Report on the Amphipoda. Repts. Voy. "Challenger," Zool., XXIX. 1888.

19. Stebbing, T. R. R. Amphipoda : I. Gammaridea. Das Tierreich Leif. XXI. 1906.

20. Stephensen, K. Revideret Fortegnelse over Danmarks Arter af Amphipoda. Videns. Medd. f. Dansk Naturhist. For. Kjøbenhavn, Bd. **84**, p. 107. 1927.

21. Unwin, Ernest E. Notes upon the reproduction of *Asellus aquaticus*. Journ. Linn. Soc. Lond. Zool., Vol. XXXIV.

22. Ussing, Hj., and Stephensen, K. *Corophium Bonelli* (M-Edw. ?) G. O. Sars, ny for Danmark, med Noter om andre Corophium-arter. Videns. Medd. f. Dansk Naturhist. For. Kjøbenhavn, Bd. **78**, p. 69. 1924.

23. Wrzesniowski, A. Vorlaufige Mittheilungen uber einige Amphipoden, 4 ; Ueber den Darmkanal und seine Anhänge. Zool. Anz., 1–2, p. 511. 1878–79.

Hydrography of the Mouth of the English Channel, 1925–1928.

By

H. W. Harvey, M.A.,

Hydrographer at the Plymouth Laboratory.

With 16 Figures in the Text.

THE temperature of the sea and the movements of water carrying with it planktonic organisms have been the subject of study since the early days of marine biological research. As investigation of cold-blooded marine animals progresses, the controlling rôle played by the temperature of the surrounding water upon their breeding, rate of growth, and general metabolism, becomes increasingly evident.

From 1902 to 1909 cruises were made throughout the English Channel by the s.s. *Huxley* four times each year, and from the data so obtained Matthews (1905–11) described the distribution of temperature at these times, as well as the distribution of salinity, and from these the general water movements were deduced. Conditions at the same time of year differed from one year to another. It was concluded that fluctuations from year to year in the annual temperature cycle and fluctuations in the inflow of water from the Atlantic would have a profound influence upon the population of marine animals and upon the fisheries. This conclusion has been borne out in this area notably by the researches of Orton (1920) upon the narrow temperature limits in which various marine animals breed, and of Ford (1929) upon the shoaling of herring for breeding purposes.

Since 1921 more frequent but less extensive cruises have been made by the s.s. *Salpa*, while surface temperature samples have been collected at intervals of about two weeks by cross-Channel steamers (see Fig. 1) for the Ministry of Agriculture and Fisheries, with the exception of the route Land's End to Ushant, on which data are collected for the Marine Biological Association. These surface data are published in the annual *Bulletin Hydrographique* of the International Council for the Exploration of the Sea. Hydrographic cruises have also been made to the west and south-west of the entrance to the Channel by French and Irish fishery research vessels, the data being published in the *Rapport Atlantique.* These data so collected throw light upon the fluctuations which have

occurred from year to year in both the movement of the water masses and in the annual cycle of temperature.

PART I. TEMPERATURE DISTRIBUTION.

The Annual Cycle.

The annual variation, or temperature cycle, differs from place to place and from time to time with the extent to which the surface layers mix with the water below, and with the depth or mass of water which is heated in summer and is cooled in winter. Further, the cycle fluctuates from year to year owing to fluctuating meteorological conditions, and on occasions owing to the inflow of water from other parts.

In shallow areas, where wave motion and turbulence due to tidal streams keep the upper layers mixed with the water below and in consequence keep the temperature nearly constant from top to bottom, the water commences to rise in temperature about a month before the vernal equinox and attains a maximum in the late summer. Such is found, for instance, in Plymouth Sound and in the shallow eastern part of the English Channel.

In the deeper waters of the Channel it is otherwise.

There is now a considerable body of data concerning the temperature cycle at Station E_1 (50° 02′ N., 4° 22′ W.) in a depth of around 71 metres. Here convection currents, wave motion, and vertical mixing set up by tidal streaming are effective in keeping the temperature almost the same from top to bottom during the winter. Later, as the water warms, receiving heat from solar radiation at the surface, there comes a time in May, June or July when heat arrives more rapidly at a depth of about 16 to 20 metres than the turbulent eddy motion of the water can carry it to greater depths. The resulting difference in density, between this upper warmed layer or epithalassa and the water below, still further damps down eddy motion at the discontinuity layer. Heat can only pass slowly through it to the water below. From this discontinuity layer to the bottom the water remains more or less isothermal, because tidal streaming over the bottom sets up eddy motion which is sufficient to pass downwards the heat which is arriving from the epithalassa.

Figure 2 shows the distribution of temperature which had been attained on August 2nd and 3rd, 1927, at Stations E_1 and E_3, 74 and 106 metres deep respectively.

Between 15 and 20 metres there is a sharp change in density, and in consequence considerable work must be done if the lighter water above is to mix with the heavier water below (Atkins, 1925). Vertical movement of water particles is tolerably free to take place between the surface and 10 or 15 metres. Hence heat from solar radiation, which is absorbed near

the surface, is freely passed on downwards from water particle to water particle to this depth by the eddying movements of the particles themselves, brought about by wave motion and the convection currents set up by cooling at night. If it were not for this mixing of the water particles carrying heat just as they carry momentum, and passing it on as in a relay race in the course of their eddy movements, the layering would be much shallower and higher temperatures would be attained near the surface, as happens in still water.

In the discontinuity layer the interchange or mixing of the water particles and their eddy movements are restrained. Hence momentum is not freely passed downwards, and this upper stratum is relatively free to slip horizontally over the heavier water, the slip taking place at the discontinuity layer. This undoubtedly takes place. At Station E_1 the water swings to and fro up and down Channel with the tides from the surface to near the bottom ; it appears that it does not swing to and fro as a whole body, but at times the upper stratum is travelling faster and slipping over the heavier water. A series of observations indicated also that the discontinuity layer oscillates vertically up and down to a slight extent.

Although the upper stratum is distinct, the many series of observations made at E_1 do not show sharp differences in salinity between this epithalassa and the heavier water ; there is no reason to suppose that the warm upper stratum flows in from other areas to cover the cooler water, yet summer land drainage doubtless flows out freely to mix with the upper stratum rather than diluting the deeper water. When an inflow of water into the E_1 area occurs during the summer, it is sometimes the case that high salinity water creeps in along the bottom.

Usually some time in August, as the intensity of solar radiation wanes, there is a gradual cooling of the upper warm layer, heat being lost from the surface by evaporation, by radiation outwards, particularly at night, and by gradual passage through the discontinuity layer into the cooler water below. Convection currents set up by loss of heat from the surface penetrate deeper and deeper, until finally the layering breaks down, often hastened by a gale, and isothermal conditions result.

At this time, usually in September or October, the deep water attains its maximum temperature (Fig. 3) unless, as happened in 1921, a mass of warmer water flows in from a neighbouring area.

During October and November the loss of heat from the mixed water is rapid. An analysis of factors leads to the inference that evaporation from the surface plays a major part in regulating the rate of cooling. During these two months in particular the vapour pressure of the relatively warm surface water exceeds the pressure of aqueous vapour in the

atmosphere (Harvey, 1925). By February or the beginning of March the minimum temperature is reached and the annual cycle completed.

While the formation of an upper warm layer is taking place in the open sea, every variant up to isothermal distribution with depth occurs as the shore or shallow areas are approached. Observations made on the line between Station E_1 and Plymouth on August 7th, 1924, reproduced in Figure 4 show this very clearly.

The water in Plymouth Sound is in connection with the large body of water in the Channel which tends to stabilise its temperature. On plotting the temperatures observed near the western end of Plymouth Breakwater, they are seen to be a little lower during the height of summer than the surface temperatures at E_1, vertical mixing being more active, and distinctly lower than the temperatures at the Varne Light vessel in the Straits of Dover, the centre of an extensive area under 40 metres in depth.

During the winter, inshore and shallower water temperatures are lower than in deep areas, similar heat losses having greater effect on shallower depths. The observations on January 7th, 1929, shown in Figure 4, illustrate this, as also the crosses in Figure 3. At the Varne Light vessel the winter temperatures are still lower. It is a fair generalisation that the annual range of temperature is greater the shallower the water and the less interchange taking place with the deeper open sea.

Surface Temperatures.

The surface temperature of the sea is usually taken from a sample drawn in a bucket and is usually taken as representative of the upper 4 to 6 inches. On a cloudy day or with a strong breeze there is rarely any distinct difference from the temperature at 5 metres, but with a clear sky during the afternoon in summer or after a frosty night in winter with a smooth sea the difference may be material, although unusual in this area. The matter is of some importance since a very great quantity of surface temperature data have been accumulated for the English Channel and North Sea, and from these charts can be drawn for the whole body of water during the winter months when isothermal conditions are known to exist. During the summer months the temperature of the upper 5 metres is so dependent upon vertical mixing due to wind, that such charts would have restricted value, except in the shallower areas, such as the eastern part of the English Channel, where vertical mixing overcomes the tendency towards layering. In view of this Table I has been compiled in order to give an idea of the source of error likely to arise in using surface temperature data. All the observations were made at about midday, while if they

had been made in the early morning doubtless some of the differences might have been greater; on the other hand, they were made on days when the sea was slight or moderate, while if the sea had been moderate or rough the differences would have been less.

TABLE I

DIFFERENCE IN TEMPERATURE (°C.) BETWEEN SURFACE SAMPLE AND WATER AT 5-METRES DEPTH AT STATION E_1.

	October.	November.	December.	January.	February.	March.
1921	+0·04°C. +0·12	−0·70° −0·04	−0·19°			
1922	+0·10	+0·01		−0·06	−0·61	−0·04
1923	+0·02	−0·18	−0·35	−0·05 −0·35	−0·11	+0·08
1924	−0·02	−0·39	−0·03	−0·06	−0·25	
1925	+0·40		−0·03	+0·01	−0·19	+0·06
1926	−0·09	−0·05	0·00 +0·08		−0·10	+0·10
1927	+0·10	+0·25	+0·12		+0·02	+0·30
1928	+0·01	0·00		+0·12	+0·17	−0·02
1929	−0·10			− ·02 − ·15	+ ·05 + ·30	0·00

FLUCTUATIONS IN THE ANNUAL CYCLE.

Not only does the maximum temperature attained at the end of summer, and the minimum temperature to which the water falls at the end of winter fluctuate from year to year, but the dates at which some particular temperature is attained differ greatly. It is perhaps the latter which is most significant to the biologist, since the breeding of many marine animals is strictly limited to a relatively narrow range of temperature. As a case in point the water near the bottom at E_1 rose to 12° C. at about the third week in June in 1921, and at the end of first week in August in 1924, and to 13° C. at about mid-July in 1921, and during the third week in September in 1924. It is obvious that such a fluctuation would have a profound effect upon any animal which breeds in the region of 12°–13° C.

The interval of about a month between each set of observations does not allow a precise value being given for the maximum and minimum temperatures attained each year by the surface water at Station E_1, but tolerably approximate values can be taken from faired curves for these temperatures and the dates they were attained in deeper water. These are shown in Table II.

TABLE II.

Approximate Maximum and Minimum Temperatures Attained by the Lower Stratum of Water at Station E_1, and Dates at which such were attained.

Year.	Maximum temperatures.	Minimum temperatures.
1921	15·4° C. third week in October	— —
1922	14·2 end September	9·5 early April
1923	13·5 first week in October	9·2 March
1924	13·1 early October	7·9 March
1925	13·6 end first week in October	9·1 late March
1926	14·5 third week in October	9·3 March
1927	13·7 early October	9·0 late March
1928	14·7 early October	8·9 early February
1929	14·0 (?) end of first week in October	8·4 early March

The isopleth diagrams in Figures 5, 6, and 7 show the temperature changes which have taken place each year at Station E_1. Black circles indicate the dates upon which series of observations were taken, and from which the isopleths are drawn.

The general distribution of temperature in the western part of the English Channel during the winter of 1927–28 is shown on the charts in Figure 8. These are compiled from surface temperatures on the cross-Channel steamship routes shown in Figure 1. They show the loss of heat during November to be most rapid in the less deep area to the eastward, which is a general phenomenon.

With regard to the fluctuations from year to year there is, I think, only one outstanding instance where the inflow of warmer water unmistakably and materially affected the cycle ; in the autumn of 1921. During other years inflow of warmer or colder water undoubtedly took place from time to time (March, 1928), but the effect of such upon the temperature cannot be clearly distinguished from the effect of fluctuating meterological conditions—solar radiation, dryness of the atmosphere leading to increased evaporation, and clear sky at night leading to increased radiation of heat into space.

In Figure 9 the observed salinities of the water at various depths at E_1 are given for the latter part of 1921, and below the integral temperature of the whole column of water from surface to bottom. An accretion of heat took place between September 15th and October 18th, a time when the water is normally losing heat. A similar curve for the following year is given below. Presumably as a result of this inflow of more saline and warmer water, a singularly warm and late autumn was experienced (Harvey, 1925).

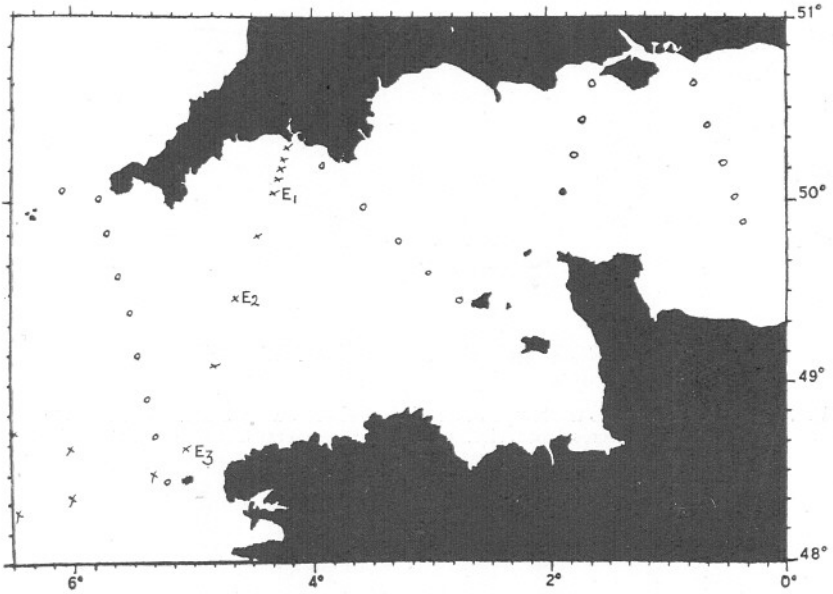


FIG. 1.—Circles indicate positions at which surface samples are taken at regular (fortnightly) intervals. Crosses indicate positions at which research vessels work stations or take surface samples.

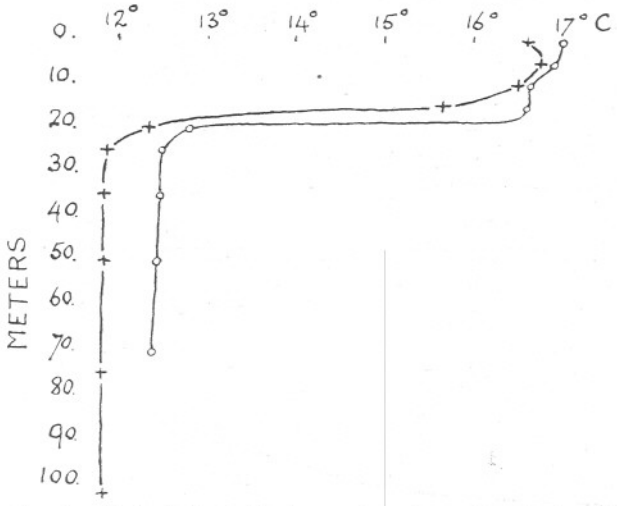


FIG. 2.—Circles indicate the temperature observed at Station E_1 on August 2nd, 1927; crosses indicate the temperature at Station E_3 on August 3rd, 1927.

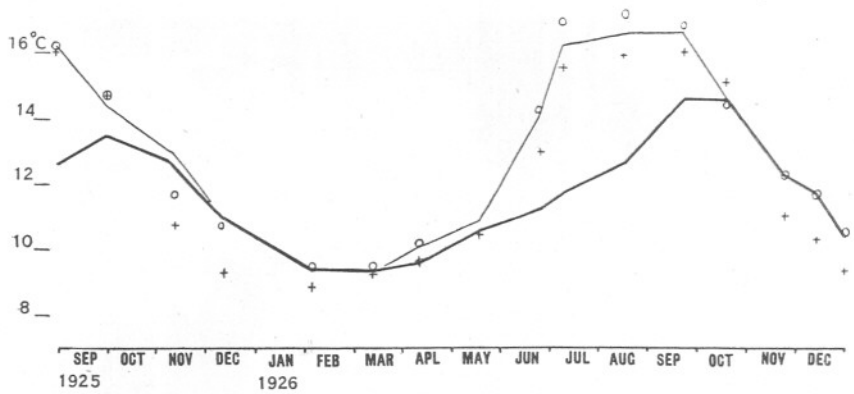


FIG. 3.—Thick line shows the temperature of the bottom water, thin line the temperature of the water at 5 metres depth, circles the surface temperatures observed at Station E_1, crosses show the surface temperatures observed off the western end of Plymouth Breakwater.

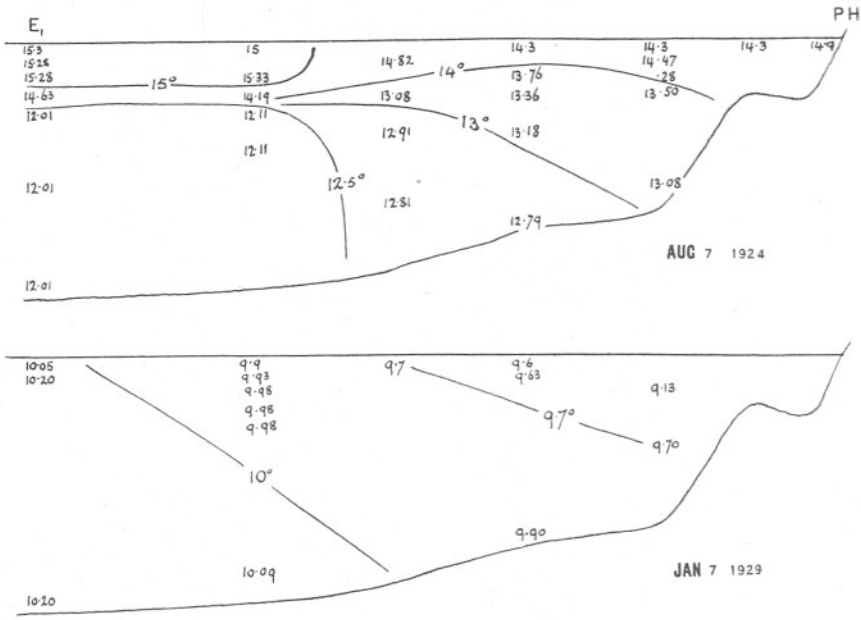


FIG. 4.—Sections between Station E_1 and Plymouth showing the distribution of temperature with depth.

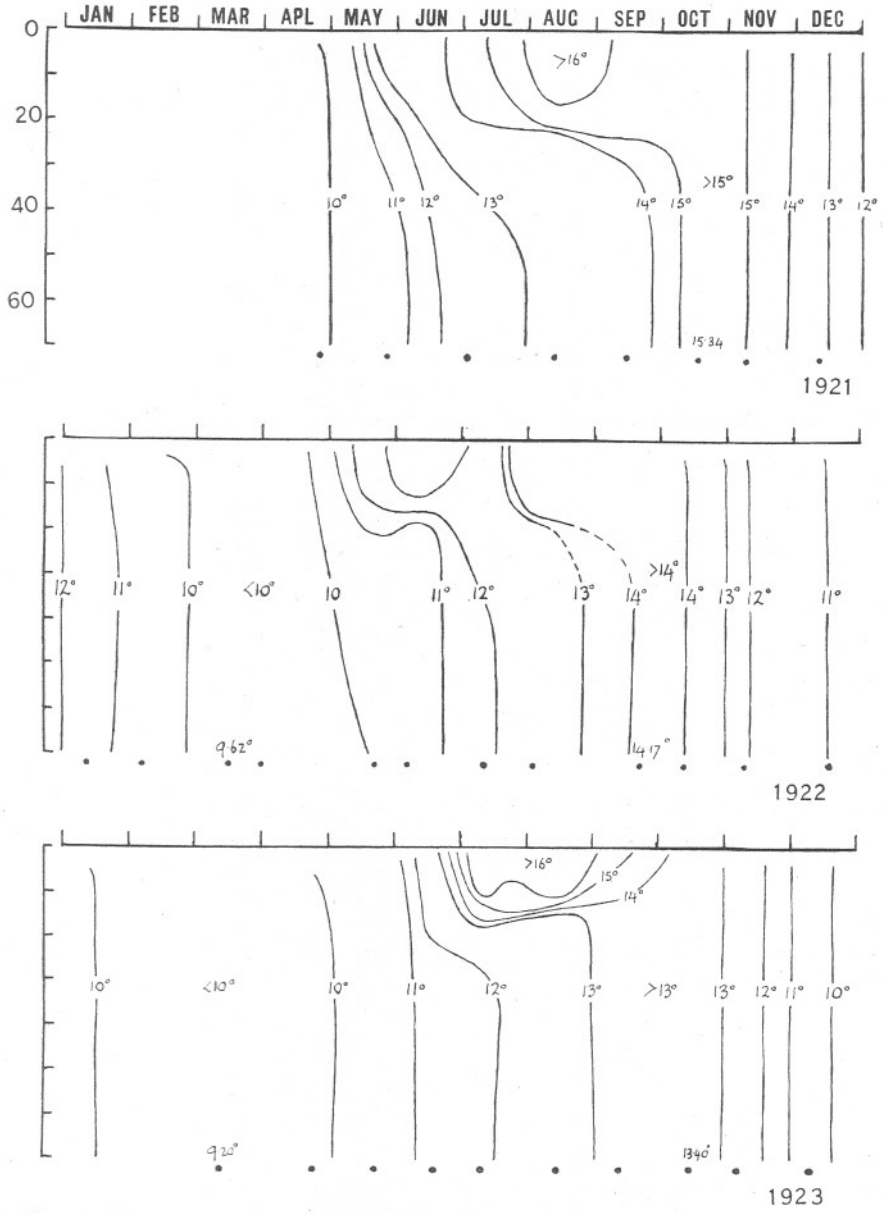


FIG. 5.—Isopleth diagrams showing the distribution of temperature with depth from April, 1921, to December, 1923, at Station E_1.

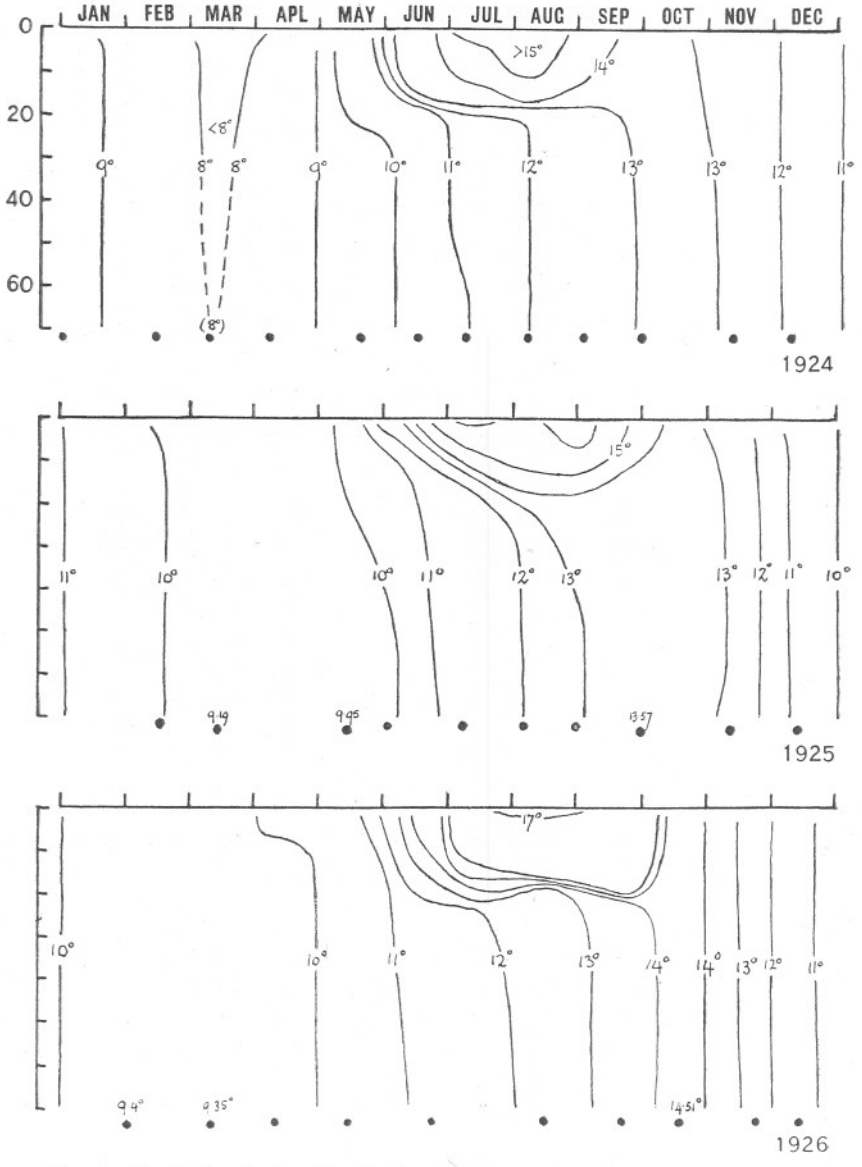


FIG. 6.—Isopleths, showing distribution of temperature with depth at Station E_1 during 1924, 1925, and 1926.

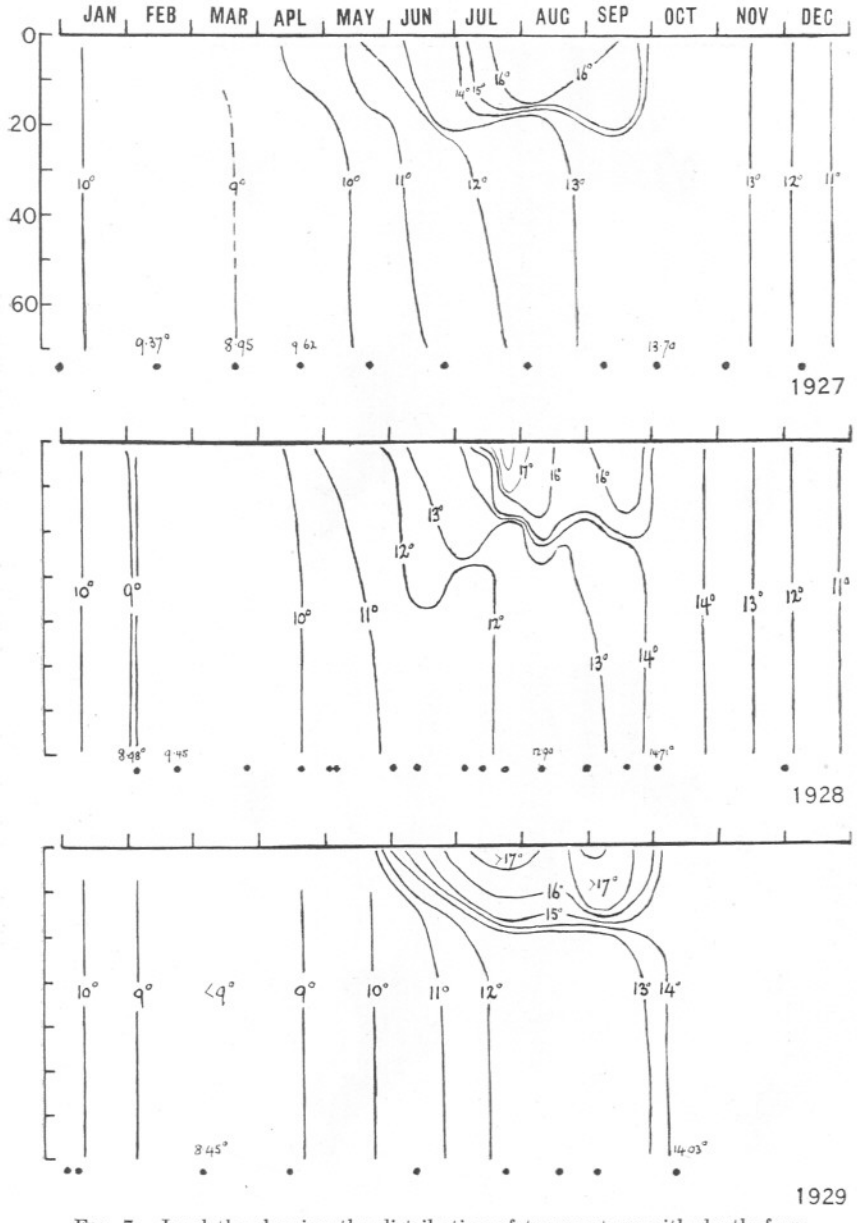


FIG. 7.—Isopleths showing the distribution of temperature with depth from January, 1927, to October, 1929.

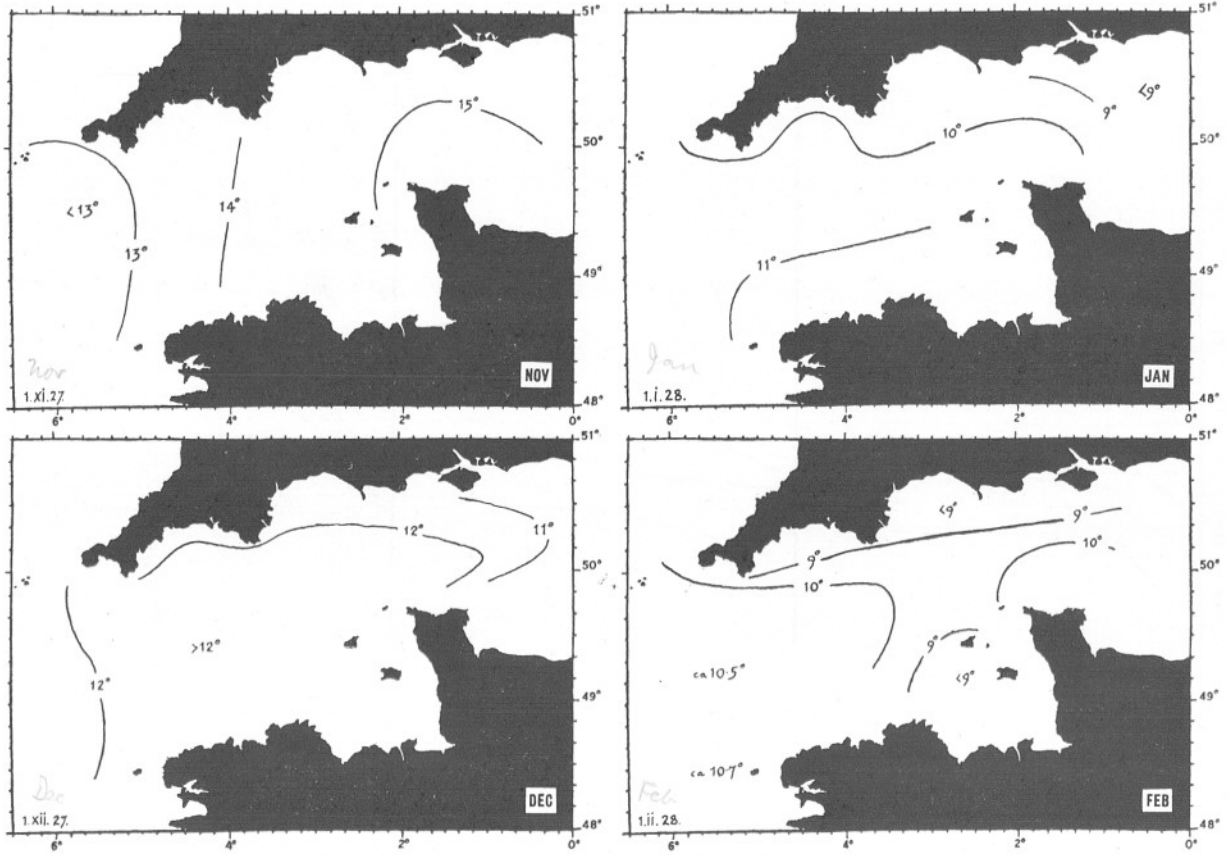


FIG. 8.—Distribution of temperature during the winter of 1927–1928.

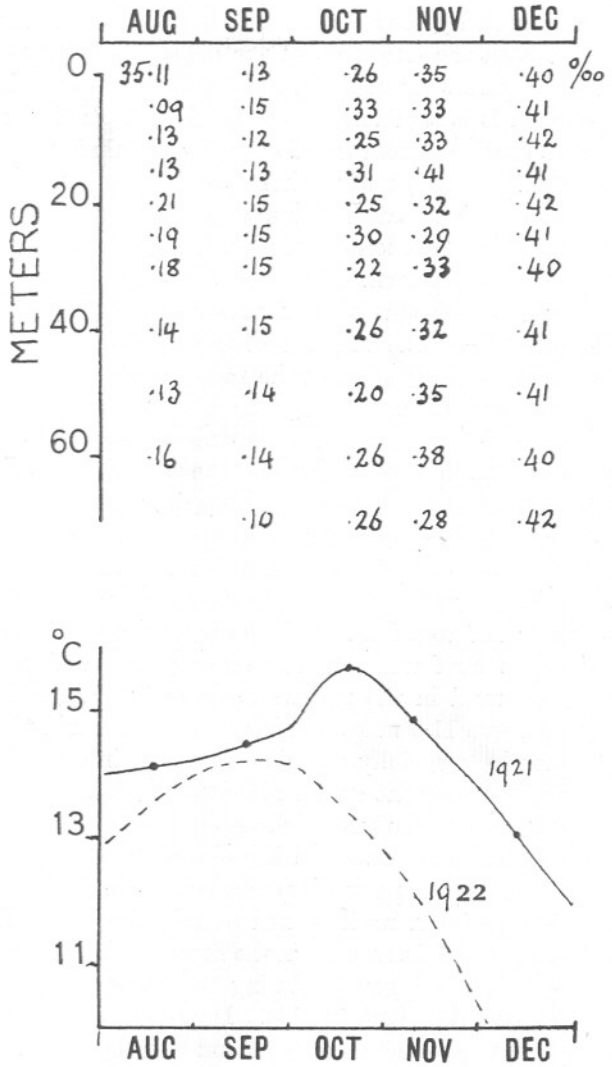


FIG. 9.—Upper diagram shows the salinity of the water observed at Station E_1 from August to December, 1921; lower diagram shows the integral mean temperature of the column of water from surface to bottom.

PART II. THE DISTRIBUTION OF SALINITY AND CIRCULATION OF THE WATER.

Our present knowledge of the circulation in the English Channel rests upon inference, with the exception of the definite proof by Carruthers (1928) that water passes through from the Atlantic into the North Sea. In this connection it is significant that the general conclusions arrived at by Matthews (1905–14) from the distribution of salinity and temperature and by Gehrke (1907) rest unaltered by subsequent observations. It does appear, however, that the circulation of the water masses, and in consequence the distribution of salinity, is more irregular and intermittent than hitherto expected.

The following brief account aims at presenting a generalised picture of the western part of the English Channel, before discussing the occurrences which are suggested by the more intense surface sampling carried out since June, 1925.

A continuous series of current measurements made by Carruthers (1928) at the Varne Light vessel shows that the residual current normally passing from the English Channel into the North Sea is occasionally held up, or even reversed for a period, by easterly and north-easterly winds, and is at other times greatly augmented by strong south-westerly winds. The mean residual movement past the Varne Light vessel at a depth of 11 metres was found to be 2·7 miles daily, into the North Sea, the maximum value so far found was 16·8 miles. The maximum residual current which occurred in the reverse direction, from the North Sea into the Channel, was 11·9 miles in a day. It was found that during the autumn months especially the flow of water into the North Sea was greatest, while during the summer months the flow was least.

Water of variable but relatively high salinity enters the mouth of the English Channel and passes eastward in the form of a tongue (Fig. 10). This tongue of water on its passage up Channel becomes more and more diluted with coastal water, itself diluted by land drainage. In spite of greater rainfall in winter, its salinity in the Straits of Dover at the Varne Light vessel is in general greater during the winter than during the summer months (Lumby, 1925, p. 14). Doubtless this is due to the increased speed of its passage up Channel and into the North Sea during the autumn and winter. A peculiar phenomenon in connection with the salinity of this tongue of water as it extends eastward has been pointed out by Lumby (1925, p. 4), who noted that during the years 1921 and 1922 the average salinity of the water increased as it passed on to the relatively shallow soundings between Newhaven and Dieppe, being higher there than where the tongue was deeper and nearer the Atlantic, on the line Southampton–St. Malo. He considered that more

saline water had crept up Channel as a subsurface current to mix with water above and so appear on reaching shallow soundings, where wave motion and tidal streaming over the bottom bring about effective vertical

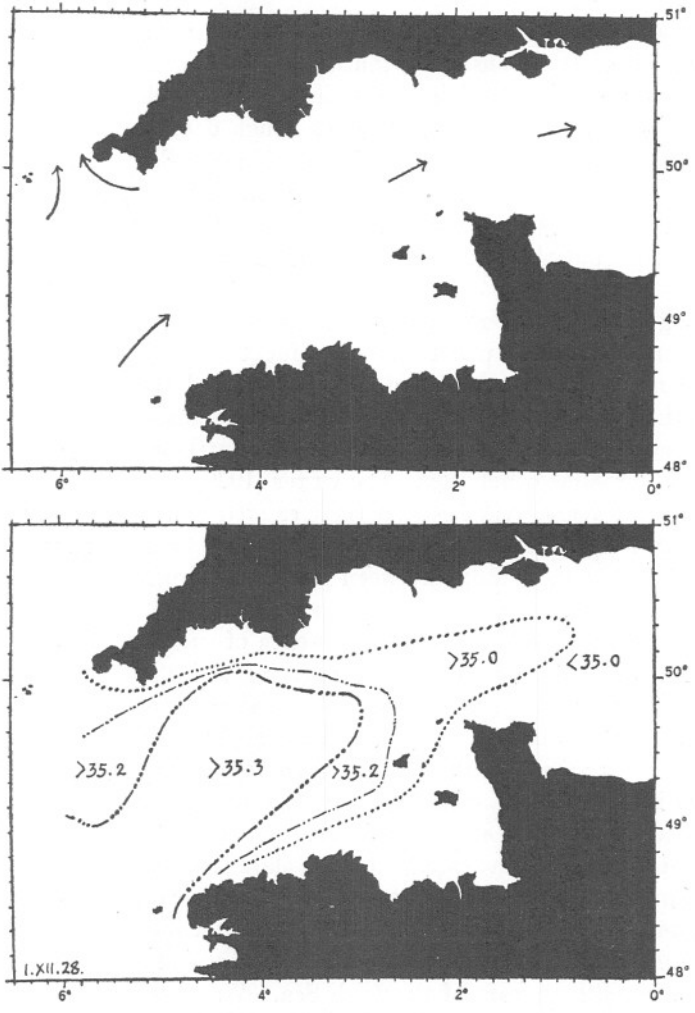


FIG. 10.—Upper diagram shows the general current system. Lower diagram shows a type of distribution of salinity expected to arise from such a system of currents.

mixing. These two years were remarkable for the inflow of highly saline water from the Atlantic. A description of the movements of bottom trailing and surface drift bottles during 1924 is given by Carruthers (1927)

who also discusses the question of cyclonic swirls set up by the penetrating tongue of water.

The shape or form of this tongue of water is very variable (Figs. 13–16). In winter the salinity is generally much the same from top to bottom ; in summer the number of cases observed where more saline water has penetrated under a layer of less saline water to any great distance are not numerous. It is considered that maps showing the surface salinity in this area are usually a fair rough picture of the salinity of the whole water mass. The picture is certainly a rough one, on account of this, of the limited intensity of sampling, and of errors likely to arise during or after rainy weather or heavy evaporation. Further, it is clear that the isohalines do not actually follow the smooth lines usually indicated in such maps, but that numerous offshoots, lacunæ and isolated patches exist.

Passing next to the circulation at the mouth of the Channel, Gehrke (1907) considered that under the centrifugal force due to the earth's rotation more water entered the English Channel than passed on into the North Sea, the surplus running out past the Lizard and Land's End. From the distribution of salinity and density, Matthews and later Lumby arrived at the same conclusion. The writer (1929) from hydrodynamical considerations found evidence that there existed a north-going difference in velocity between the surface water and the layer at 60-metres depth amounting to $1\frac{1}{2}$ miles a day between Land's End and the Scillies at the end of June, 1924.

There can be little doubt of the existence of such a residual current, superimposed on the tidal streaming, carrying water northward into the mouth of the Bristol Channel—variable in velocity and perhaps intermittent. Such a current system as suggested would be expected to give rise to a salinity distribution of the type shown in Figure 10. Changes in the current system would lead to changes in the salinity distribution ; hence the value of mapping the latter at short intervals of time in order to gauge the changes taking place in the general circulation. Such changes frequently appear to be swift and of short duration.

With regard to this general current system at the mouth of the English Channel, Matthews (1911 and 1914) found evidence of a cyclonic circulation in the southern part of the Irish Sea. Water moving northwards past Land's End and curling towards the south-east coast of Ireland moved southwards and westward to rejoin the north-going stream past Land's End. There was evidence that a similar movement of the upper layers over the stratum at 60 metres existed at the end of June, 1924 (Harvey, 1929). Matthews found evidence that the southern boundary of this cyclonic system lay further southward during the winter months. The more saline Atlantic water entering the Channel then lay closer to

Ushant, the northern part of the mouth of the Channel being blocked by the less saline water of this cyclonic system.

The water, lying at the mouth of the English Channel and forming the base of the tongue which extends eastward, is of very variable salinity. Thus in February, 1903, water of 35·5°/$_{oo}$ lay north of Ushant and in July of 1928 the whole mouth of the Channel was filled with water of under 35·0°/$_{oo}$.

As the Atlantic Stream creeps gradually northward along the edge of the continental shelf it undergoes gradual dilution : when the stream is least torpid, water of high salinity may be expected to swing from the ocean into the mouth of the English Channel under the influence of the earth's rotation. When, in addition, wind favours its passage onward and through the Straits of Dover the highest salinity at the entrance of the Channel might be expected.

These surges of the Atlantic Stream are very variable as judged by the change in latitude of the isohalines in the open ocean and the salinity of the water which penetrates, perhaps welling up, into the relatively shallow soundings at the mouth of the English Channel and in the Irish Sea.

The most notable effects recorded are those in 1903 when high salinity water persisted for over two years and again in 1921. In the early summers of 1923 and 1928 an unusual condition was observed. After heavy rains in the Loire watershed (Atkins, 1929) the English Channel filled with water of abnormally low salinity, much of which apparently came from the west coast of France, moving northward and entering the Channel past Ushant. By July, 1928, the entire Channel was filled with water having a salinity of less than 35·0°/$_{oo}$ (Figs. 15 and 16).

The Surface Salinity Diagrams.

The routes along which samples have been taken, about twice monthly, are shown in Figure 1, in which circles indicate the usual positions of sampling. The data obtained since June, 1925, when the line Plymouth–Guernsey was commenced, have been plotted in the manner shown in Figure 11. It is usually simple to draw lines marking salinities of 35·0, 35·2, 35·3, etc., and so obtain moderately true isopleths indicating the change in salinity with time and with position along the particular route. Not infrequently high salinities are found at one or two positions at a particular date, while no such high values were obtained either a fortnight previously or a fortnight later. This may mean that a narrow tongue has penetrated to the position shown and breaks up to disappear by mixing with the surrounding water mass during the ensuing fortnight, or alternatively that an outlying patch happened to be passing across the

route. In some instances further evidence can be obtained from stations in the neighbourhood which have been sampled at various depths within a few days of the occurrence by a research vessel.

From these isopleth diagrams 43 charts have been prepared showing the distribution of surface salinity at the beginning of each month. Lines are drawn connecting up the positions at which salinities of 35·0, 35·2, 35·3, etc., occur on each route, wherever possible due regard being paid to data obtained shortly before or after at various depths by the research vessels.

There can be little doubt that these boundary lines are in fact very

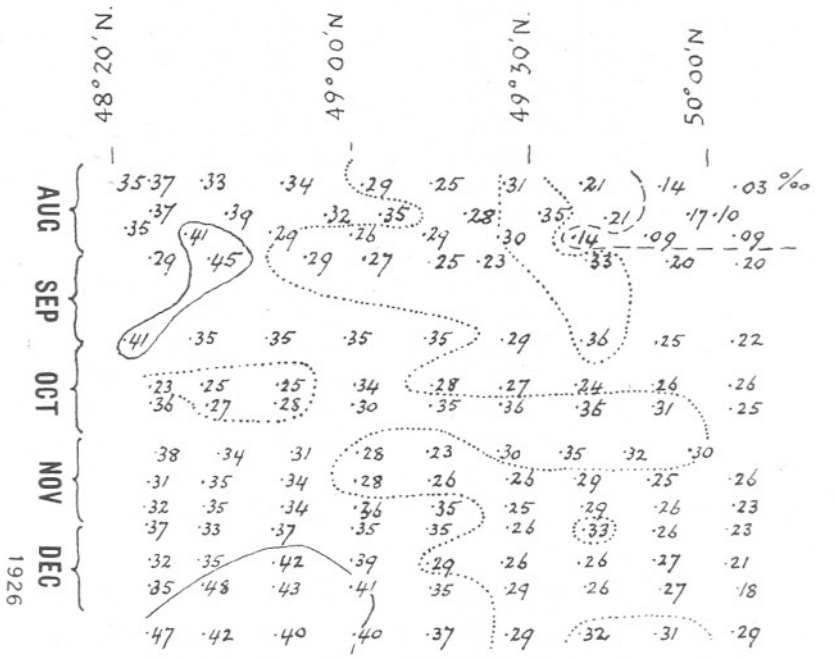


Fig. 11.—Portion of surface salinity isopleth diagram across the mouth of the English Channel (line Longships L.V. to Ushant).

irregular, with indentations, lacunæ, and outlying patches, but the fair lines drawn in such diagrams are the only means of indicating the general distribution without having data from impracticably intense sampling. Further, on some occasions less saline water lies over more highly saline or *vice versa*, the isohalines lying obliquely, not vertically; an outlying patch may be near the surface and not extend to the bottom, as was found by Matthews on occasions.

However, on taking the available evidence as a whole, a conclusion does seem justifiable that such charts give a tolerable rough picture of the

distribution of the water masses on most occasions. Any inferences regarding the movements of the water masses, as deduced from the changes they bring about in the distribution of surface salinity, rest upon the validity of the above conclusion. In the area under discussion there have been only a limited number of stations worked from top to bottom within two or three days of each other since June, 1925. If we consider a wide area, however, the distribution in February, 1927, is interesting because the French, Irish and our own vessels worked lines of stations all between the 15th and 18th. In Figure 12 the surface salinities along the steamship routes marked with circles are filled in from isopleths, and the actual observed salinities along the routes followed by the research vessels are for the most part shown in the sections. In the deep water south of Ireland the isohalines are not usually vertical—the presence of layers of more saline water sandwiched between less saline water above and below was particularly noticeable during the summer of 1929. Towards the eastern end of the English Channel and in the shallower part of the North Sea the salinity is usually the same from top to bottom. In such areas, therefore, changes in the distribution of surface salinity are more nearly representative of the movements of the water masses.

Turning next to the 43 distribution diagrams from June, 1925, to December, 1928, we find during this time an irregular inflow of high salinity water from the Atlantic into the mouth of the Channel and its disappearance. The most marked and lasting instances are shown in Figures 13, 14 and 16 respectively, while in Figure 15 is shown an incursion of low salinity water rounding Ushant and passing into the English Channel.

From June, 1925, to the end of 1926 water having a salinity of over 35·3°/$_{oo}$ usually lay to the westward of the line Lizard–Ushant. However, during the month of January, 1926, there was a marked incursion of this water into the Channel extending to about 2° 40′ W. long. (Fig. 13). By the beginning of March it appeared to have mostly moved north-westward and on April 1st was only found in the neighbourhood of the Scillies. During the next three months there was a fall in salinity in the mouth of the Channel and at the beginning of July the mouth was filled with water having a salinity less than 35·2°/$_{oo}$. It is not clear how this fall in salinity arose. There is no reason to suppose that on the whole low salinity water from the North Sea moved into the Channel during the period February to June, nor is there any decided indication of low salinity inshore water from the west coast of France entering the English Channel through the Le Four Channel or close to Ushant.

If we consider the distribution of the water masses having a salinity greater than 35·3°/$_{oo}$ on February 1st, 1926 (Fig. 13), it is difficult to conceive how this great mass of water can have become diluted by

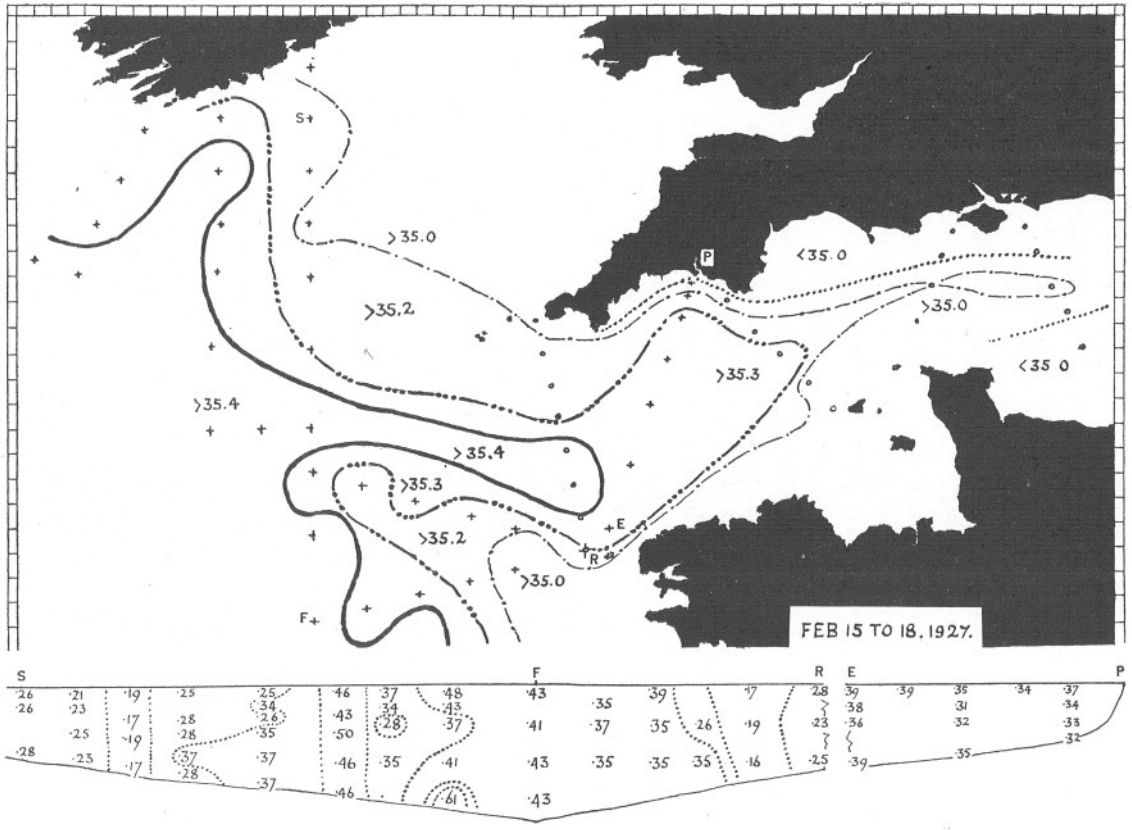


FIG. 12.—Chart showing the distribution of surface salinity, February 15th to February 18th, 1927. Sections P to E, R to F, F to S, showing the distribution of salinity with depth between the same dates.

infiltration and mixing along the edges within two months to give rise to the condition shown for April 1st. It seems much more probable that most of it had slowly swirled away north-westward, retaining its characteristic salinity, and had been largely replaced. The same argument applies even more clearly to the changes portrayed during March, April, May, and June, 1927, in Figure 14. Even in the case of a small patch or outlier of water, having a salinity greater than that of the surrounding water mass, and a surface area of no more than one or two hundred square miles, it is difficult to conceive that it would mix horizontally with the surrounding less saline water at all rapidly. Rather it might be expected that much of it would retain its characteristic higher salinity for several weeks or more.

From July, 1926, to December no samples were obtained on the Plymouth–Guernsey route, and the other data do not show any remarkable changes.

From December, 1926, to March, 1927, a decided inflow of Atlantic water into the mouth of the Channel is shown in Figure 14. The inflow indicated as taking place during December represents a volume of water of over 120 cubic miles. Current measurements at the Varne Light vessel indicate that during this month of December about 18 cubic miles of water per day passed from the North Sea into the English Channel—a reversal of the usual direction of the residual drift. Hence, in order to make way for the incoming Atlantic water, it is not improbable that over 120 cubic miles of water passed out of the Channel round the Lizard and Land's End. Assuming that this west-going stream extends for about 12 miles off shore, its velocity residual to the to and fro tidal streaming would average about 9 miles per day, perhaps rather more, during this particular month. Tidal stream observations off the Lizard in calm weather, probably only in summer, indicate a residual component in a westerly direction. " Off the Lizard the streams are of nearly equal duration, the west-going stream running . . . at a maximum rate of 3 knots near the rocks ; and the east-going stream . . . at a maximum rate of 2 knots at springs " (*The Tides and Tidal Streams of the British Isles*, Tizard, p. 43, 1909). During March, 1927, the $35{\cdot}3^{\circ}/_{\circ\circ}$ salinity water penetrated far into the Channel in the form of a narrow tongue (Fig. 14) ; some 35 cubic miles of water passed during the month into the North Sea helping to draw this tongue westward. During April, May, and June this formation broke up and there is indicated a gradual retreat north-westward of the higher salinity water.

From July, 1927, to March, 1928, there were no considerable intrusions of high salinity water.

During March and April, 1928, the mouth of the Channel filled up with low salinity water (Fig. 15), unusually transparent and rather warmer

than usual for the time of year. It is suggested (Atkins, 1929) that this water came in part northward from the west coast of France, rounding Ushant into the English Channel, and in part from drainage from the Seine watershed. In the Loire and Seine basins the rainfall during February was approximately 75% above normal, and 50 to 60% above normal for the three months January, February and March. This low salinity water possibly overlay water of higher salinity in the neighbourhood of Ushant, at all events such a condition was found later on May 8th (Fig. 15, section).

Such a condition was only observed once before since 1921, when an upper layer of water having a salinity less than 35·0°/$_{oo}$ was found extending some 60 miles north of Ushant in April, 1923. During this year also the rainfall in the Loire and Seine basins was exceptionally high, approximately 100% above normal for the month of February.

The next change of considerable extent is the inflow of higher salinity water commencing in July, 1928, and culminating on or after December, 1928 (Fig. 16).

The proofs of this paper have been read by Lieut.-Comdr. J. R. Lumby, to whom I am further indebted for several suggestions.

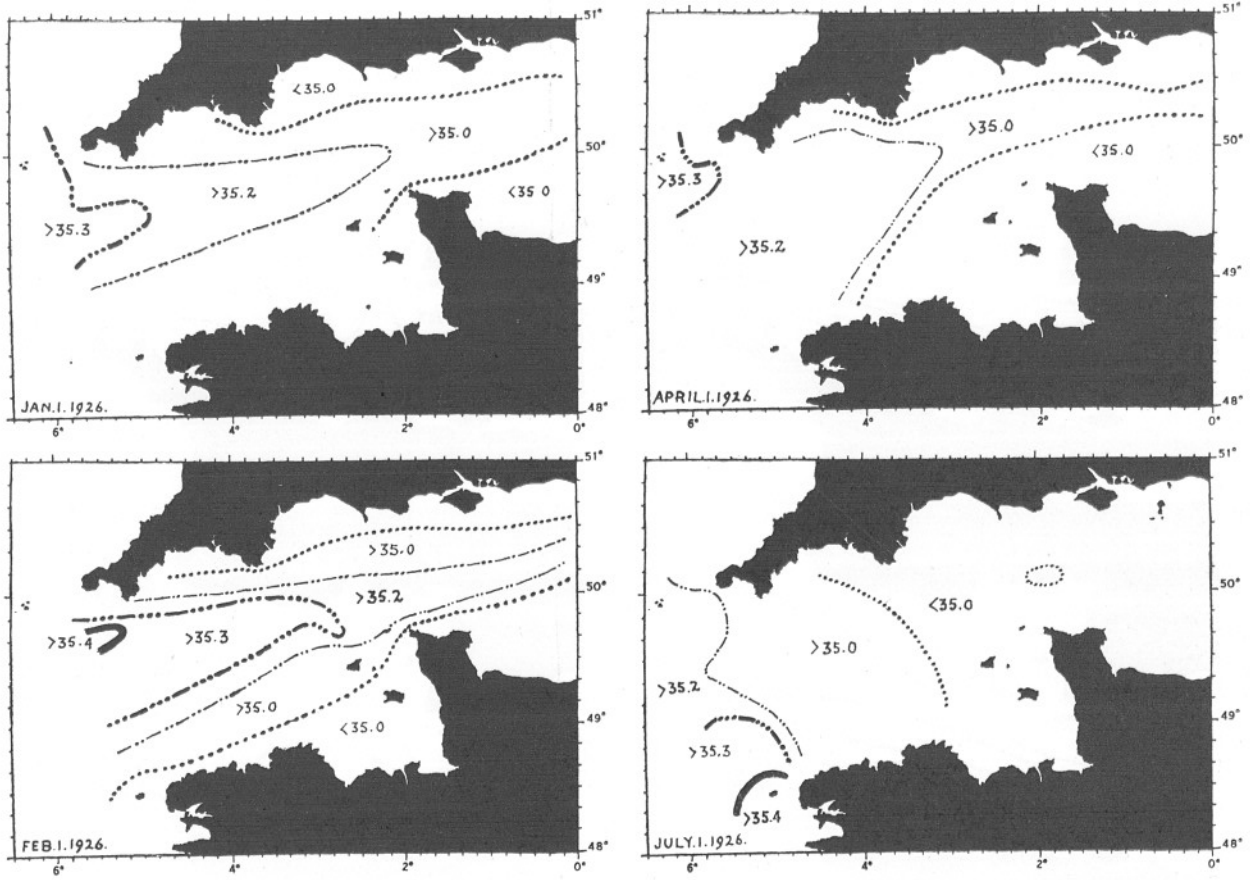

JAN.1.1926.
<35.0
>35.0
>35.2
>35.3
<35 0
APRIL.1.1926.
>35.0
<35.0
>35.3
>35.2
FEB.1.1926.
>35.0
>35.2
>35.4
>35.3
>35.0
<35.0
JULY.1.1926.
<35.0
>35.0
>35.2
>35.3
>35.4
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 13.

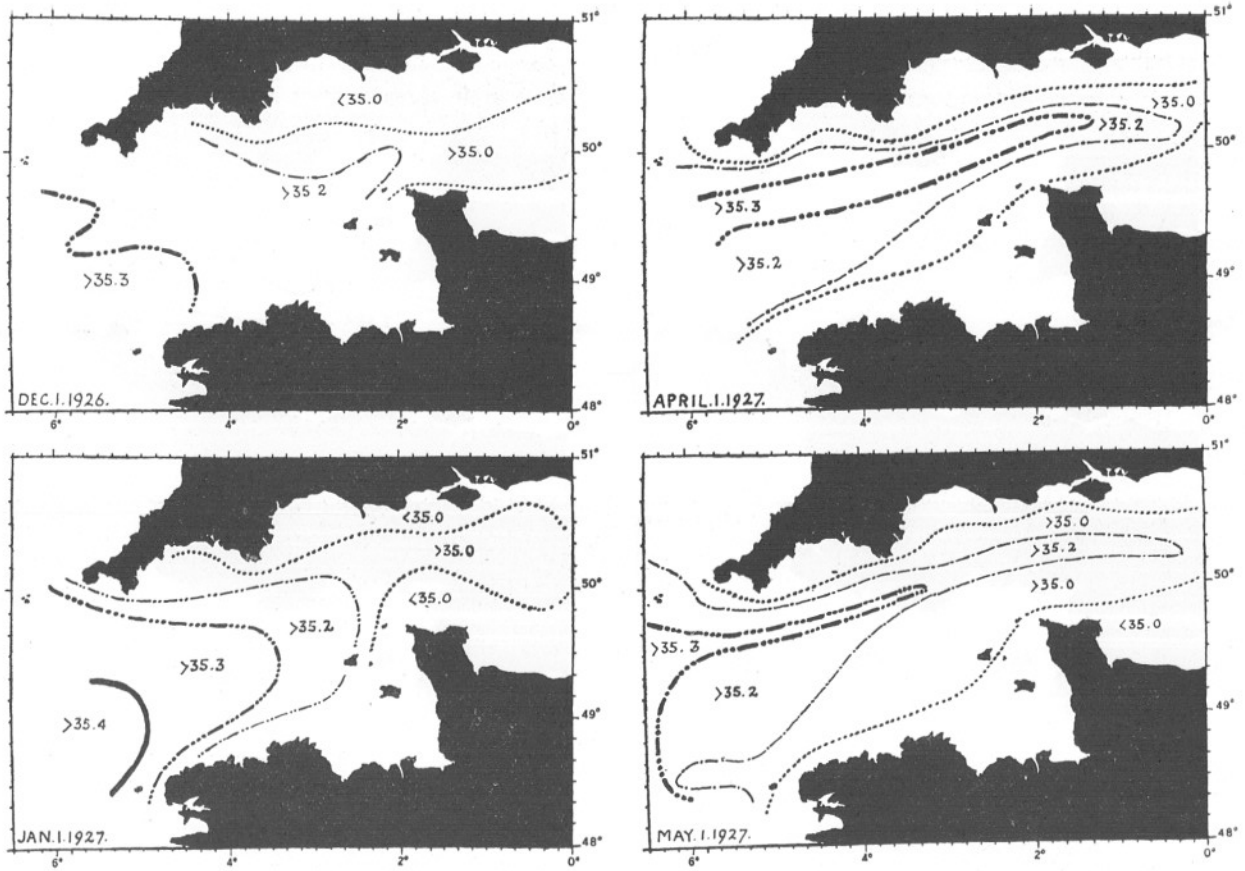

<35.0
>35.0
>35.2
>35.3
DEC.1.1926.
>35.0
>35.2
>35.3
APRIL.1.1927.
<35.0
>35.0
>35.2
>35.3
>35.4
JAN.1.1927.
>35.0
>35.2
>35.0
<35.0
>35.3
>35.2
MAY.1.1927.
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 14.

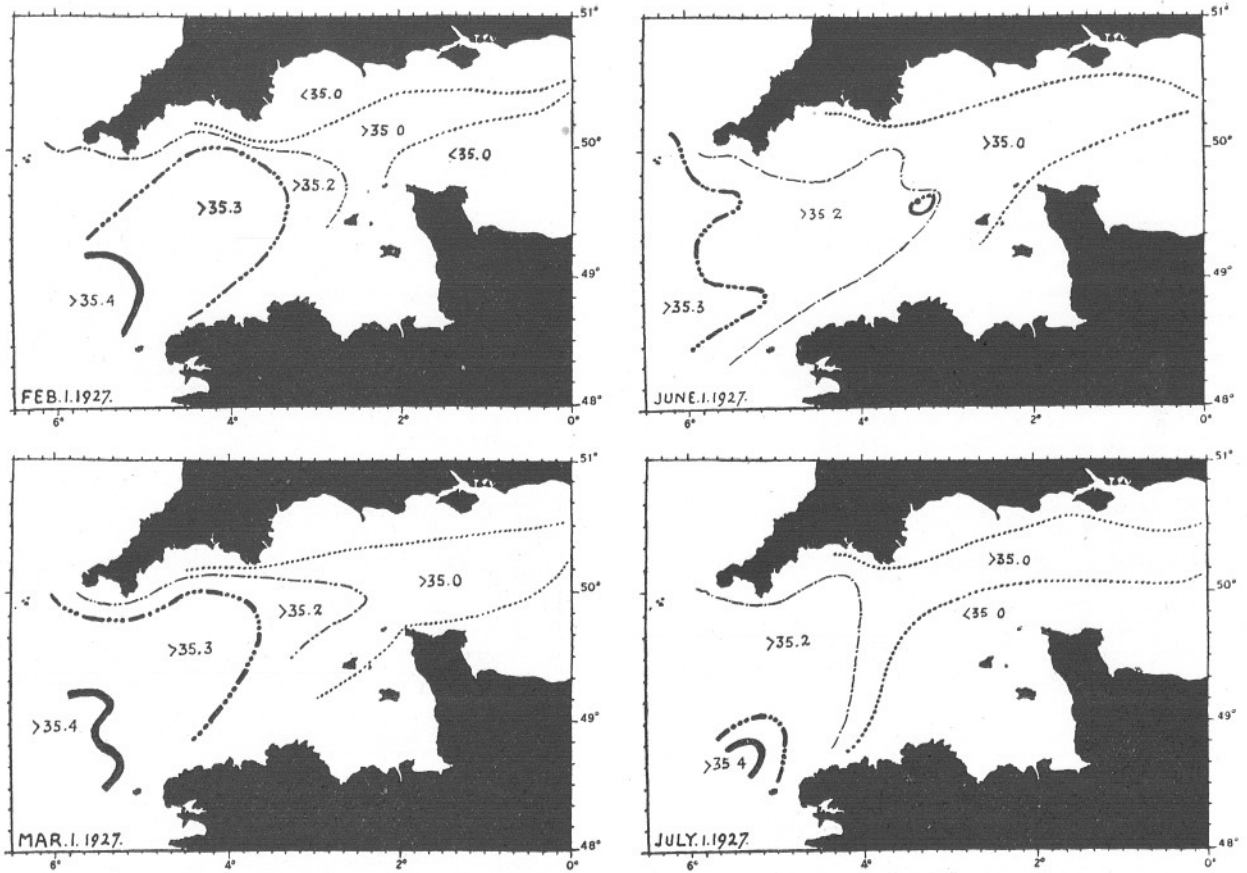


FIG. 14 (*continued*).

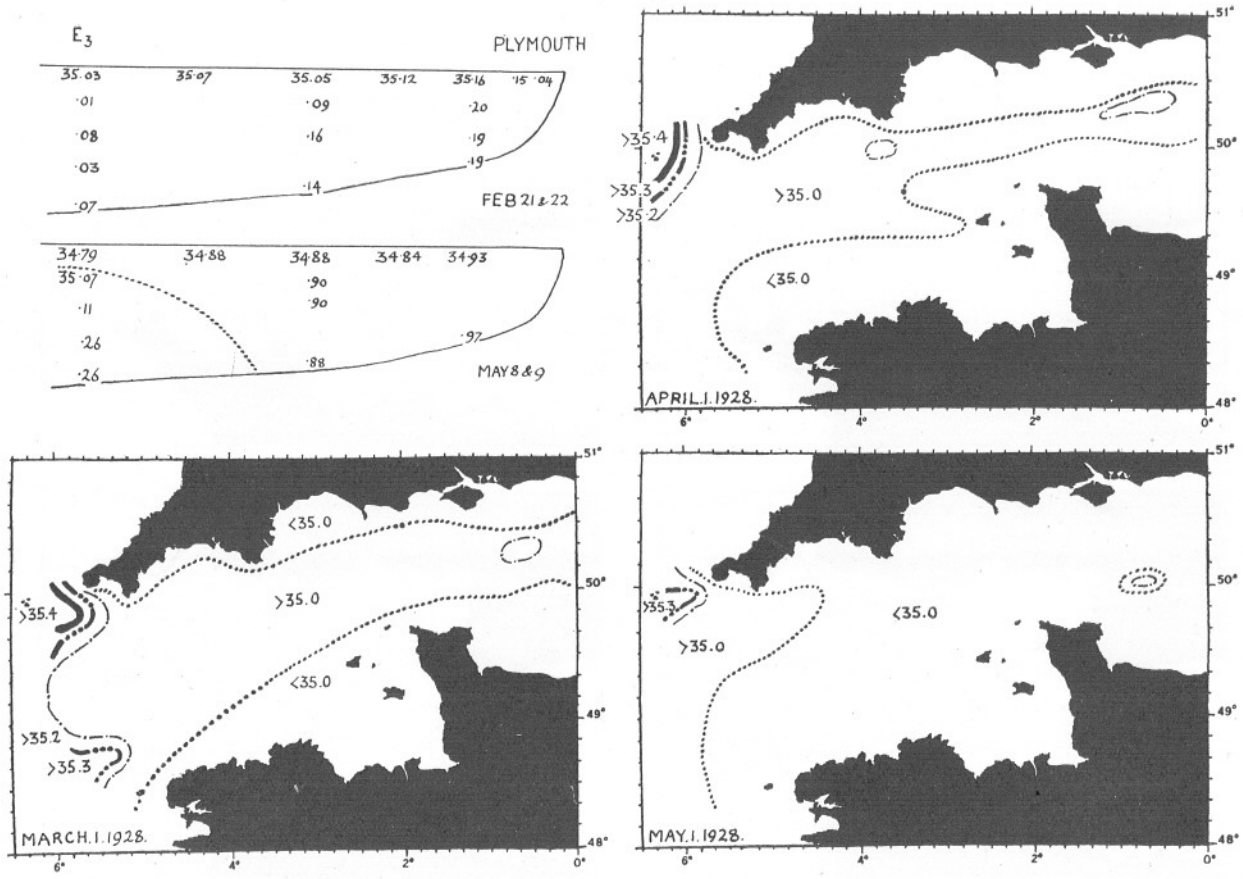

E3
PLYMOUTH
35·03 35·07 35·05 35·12 35·16 35·04
·01 ·09 ·20
·08 ·16 ·19
·03 ·19
·14
·07
FEB 21 & 22
34·79 34·88 34·88 34·84 34·93
35·07 ·90
·11 ·90
·26 ·97
·88
·26
MAY 8 & 9
>35·4
>35·3
>35·2
>35·0
<35·0
APRIL. 1. 1928.
MARCH. 1. 1928.
MAY. 1. 1928.
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 15.

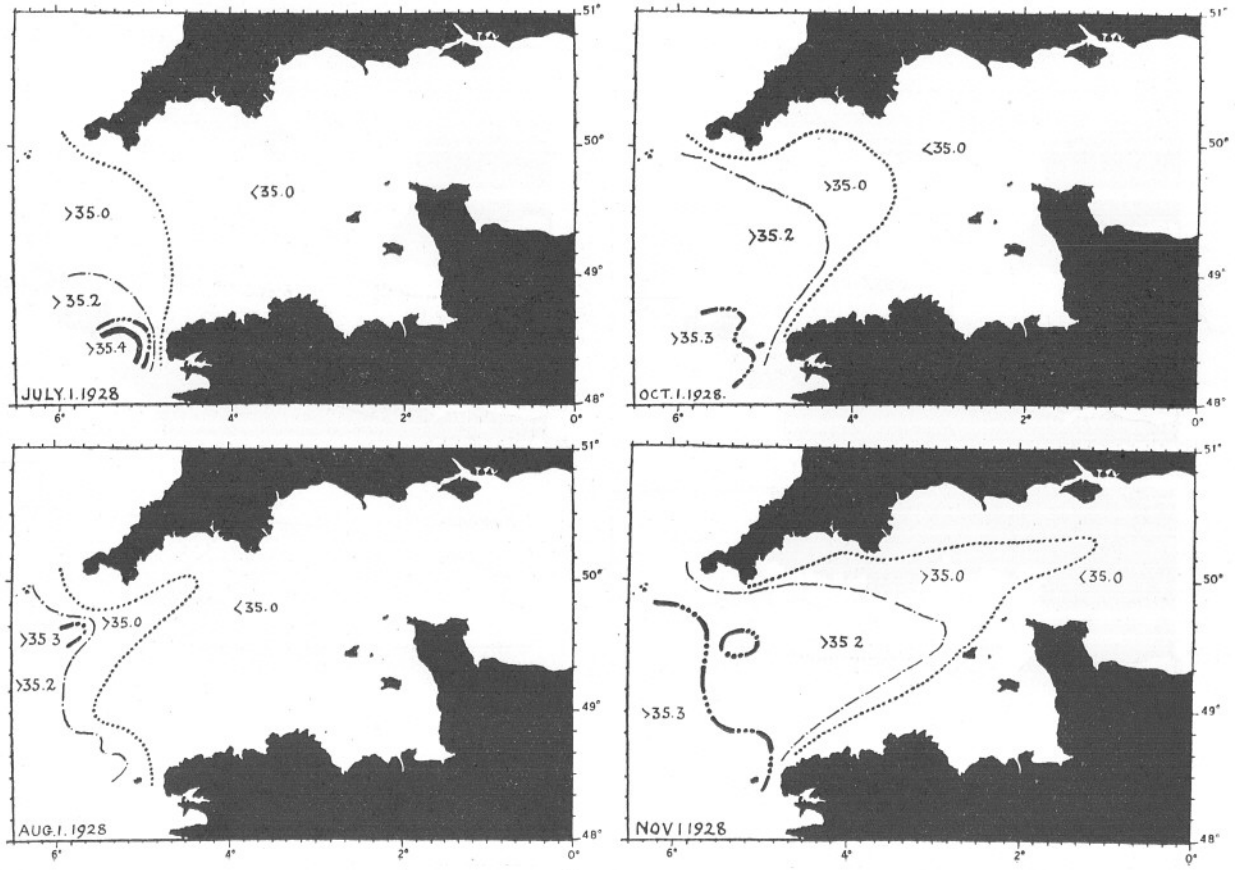

JULY 1. 1928
<35.0
>35.0
>35.2
>35.4
OCT. 1. 1928.
<35.0
>35.0
>35.2
>35.3
AUG. 1. 1928
<35.0
>35.0
>35.3
>35.2
NOV 1 1928
>35.0
<35.0
>35 2
>35.3
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 16.

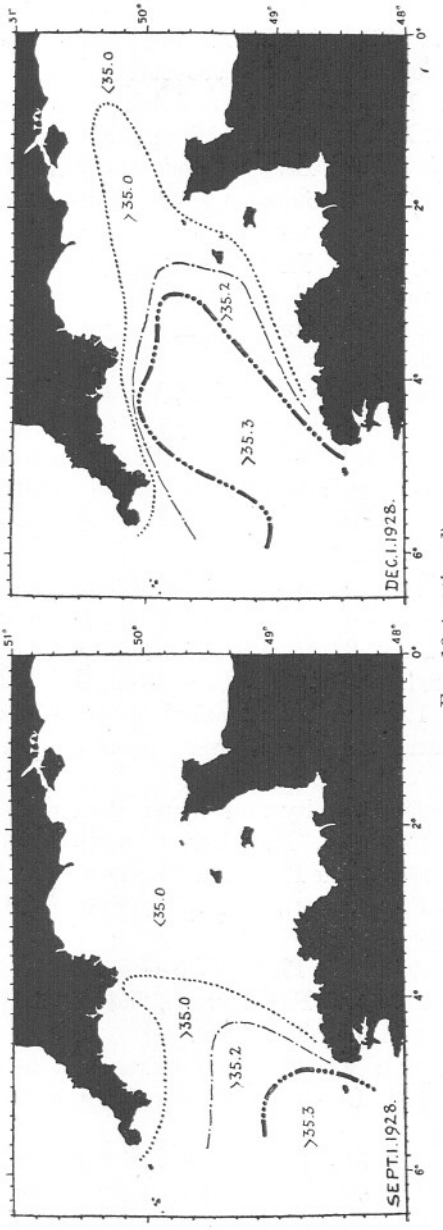


FIG. 16 (*continued*).

REFERENCES.

ATKINS, W. R. G. 1925. On the Thermal Stratification of Sea-water. Journ. Mar. Biol. Assn., **13**, pp. 693–699.

ATKINS, W. R. G. 1929. See Poole and Atkins, Photoelectric Measurements. Journ. Mar. Biol. Assn., **16**, pp. 297–356.

CARRUTHERS, J. N. 1927. Investigations upon the Water Movements of the English Channel, Summer, 1924. Journ. Mar. Biol. Assn., **14**, pp. 685–721.

CARRUTHERS, J. N. 1928. The Flow of Water through the Straits of Dover. Fish. Invest., Series 2, Vol. 9, No. 1.

DANOIS, E. LE. Rapport Atlantique, 1921 to 1928. Cons. perm. Internat. pour l'explor. de la Mer.

FORD, E. 1929. Herring Investigations, V. Jour. Mar. Biol. Assn., **16**, pp. 1–24.

GEHRKE, J. 1907. Mean Velocity of the Atlantic Currents running North of Scotland and through the English Channel. Publ. de Circ., No. 40.

HARVEY, H. W. 1924. Hydrography of the English Channel. Rapport Atlantique, 1924, pp. 60–89.

HARVEY, H. W. 1925. Evaporation and Temperature Changes in the English Channel. Journ. Mar. Biol. Assn., **13**, pp. 678–692.

HARVEY, H. W. 1925. Water Movement and Sea Temperature in the English Channel. Journ. Mar. Biol. Assn., **13**, pp. 659–664.

HARVEY, H. W. 1929. Hydrodynamics of the Waters south-east of Ireland. Journ, de Cons. Internat., pour l'explor. de la Mer, **4**, pp. 80–92.

LUMBY, J. R. 1925. Salinity and Water Movements in the English Channel during 1920–23. Fish. Invest., Series 2, Vol. 7, No. 7.

MATTHEWS, D. J. 1905. The Physical Conditions in the English Channel, 1903. N. Sea Fish. Invest., 1st Report (Southern Area), 1902–1903, Cd. 2670, 1905.

MATTHEWS, D. J. 1909. The Physical Conditions in the English Channel, 1904 and 1905. N. Sea Fish. Invest., 2nd Report (Southern Area), 1904–1905, Part II, Cd. 4641, 1909.

MATTHEWS, D. J. 1911. The Physical Conditions in the English Channel, 1906. N. Sea Fish. Invest., 3rd Report (Southern Area), 1906–1908, Cd. 5546, 1911.

MATTHEWS, D. J. 1914. The Salinity and Temperature of the Irish Channel and the waters south of Ireland. Fisheries, Ireland, Sci. Invest., 1913, No. 4, 1914.

ORTON, J. H. 1920. Sea Temperature, Breeding and Distribution in Marine Animals. Journ. Mar. Biol. Assn., **12**, pp. 339–366.

Seasonal Variations in the Phosphate and Silicate Content of Sea-Water in Relation to the Phytoplankton Crop. Part V. November 1927 to April 1929, Compared with Earlier Years from 1923.

By

W. R. G. Atkins, Sc.D., F.R.S.,

Head of the Department of General Physiology at the Plymouth Laboratory.

With 12 Figures in the Text.

Introduction.

In the previous numbers of this series (1923, 1925, 1926, 1928) it was fully established that the phosphate and silicate content of sea-water becomes greatly reduced in spring and summer. It is possible to calculate a minimum value for the phytoplankton crop from the amount of phosphate used up, also to ascertain the production up to and between various dates; such information has a direct bearing on the supply of food for copepods and other animals upon which young fish feed. The accumulation of data of this type should in time permit of some generalization as to the favourableness or otherwise of any season with respect to the survival of relatively large numbers of young fish of various species in the locality studied. The present paper is a further contribution towards the amassing of seasonal productivity data which has been in progress since March 1923, with a gap from March to October, inclusive, during 1927. Information has moreover been sought as to the extent to which the removal of the phosphate approaches completion; the analyses of water samples low in phosphate have been carried out with a rather greater degree of accuracy than heretofore, by using a more exact method of allowing for the reagent blank, by using weaker standard solutions and by ensuring that in nearly every case the analyses were performed on the day following that on which the water samples had been taken. When the cruise extended for two days this was not possible as regards samples taken on the first day. Furthermore, measurements have been made (Poole and Atkins, 1928) of the illumination, both aerial and submarine, obtaining when the samples were taken.

Seasonal Variation in Phosphate Concentration of Water at International Hydrographic Station E1.

The data from November 1927 to April 1929 are shown in Table 1, also records of silica content, temperature, vertical illumination, in air and at 10 and 20 m., together with the percentages of the illumination penetrating to these depths. The variation of phosphate with depth is shown in Figure 1, in which data from an earlier paper, but not previously plotted, have been incorporated. The phosphate-depth lines move to the left as the year goes on and concentration decreases. Then follows a period when the water may be almost or quite devoid of phosphate down to 20 m., while simultaneously regeneration preponderates in the deeper water. A little later active regeneration takes place at the surface,

TABLE 1.

STATION E1. The first line shows the dates on which samples were taken and top portion of the table gives phosphate results as mg. P_2O_5 per m.^{3}, A denoting date surface and bottom. Below these are temperatures. In the lowermost section, opposite V, electrically in air. Immediately below are the percentages of the illuminations reaching refer to measurements made about midday, the values opposite V, from which they are

	1927		1928											
M	4/11	9/12	31/1	21/2	1/3	27/3	5/4	19/4	2/5	7/5	8/5	4/6	13/6	4/7
0	19†	31	43‡	27	33	28	24	24	10	9	9	9	4	12
5	20	—	35	27	26	25	25	23	10	9	—	9	3·5	4·5
10	—	—	36	—	28	—	—	—	—	10	—	—	5	4·5
15	—	—	—	—	—	25	—	—	10	22	—	—	—	3·5
20	—	—	—	—	—	—	—	—	17	18	—	9	5	—
25	—	—	—	—	—	26	—	—	18	18	—	—	—	4
30	—	—	—	—	—	—	—	—	—	19	—	10	—	15
35	—	—	—	—	—	—	—	—	—	—	—	9	7	—
40	—	—	—	—	—	—	—	—	—	—	—	—	10	18
50	—	—	—	—	—	—	26	—	—	—	—	—	14	19
70	25	31	36	28	29	41	27	23	20	19	20	13	14	25
A	8/11	12/12	1/2	27/2	2/3	29/3	7/4	20/4	3/5	9/5	11/5	6/6	14/6	6/7
0	313	260	260	220	220	170	130	78	92	—	—	—	59	33
70	326	300	260	210	210	176	130	78	78	—	—	78	78	78
A	7/11	10/12	1/2	28/2	2/3	30/3	10/4	20/4	3/5	—	—	6/6	18/6	6/7
0	13·4	12·1	9·1	9·7	9·7	9·6	9·8	10·1	11·4	12·5	12·4	12·1	13·1	14·1
5	13·5	11·9	9·0	9·5	9·5	9·6	9·8	10·1	11·3	12·2	—	11·9	13·1	13·9
10	,,	,,	,,	,,	9·3	,,	,,	,,	11·1	10·9	—	—	12·7	13·6
15	,,	,,	,,	,,	,,	,,	,,	10·0	10·5	10·3	—	11·9	—	13·4
20	,,	,,	,,	,,	,,	,,	,,	,,	10·3	10·3	—	11·9	12·4	13·4
25	,,	,,	,,	,,	9·3	,,	9·7	,,	,,	,,	—	11·9	—	13·2
30	,,	,,	,,	,,	,,	,,	—	10·0	10·2	10·2	—	11·9	12·3	11·8
40	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	—	11·5	11·8	11·7
70	13·5	11·9	9·0	9·5	9·2	9·6	—	10·0	10·2	10·2	10·2	11·1	11·2	11·7
V	—	30·8	—	—	66·5	66·5	86	134	—	86·5	—	—	48·5	126
10	—	23%	—	—	24%	15%	21%	35%	—	32%	—	—	30%	18%
20	—	8%	—	—	9%	5%	6%	16%	—	14%	—	—	11%	4%
10		7·1			16·0	10·0	18·1	47·0		27·7			14·5	22·7
20		2·5			6·0	3·3	5·2	21·4		12·1			5·3	5·0

† At L4, 20 mg. surface and 22mg. bottom. ‡ At L4, 92 mg. surface and 32 mg. bottom.

as on September 22nd and October 19th, 1926, also August 16th and 29th, 1928. The vertical mixing of the water, which occurs late in September or early in October, may be followed by a diatom outburst, as shown by the decrease in the mean phosphate concentration of the column. Mixing is usually rapid throughout the isothermal column which obtains in winter, but at times regeneration may be sufficiently rapid at the surface to give markedly greater values, as on November 24th, 1926, March 21st, 1927, and January 2nd, 1929. This appears to be due to the decomposition of organic matter floating up to the surface.

In Figure 2 the phosphate data for 5 m. and bottom, 70 m.—the depth of water is about 70–73 m. actually—are shown throughout the same years. In order to avoid the irregularities introduced by surface regeneration in hot summer weather, when according to Marshall and Orr (1928)

TABLE 1 (*contd.*)

observations made from 1927–1929. The first column records depths in metres. The on which analyses were performed. The next portion shows silicate as mg. SiO_2 per m.^{3}, are shown the vertical illuminations in thousands of metre candles, as measured photo- 10 and 20 m. At the bottom the actual illuminations at these depths are given; they calculated, being the maxima observed for the day.

	1928								1929				
M	11/7	23/7	9/8	16/8	29/8	18/9	2/10	30/11	2/1	7/1	4/3	26/3	11/4
0	8·5	0	0·5	34	24	5	11	26·5	48	40	31·5	4	13·5
5	1·5	0	0	1	3·5	5	12·5	27	33·5	37	31·5	29	11·5
10	2	1·5	0	0	9	—	—	—	—	—	—	30	11·5
15	2	1·5	0·5	6	10	5·5	—	—	—	—	—	—	12·5
20	4	10·5	1	5·5	15	10	—	—	—	—	—	—	12·5
25	8·5	15	10	17	—	25	13	—	—	—	—	31	14
30	20	13	13	17·5	15	25	—	—	—	—	—	—	14
35	—	—	—	—	—	—	—	—	—	—	—	—	—
40	19	13	—	—	—	—	—	—	—	—	—	—	14
50	—	14	12	12·5	19	—	—	—	—	—	—	34·5	—
70	24	14	19	13	19	25	13	29	33·5	35·5	31·5	36	17·5
A	12/7	24/7	11/8	18/8	30/8	19/9	4/10	1/12	4/1	9/1	6/3	28/3	12/4
0	33	59	98	—	120	98	163	196	183	—	220	—	—
70	78	137	130	—	130	210	163	196	183	—	228	—	—
A	12/7	25/7	11/8	—	31/8	20/9	4/10	3/12	4/1	—	6/3	—	—
0	16·1	18·2	16·6	16·0	15·9	16·8	14·9	12·1	10·5	10·0	8·5	9·2	8·8
5	14·8	18·1	16·5	15·8	15·7	16·6	14·7	12·1	10·7	10·2	8·5	8·7	8·8
10	14·1	17·4	16·4	15·8	15·7	16·5	14·7	—	—	—	—	8·7	8·8
15	13·7	15·1	16·3	15·7	15·1	16·3	14·7	—	10·7	—	—	8·7	—
20	13·2	12·7	15·9	14·9	13·6	15·5	—	—	—	—	—	—	—
25	12·3	12·6	13·4	12·7	13·6	13·8	14·7	12·1	—	—	—	—	—
30	11·8	12·6	13·0	12·7	13·4	13·7	—	—	—	—	—	—	—
40	11·8	12·5*	12·9	12·7	12·9	13·5	14·7	—	10·7	—	—	—	—
70	11·8	12·9*	12·9	12·9	12·7	13·5	14·7	12·1	10·7	10·2	8·5	8·6	8·8
V	130	120	56	—	111	78	65	15·3	15	—	—	—	—
10	25%	47%	16%	—	24%	36%	16%	18%	24%	—	—	—	—
20	6%	16%	2%	—	8%	16%	4%	5%	9%	—	—	—	—
10	32·5	56·4	9·0		26·7	28·1	10·4	2·7	3·6	—	—	—	—
20	7·8	19·2	1·1		8·9	12·5	2·6	0·8	1·4	—	—	—	—

* Confirmed by duplicate observations.

the light near the surface is far too bright for effective photosynthesis by diatoms, the 5 m. values have been plotted. In July and August the surface concentrations may reach zero. The "zero" concentration really means less than 0·5 mg. P_2O_5 per m^3., or quite certainly less than 1 mg. when compared most carefully with reagent blanks. Presumably

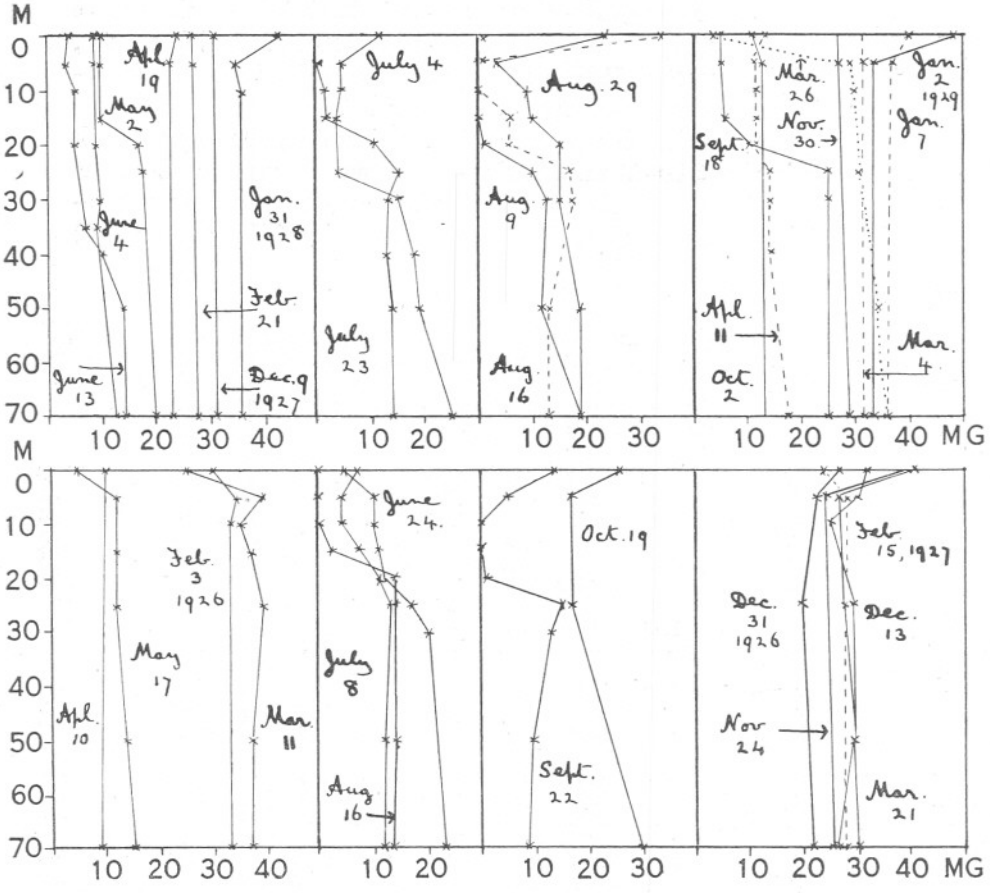


FIG. 1. Variation of phosphate concentration with depth at Station E1. The lower portion concerns 1926 up to February 1927; the upper portion concerns December 1927 to April 1929. For the sake of clearness the curves for the months have been plotted in four panels, in both upper and lower portions. Phosphate is shown as mg. P_2O_5 per m^3. From data of Table 3 (Atkins, 1928) and Table 1, this paper.

it is on account of their minute size that the diatoms are so effective in removing phosphate.

The chief interest in Figure 2 lies, however, in the evidence it affords as to the date of the main spring outburst of phytoplankton, which, it may be seen, occurs much later in some years than in others. The

magnitude of the crop depends upon the change in the water as a whole ; this will be considered later.

While the upper water is almost devoid of phosphate, regeneration proceeds apace in the bottom water, as shown by the peaks in the lower curve. The phosphate thus set free is gradually brought up into regions of better illumination and is used up by the phytoplankton, so that it

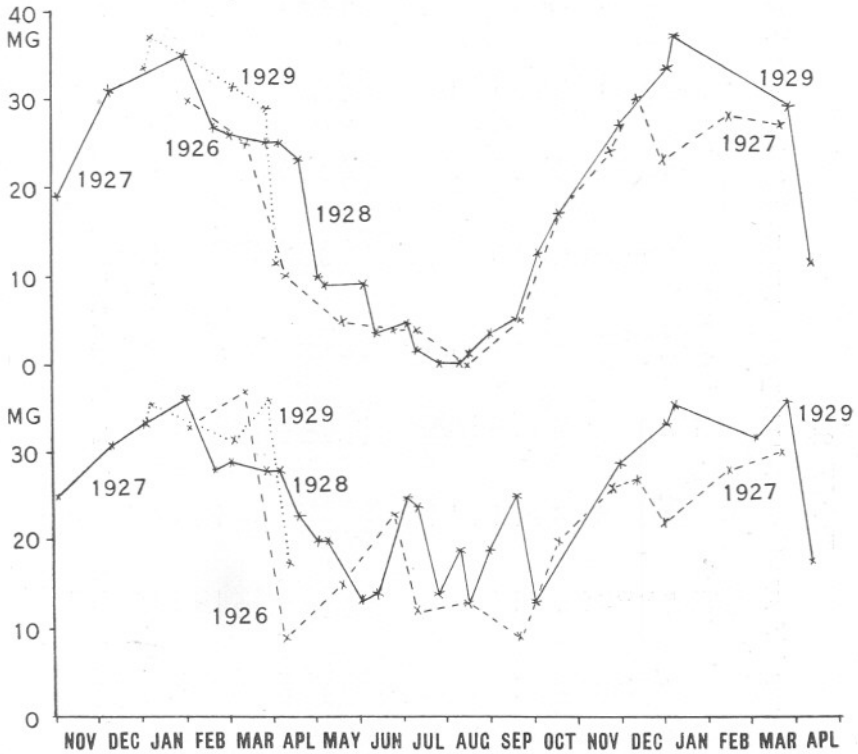


FIG. 2. Seasonal variation of phosphate concentration at Station E1. The upper portion gives the values at 5 m. and the lower those at the bottom, 70 m. The periods concerned are February 1926–March 1927, and November 1927–April 1929. Data for 1929 appear twice on the graphs, to compare with winter 1927 and the springs 1926 and 1928. Phosphate is shown as mg. P_2O_5 per m^3. From data of Table 3 (Atkins, 1928) and Table 1, this paper.

never reaches the surface as free phosphate. Even during summer there is a slow mixing of surface and bottom water as is shown by the way the bottom temperature gradually creeps up.

SEASONAL VARIATION IN PHOSPHATE CONCENTRATION OF WATER AT INTERNATIONAL HYDROGRAPHIC STATIONS E1, E2, AND E3.

The positions of these stations are roughly as follows : E1, 10 miles S.W. of Eddystone Lighthouse ; E2, Mid-Channel ; E3, 7 miles W. of

TABLE 2.

PHOSPHATE AS MG. P_2O_5 PER M.^{3} AND TEMPERATURES AT STATIONS E1, E2, AND E3.

	1927 Nov. 4		1928 Feb. 21–22.			May 7–9.			Aug. 16–17.			1929 Jan. 7.		March 26–27.		
M	E1	E2	E1	Ec	E3	E1	E2	E3	E1	E2	E3	E1	E2	E1	E2	E3
0	19	22	27	11	23	9	7	10‡	34	14·5	4	40	48·5	4	27·5	29
5	20	30	27	24	—	9	7	—	1	0	4	37	39	29	31	26·5
10	—	—	—	—	—	10	8	13	0	0	2	—	—	30	31·5	26
15	—	—	—	—	—	22	17	18	6	1	2	—	—	—	—	—
20	—	—	—	—	—	18	20	25	5·5	4	26	—	—	—	—	—
25	—	—	—	—	—	18	—	26	17	16	29	—	—	31	—	—
30	—	—	—	—	—	19	19	—	17·5	16·5	—	—	—	—	—	—
40	—	—	—	—	—	—	—	—	—	19·5	—	—	—	—	—	—
50	—	—	—	—	—	—	—	—	12·5	—	30	—	—	34·5	—	—
60	—	—	—	—	—	—	—	—	—	27	—	—	—	—	—	—
70	25	—	28	—	—	19	—	—	13	—	—	35·5	—	36	—	26
80	*	29	*	25	—	*	21	—	*	27	—	*	37·5	*	31·5	—
100		*		*	25		*	28‡		*	29·5		*		*	26
0	13·8	13·4	9·7	10·2	10·3	12·5	12·3	11·9	16·0	16·9	16·6	10·1	10·6	9·2	9·4	9·8
5	13·5	13·5	9·5	9·9	10·3	12·2	12·2	11·9	15·8	16·7	16·6	10·2	10·7	8·7	9·3	9·8
10	—	—	9·5	9·9	—	10·9	12·2	11·9	15·8	16·7	16·5	—	—	8·7	9·3	9·8
15	—	13·5	—	—	—	10·3	10·9	11·7	15·7	16·2	16·0	—	—	8·7	9·3	—
20	—	—	—	—	—	10·3	10·7	11 4	14·9	15·5	13·9	—	—	—	—	—
25	—	13·5	9·5	9·9	10·3		10·6	11·0	12·7	13·5	12·7	—	—	—	—	—
30	—	—	—	—	—	10·2	10·6	11·0	12·7	13·4	12·7	—	—	—	—	—
40	—	—	—	—	—		—	—	—	13·3	12·6	—	—	—	—	—
50	—	13·5	9·5	—	—		10·5	—	12·7	13·1	12·6	—	—	—	—	—
70	13·5	—	9·5	—	—	10·2	—	—	12·9	—	12·3	10·2	—	8·6	—	—
80	*	13·5	*	9·9	—	*	10·5	—	*	13·1	—	*	10·7	*	9·3	—
100		*		*	10·3		*	11·0		*	12·2		*		*	9·8

Mid-way surface phosphate values:— Feb., E1–E2, 24: E2–E3, 8; May, E1–E2, 7: E2–E3, 10; Aug., E1–E2, 13·5: E2–E3, 3; Jan., E1–E2, 49: March, E1–E2, 18·5· E2–E3, 36·5.

‡ Silica 80 mg. surface and bottom.

Ushant. The observations at E2 and E3 are at too great intervals of time to enable one to study the changes as closely as at E1. It may be said, however, that in general conditions at E2 are much the same as at E1. There is evidence, however, that a spring phytoplankton outburst may originate at E2 before there are any signs of it at E1. Thus on February 21st, 1928, the phosphate concentration at the surface was reduced to 11 mg. at E2, and to 8 mg. half-way on towards E3. Again, on March 11th, 1926, the values 11 mg., 0 mg., 5 mg., and 7 mg., were obtained, respectively, half-way between E1 and E2, at E2, half-way on to and at E3. Also on February 15th, 1927, 13 mg. was found for E2. It may thus be seen that the rapid utilization of phosphate by the phytoplankton depends purely upon the local conditions and may arise far out at sea. It need not depend upon anything washed out from the land.

Furthermore, references are found in the literature to phytoplankton outbursts attributed by various authors to enrichment of the sea-water by river water. The latter is, however, as a rule, far poorer in both phosphate and nitrate than is sea-water in winter or early spring. In silicate alone is river water richer than sea-water, but silicate has never been shown to be a limiting factor in diatom production in sea-water, and in spring silicate is present in the sea in abundance. Pending the production of direct analytical evidence as to the correctness of this theory of enrichment by fresh water, the author is unwilling to regard it as correct, save in comparatively landlocked basins.

Station E3 may be low in phosphate down to 15 m., but the deeper colder water is never greatly depleted, since there is so much vertical mixing thereabouts and the depth is considerably greater than at E1 or E2.

The Rapid Regeneration of Phosphate in Winter and the Water of an Offshore Wind.

Rough weather prevailed before and after Christmas 1927, but on January 2nd, 1928, it seemed just possible to get to E1 for routine water samples and to measure submarine illumination in mid-winter. Now it so happened that a rather unusual condition was observed, there was a steep gradient in phosphate concentration along the inshore stations, from L1 near the Laboratory to E1, 22 miles out.

The water at the Breakwater, L2, was just three times as rich in phosphate as that at E1 ; one might have concluded that the fresh water was enriching the sea-water, but this obviously required that the sea-water at L2 must have been diluted with fresh water to a very great extent, the salinity at E1 being 35·34°/$_{oo}$, rather a high value typical of

Atlantic water. It was found, however, that even at L1 the salinity was 30·29°/$_{oo}$.

TABLE 3.

PHOSPHATE AS MG. P_2O_5 PER M^3., PHOSPHATE IN STORED SAMPLES, TEMPERATURES AND SALINITY IN PARTS PER THOUSAND. BETWEEN JANUARY 2ND AND 7TH, 1929, THE PREVAILING WIND WAS OFFSHORE, MAINLY FROM N.E. AT THE BOTTOM OF THE TABLE SILICATE ANALYSES ARE SHOWN AS MG. SiO_2 PER M^3.

Jan.	m.	L1	L2	L3	L4	L5	L6	E1	Mid E1–E2	E2
2†	0	161	143	125	125	93	125	48	—	—
2	5	—	—	—	—	—	—	33·5	—	—
2	70	—	—	—	—	—	—	33·5	—	—
7¶	0	—	—	39	49·5	48	48	40	49	48·5
7	5	—	—	—	35	—	36	37	37	39
7	10	—	—	34	—	—	—	—	—	—
7	25	*	*	34	—	—	—	—	—	—
7	40			*	34	—	—	—	—	—
7	60				*	*	34·5	—	—	—
7	70						*	35·5	36	37·5
				PHOSPHATE IN STORED SAMPLES.						
2‡	0	—	—	360	310	150	52	46**	—	—
				TEMPERATURE.						
2	0	8·9	8·5	9·4	10·2	10·3	10·6	10·5	—	—
7	0	—	—	8·8	9·6	9·7	9·9	10·1	10·3	10·6
7	5	—	—	9·2	9·6	—	9·9	10·2	10·4	10·7
7	B	—	—	9·7	9·9	—	10·1	10·2	10·4	10·7
				SALINITY, °/$_{oo}$.						
2	0	30·29	—	—	—	—	—	35·34††	—	—
7	0	—	—	—	35·18	35·19	35·33	35·37	35·41	35·36
7	5	—	—	34·78	35·13	—	35·23	35·37	35·35	35·33
7	B	—	—	35·03	35·21	—	35·28	35·35	35·35	35·37
				SILICA.						
2	0	870‡‡	686‡‡	466	246	190	217	183	—	—

† Jan. 2nd analysed Jan. 4th. ¶ Jan. 7th analysed Jan. 9th. ‡ Jan. 2nd analysed again on Jan. 9th. ** 70 m. sample gave 37 mg. * Bottom reached before depth indicated. †† Isohaline column. B, denotes bottom. ‡‡ Subject to a correction for tint in water, but as they stand they agree well with results in Table 1 of Atkins, 1926, p. 92, when latter are corrected by new factor.

This remarkable phosphate gradient was, moreover, shown to be a surface phenomenon only at E1 on January 2nd.

Between January 2nd and 7th the prevailing wind was offshore, mainly from the N.E. Under these conditions the fishermen at Plymouth say that it is almost useless to fish, as nothing worth while is caught. The idea prevails that the water is then very clear. On January 2nd photo-electric measurements did not show any exceptional clearness, and at E1 the Secchi disc could only be seen 9 m. down, as against a

maximum of 22 m. The 9-m. value is probably somewhat low, perhaps even as much as 3 m.—for the sea was very rough, with a heavy easterly swell. It was thought that the high phosphate concentration near the coast would give an indication as to whether surface water was being blown out to sea and replaced by deeper water moving nearer inshore. Accordingly on January 7th, the weather being exceptionally cold, temperature, phosphate and salinity depth series were worked from L3 to E2, as shown in Table 3. From L4 to E2 the surface phosphate was closely the same, save for E1, which was lower. Furthermore, the whole water column was somewhat richer at E2 than at the stations nearer land. Again the salinity results show a uniform Atlantic water from E1 to E2, and at L6, surface, with only very slight dilution, 3 parts in 1000 at L6, 5 m., and very little more at L4 throughout the water-column. There is therefore no evidence whatever that any extensive movement of the surface water was occasioned by the prevailing offshore wind or that the high values for phosphate in the surface waters were in any way connected with the wind. They arose through the decomposition of material rich in phosphate floating up to the surface all over the area studied, though the possibility is not precluded that a certain amount of seaweed and particulate matter may drift out to sea through wind action. Further evidence of enrichment through decomposition is offered by the fact that certain of the water samples taken on January 2nd and stored till January 9th gave even higher values than when freshly drawn.

A Comparison of the Phosphate Content of the Water at E1 in Different Years.

In Table 4 the mean values of the phosphate content of the water-column are shown, from 1923–1929. There is usually a maximum in January. For the seven years the mean maximum was 35·1 mg., varying from 37·0 to 31·0 mg. Very strangely there were mid-winter phyto-plankton outbursts in mid-December 1925 and late December 1926.

The minimum values for the water-column were found in June, July, or August, with secondary minima in April or May. For the five summers studied the mean minimum was 7·6 mg., varying from 8·7 to 5·1 mg.

The data are shown in Figure 3, the years being continued into the January following to show the winter maxima or depressions. The most striking thing about the curves, apart from their general similarity, is the rapid fall in the spring of each year. The fall, however, differs from year to year both as regards its date and its rate, as shown by the slope of the curve. Tables 5 and 6 have been prepared to facilitate the comparison of the years, as indicated in their headings. The dates are shown at which certain phosphate concentrations were reached at

TABLE 4.

PHOSPHATE CONTENT OF THE WATER-COLUMN, SURFACE TO BOTTOM, 70 M., AT STATION E1, EXPRESSED AS MG. P_2O_5 PER M^3. THE MONTHS ARE DIVIDED INTO THREE PORTIONS EACH, EQUAL IN LENGTH.

		1923	1924	1925	1926	1927	1928	1929
Jan.	I	—	*37·0*	—	—	21·6	—	*36·5*
,,	II	—	—	*31·9*	*40·0**	—	—	—
,,	III	—	—	—	—	*36·2*	—	—
Feb.	I	—	—	—	33·0	—	—	—
,,	II	—	32·0	31·1	—	27·9	27·8	—
,,	III	—	—	—	—	—	—	—
Mar.	I	*37·0*	—	—	36·4	—	28·5	31·5
,,	II	—	22·1	28·3	—	29·0	—	—
,,	III	—	—	—	—	—	25·8	31·4
April	I	—	15·0	—	—	—	25·6	—
,,	II	—	—	—	9·5	—	23·1	14·4
,,	III	27·7	—	8·5	—	—	—	—
May	I	—	—	—	—	—	17·2	—
,,	II	—	12·1	9·2	12·9	—	—	—
,,	III	11·6	—	—	—	—	—	—
June	I	—	—	15·8	—	—	10·6	—
,,	II	13·2	9·1	—	—	—	**8·3**	—
,,	III	—	—	—	16·0	—	—	—
July	I	—	**8·7**	6·9	10·5	—	13·7	—
,,	II	**7·4**	—	—	—	—	14·2	—
,,	III	—	—	—	—	—	10·2	—
Aug.	I	—	10·1	19·2	—	—	9·4	—
,,	II	16·1	—	—	10·4	—	12·0	—
,,	III	—	—	—	—	—	15·3	—
Sept.	I	—	16·1	**5·1**	—	—	—	—
,,	II	13·9	—	—	—	—	19·0	—
,,	III	—	—	—	**8·6**	—	—	—
Oct.	I	—	14·9	18·2	—	—	12·8	—
,,	II	16·0	—	—	18·2	—	—	—
,,	III	—	—	—	—	—	—	—
Nov.	I	20·0	—	—	—	23·5	—	—
,,	II	—	20·1	25·9	—	—	—	—
,,	III	—	—	—	25·6	—	27·9	—
Dec.	I	—	32·0	—	—	*31·0*	—	—
,,	II	34·0	—	18·6	29·8	—	—	—
,,	III	—	—	—	21·6	—	34·0	—

* This is really a surface value for L6, but L3–L6 gave the same value for phosphate, but it may possibly be too high for E1. Weather was too bad to get to E1 or to do the depth series.

surface and bottom, also the temperatures of the water on those dates. Both dates and temperatures are then compared with those of the first year of the series, 1923. Now the phosphate depletion is a measure of

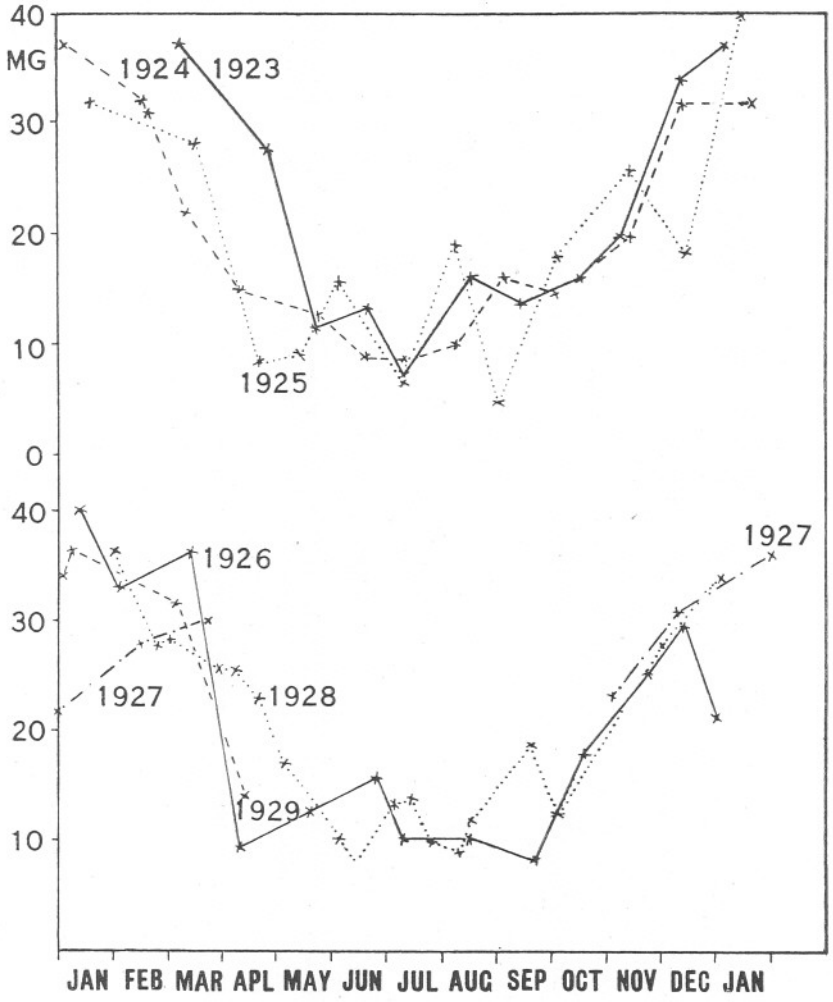


FIG. 3. Mean phosphate concentration of the whole water-column, 70 m., at Station E1 expressed as mg. P_2O_5 per m^3. The upper portion shows the values throughout the years 1923, 1924 and 1925, the lower those for 1926, portions of 1927, 1928 and the spring of 1929. From data of all papers of the series, and Table 4.

the phytoplankton production, which is only secondarily affected by temperature. The latter has been included mainly on account of its influence upon the rate of hatching of fish eggs and upon the rate of growth of animals.

TABLE 5.

DATES AND TEMPERATURES WHEN CERTAIN PHOSPHATE CONCENTRATIONS WERE REACHED AT E1, SURFACE. TAKING THE 1923 DATES AND TEMPERATURES AS ARBITRARY STANDARDS THE ADVANCES OR RETARDATIONS OF THE OTHER YEARS ARE RECORDED IN DAYS AND DEGREES.

mg.	1923	1924	1925	1926	1927	1928	1929	1924	1925	1926	1927	1928	1929
30	March 30	Feb. 18	Feb. 25	Feb. 3	Feb. 6	Feb. 13	March 18	41	33	55	52	46	12
30	9·7°	8·4°	9·6°	9·5°	9·2°	9·5°	8·9°	−1·3°	−0·1°	−0·2°	−0·5°	−0·2°	−0·8°
20	April 28	Feb. 28	March 20	March 21	—	April 22	April 4	59	39	38	—	6	24
20	10·2°	8·0°	9·4°	9·7°	—	10·4°	9·0°	−2·2°	−0·8°	−0·5°	—	+0·2°	−1·2°
10	May 10	April 28	April 6	April 10	—	May 2	April 13	12	34	30	—	8	27
10	11·0°	9·4°	9·5°	10·2°	—	11·4°	8·8°	−1·6°	−1·5°	−0·8°	—	+0·4°	−2·2°
2·5	May 21	June 18	April 18	July 21	—	July 6	—	−28	33	−61	—	−46	—
2·5	11·4°	13·7°	9·7°	17·0°	—	14·7°	—	+2·3°	−1·7°	+5·6°	—	+3·3°	—
2·5	Sept. 15	Aug. 24	Sept. 10	Sept. 6	—	Aug. 25	—	+22	5	+9	—	+21	—
2·5	15·0°	15·0°	16·0°	16·9°	—	16·0°		0·0°	+1·0°	+1·9°	—	+1·0°	—
10	Sept. 28	Oct. 20*	Oct. 6	Oct. 3	—	Sept. 28	—	−22	−8	−5	—	0	—
10	14·0°	12·9°	14·3°	15·9°	—	15·5°		−1·1°	+0·3°	+1·9°	—	+1·5°	
20	Nov. 7†	Nov. 22	Nov. 1‡	Nov. 6	Nov. 6	Nov. 5	—	−15	+6	−1	−1	−2	—
20	12·2°	12·3°	12·6°	13·3°	13·7°	13·6°		+0·1°	+0·4°	+1·1°	+1·5°	+1·4°	—
30	Dec. 1	Dec. 6	Jan. 2§	Dec. 12	Dec. 3	Dec. 14	—	−5	−32	−11	−2	−13	—
30	10·9°	11·9°	10·2°	11·7°	12·1°	11·4°		+1·0°	−0·7°	+0·8°	+1·2°	+0·5°	—

* Also on Sept. 2, giving +26. † Also on Oct. 11. ‡ Also on Dec. 21. § 1926.

TABLE 6.

DATES AND TEMPERATURES WHEN CERTAIN PHOSPHATE CONCENTRATIONS WERE REACHED AT E1, BOTTOM. TAKING THE 1923 DATES AND TEMPERATURES AS ARBITRARY STANDARDS, THE ADVANCES OR RETARDATIONS OF THE OTHER YEARS ARE RECORDED IN DAYS AND DEGREES.

mg.	1923	1924	1925	1926	1927	1928	1929	1924	1925	1926	1927	1928	1929
30	April 14	Feb. 20	March 17	March 17	March 21	Feb. 17	April 1	54	28	28	24	57	13
30	9·6°	8·6°	9·2°	9·5°	9·0°	9·4°	8·7°	−1·0°	−0·4°	−0·1°	−0·6°	−0·2°	−0·9°
20	May 9	March 17	April 11	March 27	—	May 2	April 9	53	28	43	—	7	30
20	10·2°	8·0°	9·4°	9·5°	—	10·2°	8·8°	−2·2°	−0·8°	−0·7°	—	0·0°	−1·4°
15	May 20	April 9	April 26	April 2†	—	May 25	April 14	41	24	48	—	−5	36
15	10·4°	8·3°	9·5°	9·5°	—	10·8°	8·9°	−2·1°	−0·9°	−0·9°	—	+0·4°	−1·5°
15	Oct. 20*	Aug. 15	Sept. 19§	Oct. 6‡	—	Oct. 9§§	—	66	31	14	—	+11	—
15	13·2°	12·1°	13·0°	14·6°	—	14·4°	—	−1·1°	−0·2°	+1·4°	—	+1·2°	—
20	Nov. 6	Nov. 4	Sept. 29	Oct. 18	—	Oct. 28	—	2	38	19	—	9	—
20	12·3°	12·9°	13·5°	14·5°	—	13·5°	—	+0·6°	+1·2°	+2·2°	—	+1·3°	—
30	Dec. 1	Dec. 4	Dec. 28	—**	Dec. 3	Dec. 8	—	−3	−27	—	−2	7	—
30	11·0°	11·9°	10·5°	—	12·2°	11·8°	—	+0·9°	−0·5°	—	+1·2°	+0·8°	—

* Also June 4 and July 27. † Also July 4. ‡ Also May 18. § Also May 20 and July 19.
** Max. 27 mg. Dec. 13. §§ Also July 24 and Aug. 14.

It may be seen that 1924, 1926 and 1929 are early years, 1928 being late, with 1923 even later. The differences are, moreover, very striking since 1924 and 1926 are 6 to 7 weeks ahead of 1923 and 1928. The earliest spring, 1924, happened also to be the coldest, both at the time of the vernal outburst and in general. It must accordingly have been

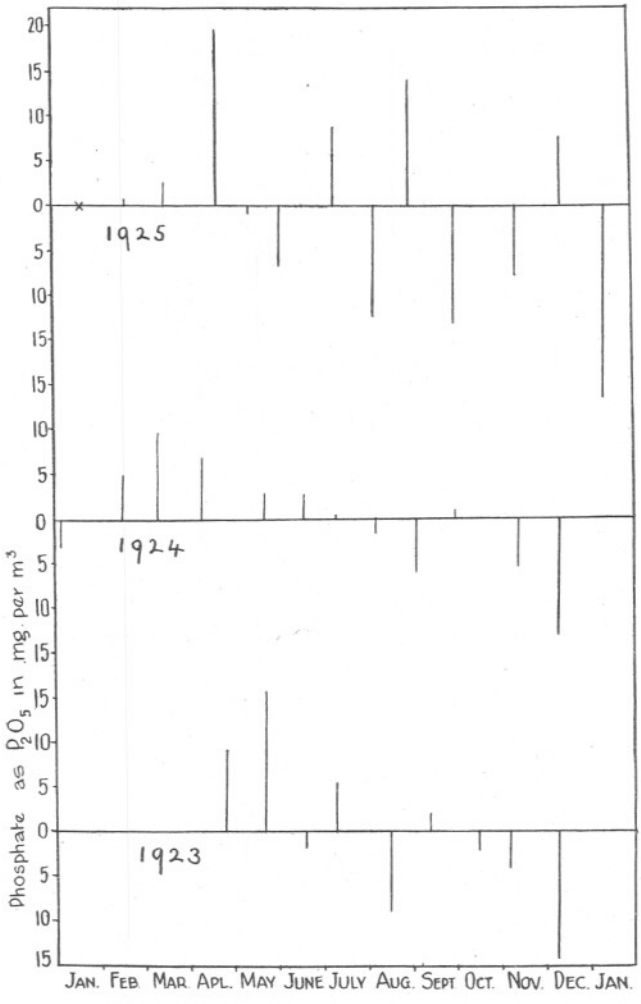


FIG. 4. The production of phytoplankton, at Station E1, may be deduced from the uprights above the zero line; in reality these lines show the difference in the mean phosphate concentration of the water-column, expressed as mg. P_2O_5 per m^3., between two successive observations. Decrease in phosphate, being equivalent to production of phytoplankton, is shown above the zero line. From data of Table 3 (Atkins, 1926).

[Reprinted from Fig. 4, *Jour. Mar. Biol. Assoc.*, 1926, **14**, 454.]

one in which the hatching of fish eggs went on most slowly. This year therefore should be an outstanding one as regards suitability or otherwise for various species of young fish. The next year to 1924 as regards low temperature was 1929, a moderately early year, though not as early as 1924 or 1926—or even as 1925 as regards the surface.

The autumnal regeneration of phosphate seems to proceed rather more

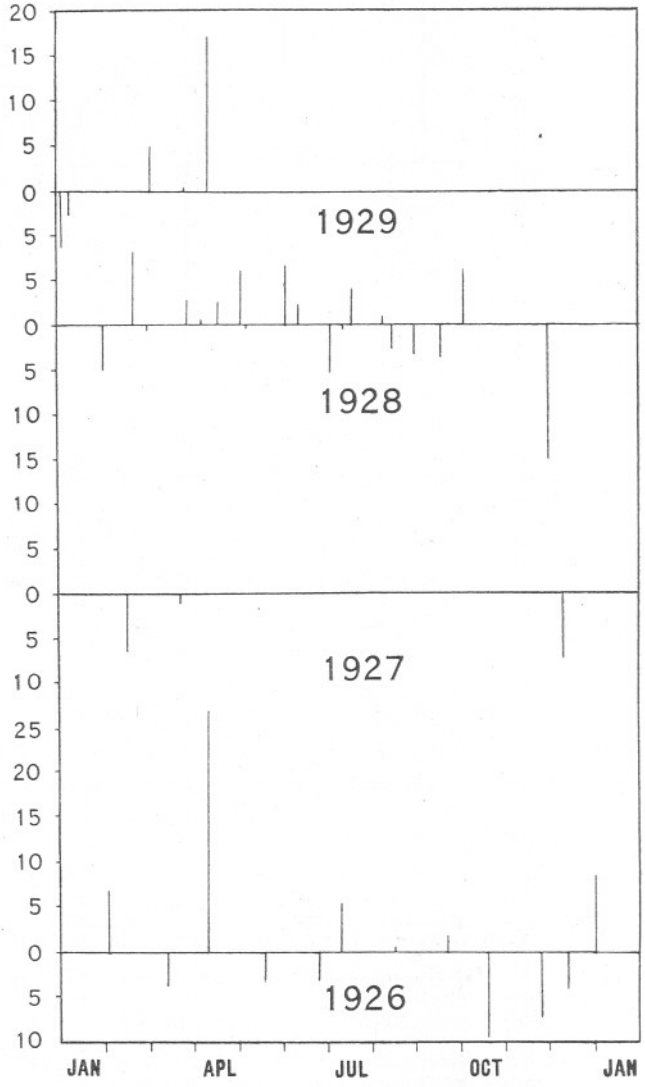


FIG. 5. Similar to Fig. 4, but for years 1926–1929, spring. From data of Tables 4 and 7.

regularly as to date and temperature than does the vernal consumption process.

It is possible to make further use of the data of Table 4, which gives the mean phosphate concentration of the water-column, because the differences between consecutive values are a measure of the consumption or regeneration of phosphate. Such differences are shown in Figures 4 and 5 as perpendiculars above or below the zero line, erected at distances on the abscissæ corresponding to the date of the second of each pair of analyses.

In comparing these two figures it is obvious that the height of a perpendicular depends to some extent on the frequency of the observations. The diversity of the years is, however, brought out very clearly. Thus the two late years, 1923 and 1928, are in some respects quite different; 1928 began as a rather early year but did not maintain its productivity; 1924 began very early and its further progress, both as regards production of phytoplankton and regeneration of phosphate, was monotonously regular. In 1925 large outbursts were followed by periods of very considerable regeneration; both 1925 and 1926 had December outbursts; 1926 and 1929, as well as 1925, had single spring outbursts of remarkable magnitude.

During 1928 analyses were performed at shorter intervals in connection with the work on illumination. It may be seen in Figure 5 that the first perpendicular above the line is followed by a very small one below it, the second above the line by a third above it, but very small. There are further on two very small perpendiculars below the line in May and July. Obviously the rates of production of phytoplankton varied greatly. Table 7 shows such rates in terms of consumption or regeneration of phosphate, the latter being denoted by a plus sign; these were obtained as described in the heading of the table, and are shown in Figure 6, the construction of which is given in the legend.

The phenomenon that is brought out most clearly in Figures 4, 5, and 6 is that production of phytoplankton is not a process that proceeds uniformly at a slow rate, or at an ever-increasing rate, till limited by lack of phosphate. Such a deficiency does ultimately limit it, but in between productivity proceeds in a series of bounds, with periods of no change of rate or with periods of decay in between. Since phosphate consumption is never very great below 25 m. at E1, in the absence of vertical mixing, this depth has been selected as one above which the main region of photosynthesis lies. The illumination at 25 m. is from about 1·0 to 10·4 per cent of full daylight. Vertical mixing, however, introduces complications, especially as the main spring outburst occurs before the formation of the epithalassa. Moreover, in autumn, at the end of September or very early in October, the resumption of vertical

TABLE 7.

THE UPPER PORTION OF THE TABLE SHOWS PHOSPHATE CONCENTRATION, IN MG. P_2O_5 PER M.^{3}, AT STATION E1, AVERAGED FROM 0–70 M., ALSO FROM 0–25 M. AND 25–70 M., TOGETHER WITH THE DIFFERENCES, △, BETWEEN CONSECUTIVE OBSERVATIONS. THE LOWER PORTION GIVES TNE INTERVALS BETWEEN THE OBSERVATIONS, THE RATES OF PHOSPHATE CONSUMPTION OR REGENERATION, IN MG. P_2O_5 PER M.^{3} PER DAY, AND THE MEAN DATES FOR WHICH THE RATES ARE TAKEN AS APPLICABLE.

Date.	4/11/'27	9/12	31/1/'28	21/2	1/3	27/3	5/4	19/4	2/5	7/5	4/6	13/6
0–70 m.	23·5	31·0	36·2	27·8	28·5	25·8	25·6	23·1	17·1	17·3	10·6	8·3
△	—	+ 7·5	+ 5·2	− 8·4	+ 0·7	− 2·7	− 0·2	− 2·5	− 6·0	+ 0·2	− 6·7	− 2·3
0–25 m.	21·0	31·0	36·5	27·4	28·1	25·4	24·9	23·2	12·2	14·5	9·0	4·5
△	—	+10·0	+ 5·5	− 9·1	+ 0·7	− 2·7	− 0·5	− 1·7	−11·0	+ 2·3	− 5·5	− 4·5
25–70 m.	24·9	31·0	36·0	27·9	28·7	26·0	27·0	23·0	19·9	19·0	11·5	11·1
△	—	+ 6·1	+ 5·0	− 8·1	+ 0·8	− 2·7	+ 1·0	− 4·0	− 3·1	− 0·9	− 7·5	− 0·4
Interval, days	—	35	53	21	9	26	9	14	13	5	28	9
Mean date	—	21/11	4/1	10/2	25/2	14/3	31/3	12/4	25/4	4/5	21/5	8/6
Rate, 0–70 m.	—	+0·21	+0·10	−0·40	+0·08	−0·10	−0·02	−0·18	−0·46	+0·04	−0·24	−0·26
Rate, 0–25 m.	—	+0·29	+0·10	−0·43	+0·08	−0·10	−0·06	−0·12	−0·85	+0·46	−0·20	−0·50
Rate, 25–70 m.	—	+0·17	+0·10	−0·39	+0·09	−0·10	+0·11	−0·29	−0·24	−0·18	−0·27	−0·04

TABLE 7 (*continued*).

4/7	11/7	23/7	9/8	16/8	29/8	18/9	2/10	30/11	2/1/'29	7/1	4/3	26/3	11/4
13·7	14·2	10·2	9·4	12·0	15·3	19·0	12·8	27·9	34·0	36·5	31·5	31·4	14·4
+ 5·4	+ 0·5	− 4·0	− 0·8	+ 2·6	+ 3·3	+ 3·7	− 6·2	+15·1	+ 6·1	+ 2·5	− 5·0	− 0·1	−17·0
4·8	3·6	4·2	1·3	7·6	11·4	8·1	12·4	27·0	35·0	37·3	31·5	27·4	12·3
+ 0·3	− 1·2	+ 0·6	− 2·9	+ 6·3	+ 3·8	− 3·3	+ 4·3	+14·6	+ 8·0	+ 2·3	− 5·8	− 4·1	−15·1
18·6	20·1	13·6	13·8	14·4	17·4	25·0	13·0	28·3	33·5	36·0	31·5	33·7	15·6
+ 7·5	+ 1·5	− 6·5	+ 0·2	+ 0·6	+ 3·0	− 7·6	−12·0	+15·3	+ 5·2	+ 2·5	− 4·5	+ 2·2	−18·1
21	7	12	17	7	13	20	14	59	33	5	56	22	16
23/6	7/7	17/7	31/7	12/8	22/8	8/9	25/9	31/10	16/12	4/1	4/2	15/3	3/4
+0·26	+0·07	−0·33	−0·05	+0·37	+0·25	+0·18	−0·44	+0·26	+0·19	+0·50	−0·09	−0·05	−1·06
+0·01	−0·17	+0·05	−0·17	+0·90	+0·29	−0·17	+0·31	+0·25	+0·24	+0·46	−0·10	−0·19	−0·94
+0·36	+0·21	−0·54	+0·01	+0·09	+0·23	+0·38	−0·86	+0·26	+0·16	+0·50	−0·08	+0·10	−1·13

mixing may cause the upper 25 m. to show a gain in phosphate, indicating apparently a period of regeneration, whereas the whole water-column may show a reduction in phosphate, as on October 2nd, 1928. For these reasons, the values for the whole column are the most reliable, though the other two have been tabulated for the information they can yield

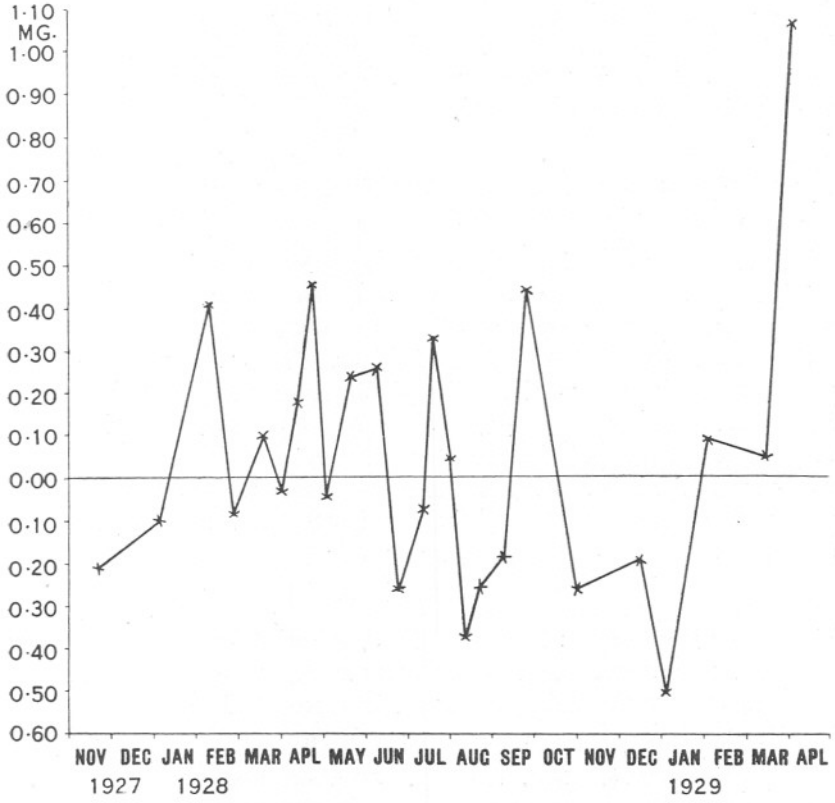


FIG. 6. The ordinates represent mg. P_2O_5 per m^3. per day, and denote the rates of change in phosphate concentration at Station E1, throughout the whole 70 m. water-column. The rates are plotted for the dates midway between those on which the water was sampled. Decrease in concentration, being equivalent to increase in phytoplankton, is plotted above the zero line. The crests are therefore times of maximal rates of production of phytoplankton, the troughs of maximal rates of decay of phyto- and zoo-plankton combined. From data of Table 7.

when considered in relation to the possible sources of error in their interpretation. The maximum consumption rate found for the whole column was 1·06 mg. P_2O_5 per $m.^3$ per day, for April 3rd, 1929, followed by 0·46 for April 25th, 1928, 0·44 for September 25th, 1928, and 0·40 for February 10th, 1928. Such rates would soon reduce the phosphate content to zero were they to be continued. For the upper 25 m. the

maxima were 0·94 for April 3rd, 1929, 0·85 for April 25th, 1928, 0·50 for June 8th, 1928, and 0·43 for February 10th, 1928. The greatest rate of all was observed in the lower region, 25–70 m., when vertical mixing was active, namely, 1·13 mg. for April 3rd, 1929, followed by 0·86 for September 25th, 1928, and 0·54 for July 17th, 1928.

The writer is indebted to Mr. H. W. Harvey for the construction of isohalines which show that there was no marked influx of water into the mouth of the English Channel during the period studied. It is accordingly legitimate to regard the cyclic processes at E1 as being those taking place in a closed system.

A Comparison of the Variation in Hydrogen Ion Concentration, Total Carbon Dioxide and Phosphate Content of Sea-water.

An extended series of measurements of the hydrogen ion concentration was made some years ago in order to obtain an estimate of the minimum weight of the phytoplankton crop from the change in the carbon dioxide content as shown by alteration in alkalinity. This was abandoned as the phosphate analyses gave the desired information more simply. It was intended, however, to institute a comparison of the two, but a few series only could be made in 1928. These are shown in Table 8, besides similar observations for 1922. When arranged in order of the monthly dates the two years are seen to agree closely, as might be expected if made in the same year.

TABLE 8.

Hydrogen Ion Concentration, pH value, of Sea-water at Station E1, Determined Colorimetrically at Sea upon freshly drawn Samples using Cresol Red and McClendon's Buffer Solutions. Comparison of Autumn 1922 with 1928.

m.	Sept. 18th, 1928.	Sept. 22nd, 1922.	Oct. 2nd, 1928.	Oct. 12th, 1922.
0	8·24	8·22	8·22	8·20
5	8·24	8·22	8·22	8·20
10	8·23	8·22	—	8·20
15	—	8·21	8·22	8·20
20	8·21	8·21	—	8·20
25	8·19	8·20	8·22	8·20
30	8·15	8·18	—	8·20
40	8·15	8·18	—	8·20
70	8·14	8·18	8·22	8·20

A comparison of the changes in phosphate and in carbon dioxide is shown in Figure 7, constructed as indicated in the legend. It may be

seen the vernal fall in carbon dioxide and in phosphate are rather similar, both are reduced during the summer, and rise in winter, though the high value of the previous winter was not reached by the carbon dioxide by January 1924. The figure makes it clear that though the phosphate is greatly reduced, in summer, throughout the whole water-column—to

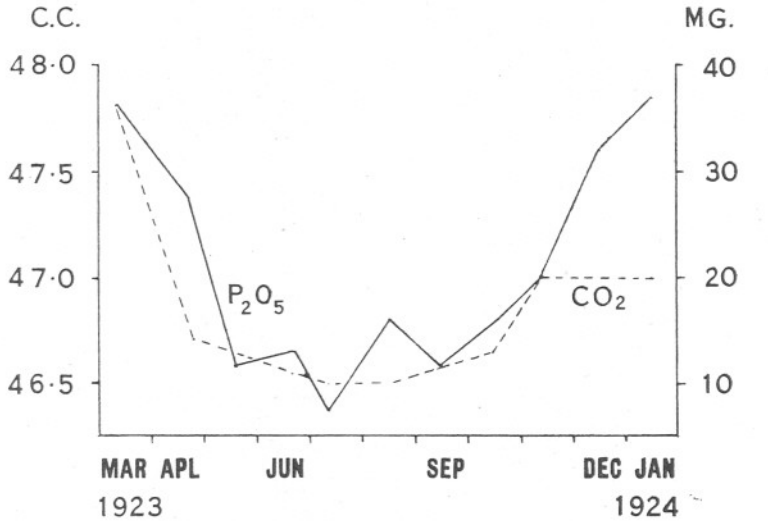


FIG. 7. The left-hand ordinates denote cubic centimetres of carbon dioxide per litre, those on the right mg. of P_2O_5 per m^3. The phosphate values are those for the whole water-column for the period shown by the abscissæ. The carbon dioxide values, broken line, denote the total amount present in the water-column, in c.c. per litre—the water being of alkaline reserve "26," namely, requiring 26 c.c. of N/10 HCl to neutralize one litre at 100° C. The carbon dioxide was found by converting the pH (logarithmic) values obtained, with cresol red and McClendon's standards (Atkins, 1924), into concentrations, cH values, for each depth, and from these a mean value for the water-column was got and converted into the pH value. From the pH values for the various dates, McClendon's (1917) curve for excess base 26 was used to read off the c.c. of CO_2 per litre. Author indebted to H. W. Harvey for this figure.

about 25 per cent of its winter value, yet the reduction in carbon dioxide is comparatively small, from 47·8 to 46·5 c.c. per litre.

THE SILICATE CONTENT OF SEA-WATER AND ITS SEASONAL VARIATION.

Table 1 shows the silicate at Station E1, expressed as mg. SiO_2 per m^3. The results have been plotted in Figure 8, surface full line and bottom broken line. For comparison a dotted curve shows phosphate, at 5 m. There is a general agreement between the curves, but the silicate curve never reaches zero. It does, however, reach a minimum of 33 in July,

which is about the limit of what is definitely detectable by the method. The surface silicate is, during the summer, rather lower than the bottom concentration. The sudden rise in the latter in September is probably associated with movement of water in from slightly further out. Of this there is definite hydrographic evidence. It is also noteworthy that whereas the phosphate one winter is closely the same as that in the following winter, when at its maximum, yet the 1928–1929 silica concentration was far below that of 1927–1928. Furthermore, in April 1928 the steep fall in silica took place some weeks before the marked fall in phosphate. This looks as if the latter was due in the main to a Phæocystis

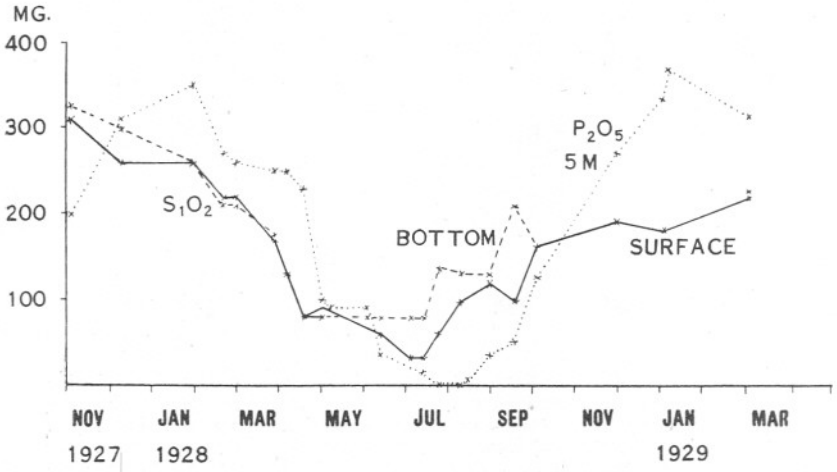


FIG. 8. The ordinates represent silicate, as mg. SiO_2 per m^3., the abscissæ show months The full line curve is that for surface water, the broken line representing concentrations found in bottom samples. For comparison a dotted curve has been given to show phosphate concentrations, as mg. P_2O_5 per m^3., at 5 metres—to avoid surface irregularities due to regeneration. For this curve the ordinate scale readings must be reduced to one-tenth to read miligrams.

outburst, and the later complete exhaustion of phosphate, when silica was increasing, may possibly have been due largely to the growth of Peridinians. In the absence of a proper examination of the plankton it is impossible to decide such questions.

Table 3 furnishes additional support to the finding of a previous year as to the steep silicate gradient existing near the land.

THE PHYTOPLANKTON AT STATION E1.

Lack of a collaborator has rendered it impossible to make regular and approximately quantitative observations on the phytoplankton and to correlate them with the changes in phosphate concentration as Marshall

and Orr (1927) have done in the Clyde. It was found, however, that *Phæocystis globosa* occurred abundantly in the tow-nets on May 2nd, 1928, the date on which the fall in phosphate concentration was also found (Table 1), temperature 10·2–11·4° C. On April 4th, 1929, every sample of water obtained by the Nansen-Pettersen bottle from surface to bottom contained Phæocystis in abundance. This also coincided with the

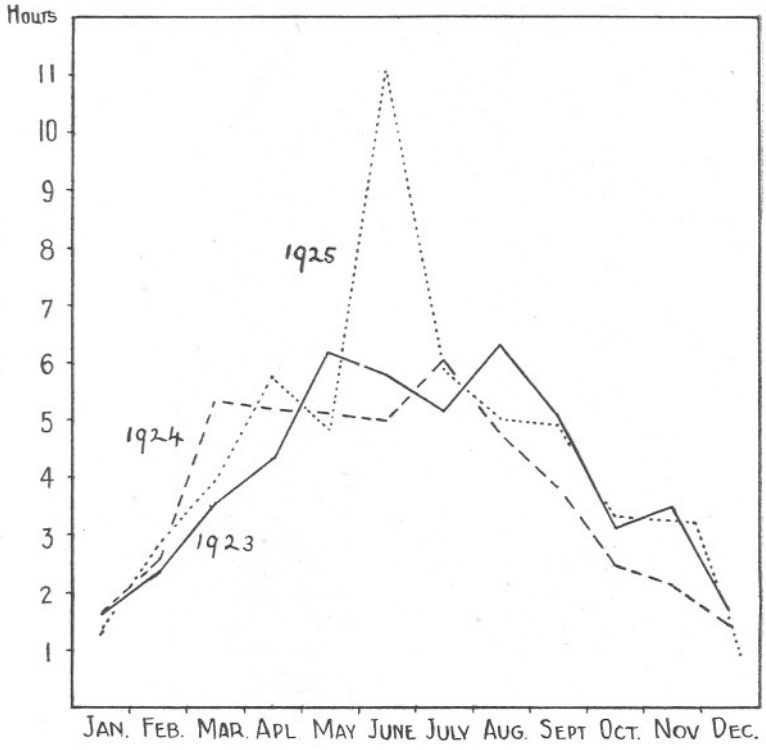


FIG. 9.—Mean monthly sunshine records, in hours per day, for England S.W. (including S. Wales), plotted for 15th of each month, 1923–1925. From Meteorological Office Records.

[Reprinted from Fig. 5 of *Jour. Mar. Biol. Assoc.*, 1926, **14**, 457.]

sudden fall in phosphate, which took place about a month earlier than in 1928, the temperature being 8·8°. Next in abundance to Phæocystis the water from the sample bottles, examined directly, without centrifuging, with a low power in a small dish, contained the following: *Lauderia borealis*, abundant; *Rhizosolenia stolterfothii*, a fair amount; *Chætoceros decipiens*, frequent; *Nitzschia delicatissima*, embedded in the jelly of Phæocystis, a small species of Gymnodinium; *Navicula membranacea*, also occasional cells of *Rhizosolenia shrubsolii*, *R. robusta*, *Skeletonema*

costatum, *Chætoceros densus*, *C. sociale*, Navicula sp., *Nitzschia closterium*, *Streptotheca tamensis*, *Hyalodiscus stelliger*, Thalassiosira sp., Pleurosigma sp., *Peridinium ovatum*, *P. pentagonum*, Dinophysis sp., *Spirodinium spirale*. The water-column being isothermal the plankton was

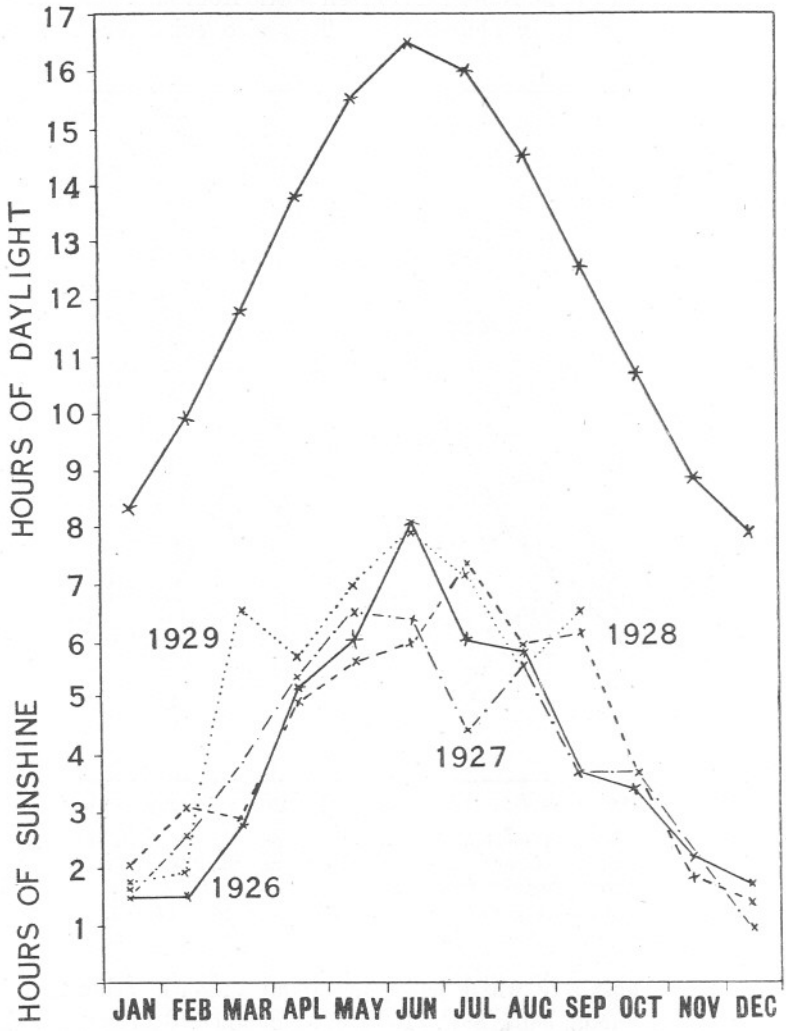


FIG. 10. As Fig. 9, 1926–1929, also mean length of daylight per day, for each month, plotted for 15th.

well distributed but seemed more abundant at 15 m. than elsewhere. The phosphate concentration was slightly lower at 5 and 10 m. than elsewhere. I am indebted to Dr. M. V. Lebour for kindly identifying the phytoplankton.

The Causes of the Difference in the times of Phosphate Consumption from Year to Year.

In an earlier paper (1926) it was shown that the years 1924 early, 1925 intermediate, and 1923 late were arranged in the order of their early spring sunshine records, as may be seen in Figure 9. A similar agreement had been found by Herdman, Scott and Dakin (1910), 1907 having an unusually early diatom crop, following, with a lag, a high value for February sunshine. Marshall and Orr (1927), however, found a remarkable constancy in the date of the vernal outburst in the Clyde area. Their phosphate estimations were checked by counting the diatom chains, a good agreement being found. In another paper (1928) the E1 observations concerning the years 1923, 1924 and 1925 were shown to be associated with predominant north-sector winds in 1924. The relation works back to the sunny weather and clear skies associated with northerly winds.

Figure 10 is similar to Figure 9, but concerns 1926–1929 ; 1926 has been classed as an early year, like 1924, but Figures 4 and 5 show that in detail the years were very different, for 1924 gave a regular series of productivity uprights, whereas in March 1926 regeneration preponderated, being associated with 2·8 hours sunshine per day. The big outburst came in April, with an average of 5·2 hours sunshine per day. After this 6 hours daily in May and 8 hours in June did not lead to the complete exhaustion of the phosphate, though the surface values were further reduced. The epithalassa having become established regeneration took place, but very low phosphate values were found in July, August and September, even with decreased sunlight. One has, however, to consider the possible effect of variations in the clearness of the water, data on which are recorded in Table 1 and are shown in Figure 11. These variations are such as to alter the illumination about eight times, much the same as is found between a dull winter day giving 15,000 metre-candles and a very bright summer or spring day with 120,000 m.c. So unless one knows the absorption coefficient it does not follow that a period of bright sunshine is necessarily one of high illumination at, say, 15–25 m., though it will probably be so at depths down to 10 m. in the open sea.

The year 1927 should have been an earlier year than 1926, with 3·9 hours daily sunshine for March. Observations up to March 21st, after which they are lacking, showed no outburst, but rather slow regeneration till March, following upon the small and unusual outburst at the very end of December 1926.

The year 1928 was studied in great detail. There was a moderate outburst late in February with small ones in the end of March and middle

of April and larger ones early in both May and June, causing the year to be grouped with 1923 as late, though it began well in February ; in this month the sunshine was 116 per cent of the normal, January having had 125 per cent. That for March was only 73 per cent, and April 89 per cent.

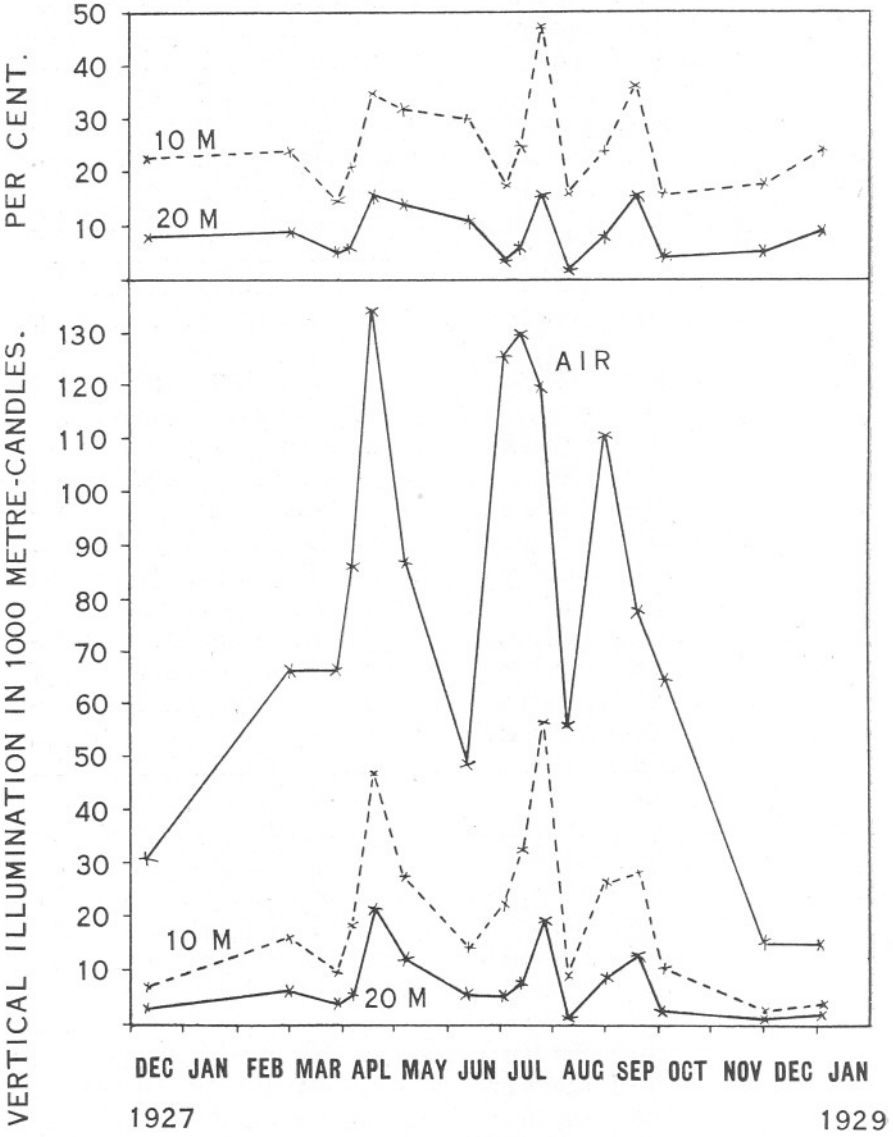


FIG. 11. The upper portion represents the percentage of the vertical illumination (received on a horizontal surface) penetrating to 10 and 20 metres, at Station E1, on the dates shown. The lower portion gives the vertical illuminations, in 1000-metre-candles, in air, at 10 and at 20 m. Data from Poole and Atkins (1929).

In 1929 the most striking feature was the great outburst early in April. After an almost normal January sunshine (104 per cent) and only 75 per cent of the normal in February, that for March had risen to 165 per cent, 6·54 hours per day. This seems obviously connected with the early April outburst. Figure 11 also shows the mean monthly length of the day for the meteorological district, namely, England S.W. and

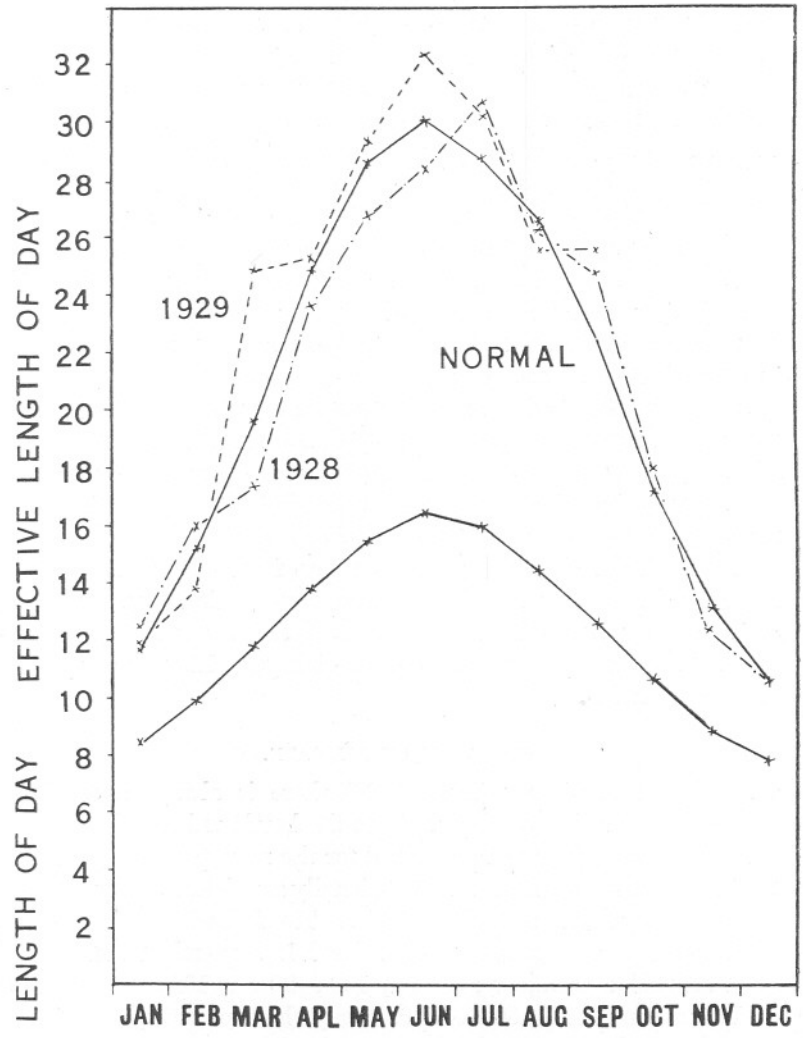


FIG. 12. The lowermost curve shows the length of day in hours for the meteorological district England S.W. (including S. Wales). The upper full curve shows the normal " effective " length of day for the district, counting each hour of sunshine as equivalent to two hours of diffuse light. (See text.) The curve with dot and dash shows the " effective " length of day for 1928 ; the curve with dashes only represents 1929.

S. Wales. It is obvious that length of day is a very important factor as regards the causation of an outburst of plant growth. Poole and Atkins (1929) found that the vertical illumination due to the sun's direct rays is about twice as great as that due to the diffuse light. Thus sunshine, which usually occurs in the midday hours, has the effect as it were of trebling the duration of the light, when at its highest, for in addition to a normal diffuse light of, say, 30,000 m.c. there will be an extra 60,000 due to sunlight; this is equivalent to three times as long at 30,000 m.c. Since, however, the sunshine hours are already included in the length of the day we can get a rough idea of the "effective length of day" by adding, to the mean length for the month, twice the mean monthly sunshine for the month of the year under consideration. This gives an approximate relative figure for the same months of different years; thus for March the normal "effective" length of day is 19·7 hours for the district, whereas that for 1928 was 17·6 and for 1929 it was 24·9 hours. The comparison is only a rough one, however, for the different months, because the average diffuse illumination varies greatly from month to month; also the sunlight is not twice as powerful as the diffuse light in the depth of winter and is more than twice as powerful in mid-summer. Figure 12 shows the mean monthly length of day for the district, also the normal "effective" length of day, obtained from the normal values of the mean monthly sunshine. The broken lines show the "effective" length of day for 1928 and 1929. The great difference in March appears to offer a rational explanation of the remarkable phytoplankton outburst early in April 1929. Pending the obtaining of accurate measurements of the daily or monthly illumination in metre-candle hours by means of a permanently exposed photo-electric cell and a Cambridge Instrument Co. "thread recorder," the curves of Figure 12 may serve as a rough approximation.

Estimation of Silicate.

As mentioned previously (1923, 1926) there is always a suspicion that a trace of silicate may dissolve from the bottle unless this has been waxed. The values given were obtained for the most part using samples from waxed bottles, but these were occasionally supplemented by analyses from the ordinary hard green glass bottles. The following values, in mg. SiO_2 per cubic metre, were obtained for E1, September 18th, 1928, analysed on 20th: 0 m., 99; 15 m., 100; 20 m., 102; 25 m., 163; 30 m., 118; 40 m., 144; 60 m., 209. Only the 0 m. sample was from a waxed bottle, but obviously the 15 and 20 m. samples agree well. The 25 m. sample is from water totally different as regards temperature and phosphate, but from this depth downwards both are almost uniform, whereas the silicate values are not. It seems possible that suspended

diatom tests and siliceous material has been dissolved in varying amount, but the glass risk is not excluded ; the tints are moreover so faint that too great reliance must not be placed in the analytical results. The degree of accuracy attainable may be judged from the following analyses of samples from E1, July 23rd, 1928, using waxed bottles : taking 100 mg. and 200 mg. standards the surface results were 55 and 60 mg. respectively and the bottom 142 and 130 mg. Nevertheless, it seems likely that such accuracy is not always obtained.

A matter of greater importance is the picric acid used in making up the standard solution, for which 36·9 mg. of picric acid has been taken as corresponding to 50 mg. p.l. of SiO_2 in solution as silicate according to Diénert and Wandenbulcke (1923). Thresh and Beale (1925) used 40 mg. of picric acid. King and Lucas (1928), however, state that 25·6 mg. of vacuum-dried, C.P. picric acid per litre gives a colour equivalent to 50 mg. p.l. of SiO_2 with the reagents. They suggest that possibly the earlier workers neglected to dry the picric acid, to which water is usually added for safety. My own standard solution was made from picric acid crystals which had been for several years in a nearly empty bottle and appeared to be quite dry ; they were further dried over sulphuric acid in a desiccator. The crystals used by Thresh and Beale were also dried over sulphuric acid in an ordinary desiccator (private communication). It seems unlikely that so large a discrepancy can be accounted for merely by the difference in drying in an ordinary and a vacuum desiccator, yet the work of King and Lucas, carried out with every precaution and with picric acid recrystallised from benzene (Benedict, 1922), renders it desirable that the standards used by different workers should be compared till uniformity is secured.

As first pointed out by Folin and Doisy (1916), impure picric acid, specially common at about that time, may be a source of error in estimating creatine and creatinine. A rather laborious purification gave a product that could be relied upon, though Benedict (1922) reported samples that were not even improved by this repetition of recrystallization of sodium picrate from water. Benedict found that recrystallization of even the " technical " grade of picric acid from hot benzene gave a product which was quite satisfactory. The impurities give a deep colour with alkali ; this is important in the creatine estimation, but affects the silica estimation far less, since it is carried out by comparison with an acid mixture. Recently, however, Benedict (1929) has found samples of picric acid which show little improvement after crystallization from benzene. He recommends the use of glacial acetic acid as a solvent for the dried picric acid, or alternatively recrystallization of the sodium salt by a modification of the Folin-Doisy method, using sodium carbonate instead of sodium hydroxide.

Through the courtesy of Dr. E. J. King it is now possible to be sure that analyses on opposite sides of the Atlantic are truly comparable. He examined my standard picric acid solution and found that it agreed exactly with his own, made up to be 36·9 mg. per litre. This, according to Diénert and Wandenbulcke, is equivalent in colour to one containing 50 mg. SiO_2 per litre. According to King and Lucas this is matched by 25·6 mg. of picric acid per litre. Apparently the fault lies in the picric acid originally used by Diénert, for the silica content of silicate can readily be checked by gravimetric analysis. Since in my earlier work I used Diénert and Wandenbulcke's factor, all the figures published must be multiplied by 1·30. Those given in this paper *are now correct by King's standard.*

Methods of Calculating the Allowance to be made for the Reagent Blank.

The analyses of phosphate were made, as heretofore, by the coeruleo-molybdic method of Denigès, using 100 c.c. of liquid in a Hehner tube. The allowance for the reagent blank is of course a perfectly general correction, necessary in all colorimetric work involving minute quantities.

The blank correction was formerly made as follows: if using as standard a 0·05 mg. per litre solution of phosphate, reckoned as P_2O_5, or 50 mg. per cubic metre, 100 c.c. of distilled water plus reagents matches 10 c.c. of standard plus reagents. The amount of the blank then corresponds to $\frac{50\times10}{100}=5$. This amount corresponds to a full column, therefore if an unknown solution matches at a reading of 40, it is clear that the standard column contains two-fifths of the blank in excess of its supposed phosphate content, whereas the unknown contains the full amount of reagents producing the blank. Accordingly three-fifths of the blank must be subtracted from the apparent amount found for the unknown, namely,

$$\frac{50\times40}{100}=20, \text{ less } 3=17.$$

This, however, is not quite correct, for the real strength of the standard has been increased by the presence of the reagents also. In general terms let k denote the true amount of the blank, c the concentration of the standard before addition of the blank-producing reagents, x the reading for the blank and y that for the unknown solution containing an amount z: then

$$k=(c+k)\times\frac{x}{100},$$

$$\text{and } z+k=(c+k)\times\frac{y}{100}$$

Now taking, as before, x=10 and y=40, with c=50 mg. per cubic metre, we get :—

$$100\,k=500+10\,k, \text{ hence } k=5{\cdot}5$$

$$\text{and } z+k=\frac{55{\cdot}5\times 40}{100}=22{\cdot}2$$

hence z=16·7, as against z=17 by the approximate correction. In view of the fact that a difference of two units on the scale corresponds to 1 mg. per cubic metre, the use of the approximate correction is not a cause of any appreciable error. However, using a weaker standard solution the error may become more serious, especially for higher values of k and lower values of y.

Thus, with k as before, viz. 5·5, y=40 and c=25, we get

$$z+k=\frac{30{\cdot}5\times 40}{100}=12{\cdot}2,$$

whence z=6·7 and the approximate method gives :—

$$z=\frac{c\times 40}{100}-\frac{60}{100}k,$$

hence z=10—3=7, which is in good agreement. However, with x=24, and c=25 we get k=6·0 by the approximate method and 7·9 by the exact one. With these values and y=30 the approximate method gives 3·3, the exact 2·0. An alternative approximation, in cases where y approaches to x, is to subtract and calculate from :—

$z=\frac{(y-x)c}{100}$, which with the above assigned values gives z=1·5, which would then be rounded off to z=2 as obviously nearer than z=1.

Since in the present paper the interest lies partly in seeing how near to complete exhaustion the phosphate content may go, it has seemed advisable to use the first approximate method when c=50, as before, and to adopt the exact formula for use with the very weak solutions estimated with standard c=25 mg. per cubic metre.

SUMMARY.

1. The phosphate content of sea-water at Station E1 ranged, during the period November 1927–April 1929, from 48 mg. P_2O_5 per m^3., to 0·0 mg. The former was an exceptional and temporary surface value during phosphate regeneration in mid-winter ; the latter was a very usual value at from 0–15 m. during July, August or even September.

2. For the whole water-column, 0–70 m., at E1 the maximum values were 36·2 and 36·5 mg. during the winters 1927–1928 and 1928–1929 respectively. The minimum value for the column was 8·3 mg. in June 1928.

3. For the seven years 1923–1929 the maximum value for the phosphate content of the whole column was 37·0 mg. in 1923 and 1924, the lowest winter maximum observed being 31·0 mg. For the seven years the mean maximum value was 35·1 mg. The five summers gave a mean minimum value of 7·6 mg. for the column, the absolute minimum being 5·1 mg. on August 31st, 1925.

4. Additional evidence has been obtained that the surface may be a region of phosphate regeneration, not only in winter, but in bright summer weather when apparently the illumination is too intense for diatoms to thrive. Normally the bottom and deeper waters are the chief sites in which regeneration becomes apparent.

5. Taking the vernal consumption of phosphate as a standard, the years 1924, 1926 and 1929 were early years, 1928 being late with 1923 even later. The differences may amount to as much as 6 or 7 weeks. The earliest spring, 1924, happened also to be the coldest. It must accordingly have been one in which the hatching of fish eggs went on most slowly. This year, therefore, should be an outstanding one as regards suitability or otherwise for various species of young fish.

6. The differences in the seasonal productivity of the various years is well brought out by erecting perpendiculars, at the proper positions on the time abscissæ, which are proportional to the differences between successive observations of the phosphate concentration of the water-column. It is seen that the production of phytoplankton, as measured by phosphate consumption, proceeds by a series of outbursts.

7. The rate of production throughout the whole water-column was as much as 1·06 mg. P_2O_5 per m^3. per day for April 3rd, 1929. For the upper 25 m. the maximum rate found was 0·94 mg. for the same date, with 1·13 mg. for the column from 25–70 m. Owing to vertical mixing with surface water poorer in phosphate this rate is fictitiously the greatest.

8. A comparison of the total carbon dioxide content of the water-column at various times during the year has shown that in a general way the minimum is reached at about the same time as the phosphate minimum. The carbon dioxide content was found to vary from 47·8 to 46·5 c.c. per litre, so it never remotely resembles complete exhaustion in the open sea.

9. There is a general agreement between the curves for seasonal variation in phosphate and in silicate, but the latter never reaches zero. The July minimum for the surface, 33 mg. SiO_2 per m^3. is very near the limit of what can be detected. The winter maxima differ more than do the phosphate max ma from year to year, that for 1927–1928 and 1928–1929 being respectively 320 and 220 mg. A sharp fall in silica content in the spring may be several weeks ahead of a similar fall in phosphate.

10. The factor for silica determination as given by King and Lucas has been adopted in preference to that of the originators of the method of colorimetric comparison against picric acid. This necessitates the multiplication of the results of my analyses, published heretofore, by the factor 1·30. The trouble has apparently been due to the presence of an impurity in the picric acid used by Diénert which may render advisable a method of purification recognised as necessary in the determination of creatine and creatinine.

11. In April 1929 a sudden fall in phosphate concentration was accompanied by a remarkably rich phytoplankton outburst. Every sample of water bottled from 0–70 m. contained lumps of Phæocystis jelly, as well as the diatom *Lauderia borealis* in abundance, though not so in every sample. *Rhizosolenia stolterfothii*, *Chætoceros decipiens*, and *Nitzschia delicatissima* were also plentiful; twelve other species of diatoms were found and four of the Peridineæ.

12. The order in which the years stand in § 5 is, in a general way, the order of spring sunshine. The variations in the clearness of the water must be taken into account in assessing the submarine illumination; such variations may cause an eight-fold variation in the upper 20 m., much the same as is found between winter and spring.

The length of the day as well as the sunshine is important in regulating the amount of photosynthesis. Crediting the day with two hours extra daylight for each hour of sunshine a graph has been constructed which shows how 1929 was in this respect ahead of 1928 in the spring. The comparison is a fair one for the same months of different years, but only rough for the different months, as the sun's altitude varies.

It should be added that the values quoted for the salinity of the water were determined in the Government Chemists' Laboratory, London.

REFERENCES.

ATKINS, W. R. G. 1924. The hydrogen ion concentration of sea-water in relation to photosynthetic changes. Pt. III. J. Marine Biol. Assoc., **13**, 437–446.

ATKINS, W. R. G. 1923. The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. *Loc. cit.*, **13**, 119–150.

ATKINS, W. R. G. 1925. Seasonal changes in the phosphate content of sea-water in relation to the growth of the algal plankton during 1923 and 1924. *Loc. cit.*, **13**, 700–720.

ATKINS, W. R. G. 1926. The phosphate content of sea-water in relation to the growth of the algal plankton. Pt. III. *Loc. cit.*, **14**, 447–467.

ATKINS, W. R. G. 1928. Seasonal variations in the phosphate and silicate content of sea-water during 1926 and 1927 in relation to the phytoplankton crop. *Loc. cit.*, **15**, 191–205.

ATKINS, W. R. G. 1923. The silica content of some natural waters and of culture media. *Loc. cit.*, **13**, 151–159.

ATKINS, W. R. G. 1926. Seasonal changes in the silica content of natural waters in relation to the phytoplankton. *Loc. cit.*, **14**, 89–99.

ATKINS, W. R. G., AND WILSON, E. G. 1926. The color metric estimation of minute amounts of compounds of silicon, of phosphorus and of arsenic. Biochem. J., **20**, 1223–1228, No. 6.

ATKINS, W. R. G., AND POOLE, H. H. 1930. The photo-electric recording of daylight. Nature, **125**.

BENEDICT, S. R. 1922. A method for the purification of picric acid for creatinine determinations. J. Biol. Chem., **54**, 239–241.

BENEDICT, S. R. 1929. A note on the purification of picric acid for creatinine determinations. *Loc. cit.*, **82**, 1–3.

DIĔNERT, F., AND WANDENBULCKE, F. 1923. Sur le dosage de la silice dans les eaux. C.R. Acad. des Sc., Paris, **176**, 1478–1480.

FOLIN, O., AND DOISY, E. A. 1916. Impure picric acid as a source of error in creatine and creatinine determinations. J. Biol. Chem., **28**, 349–356.

HERDMAN, W. A., SCOTT, A., AND DAKIN, W. J. 1910. Intensive study of the marine plankton around the south end of the Isle of Man. Pt. III. Trans. Liverpool Biol. Soc.

KING, E. J., AND LUCAS, C. C. 1928. The use of picric acid as an artificial standard in the colorimetric estimation of silica. J. Amer. Chem. Soc., **50**, 2395–2397.

MARSHALL, S. M., AND ORR, A. P. 1927. The relation of the plankton to some chemical and physical factors in the Clyde Sea area. J. Marine Biol, Assoc., **14**. 837–868.

MARSHALL, S. M., AND ORR, A. P. 1928. The photosynthesis of diatom cultures in the sea. J. Marine Biol. Assoc., **15**, 321–360.

MCCLENDON, J. F. 1917. The standardization of a new colorimetric method for the determination of the hydrogen ion concentration, CO_2 tension, and CO_2 and O_2 content of sea-water, of animal heat, and of CO_2 of the air, with a summary of similar data on bicarbonate solutions in general. J. Biol. Chem., **30**, 265–288.

POOLE, H. H., AND ATKINS, W. R. G. 1928. Photo-electric measurements of submarine illumination throughout the year. J. Marine Biol. Assoc., **16**, 297–324.

THRESH, J. C., AND BEALE, J. F. 1925. The examination of waters and water supplies. London.

CORRIGENDUM.

In the *Journal of the Marine Biological Association*, Vol. XVI., No. 3, 1930, pp. 848 and 851, a factor is given for converting silica, estimated by Diénert's and Wandenbulcke's standard, into the value now believed to be correct according to King and Lucas. The factor used was 1·30, in error for 1·44. The values stated to be correct by King's standard are therefore almost 10 per cent too low. I am indebted to Prof. Thomas G. Thompson for pointing out this extraordinary blunder, which I much regret.

W. R. G. Atkins.

A Study of the Spring Diatom Increase in Loch Striven.

By

S. M. Marshall, B.Sc.,
Assistant Naturalist,

And

A. P. Orr, M.A., B.Sc., A.I.C.,
Chemist,
Marine Station, Millport.

With 15 Figures in the Text.

THE spring diatom increase in the open sea and probably also in inshore waters is one of the most important annual biological events and information regarding it or its causes is likely to be of value. In an inshore area changes are not only more pronounced, but also take place more rapidly than in the open sea and, for this reason among others, the increase was studied in Loch Striven, a well-sheltered loch in the Clyde Sea Area. A general description of the weekly changes occurring in this loch has already been made (Marshall and Orr, 1927). The changes during the spring, however, are so rapid that an examination at even closer intervals during this period was thought advisable. Such an examination was made in 1927 and 1928, the interval between successive visits being generally two days. The methods used were the same as those described in the above-mentioned paper.

During the spring increase in Loch Striven in the years studied the sea was an almost pure culture of *Skeletonema costatum*. The other diatom species which occurred were few enough to be negligible and animal life was scarce. Before the increase began Skeletonema formed over 96% of the diatoms. On March 19th, 1928, of the first thousand cells counted, only five cells were not Skeletonema, on the 22nd less than 10, and on the 26th only 13. Thus the changes occurring were due almost entirely to one diatom species.

The spring increase of 1926 has been described in the paper referred to (Fig. 7). Visits were made only about once a week and the depths worked were 0, 5, 10, 20 and about 30 fathoms. The increase was regular in form, beginning at the surface and sinking gradually into

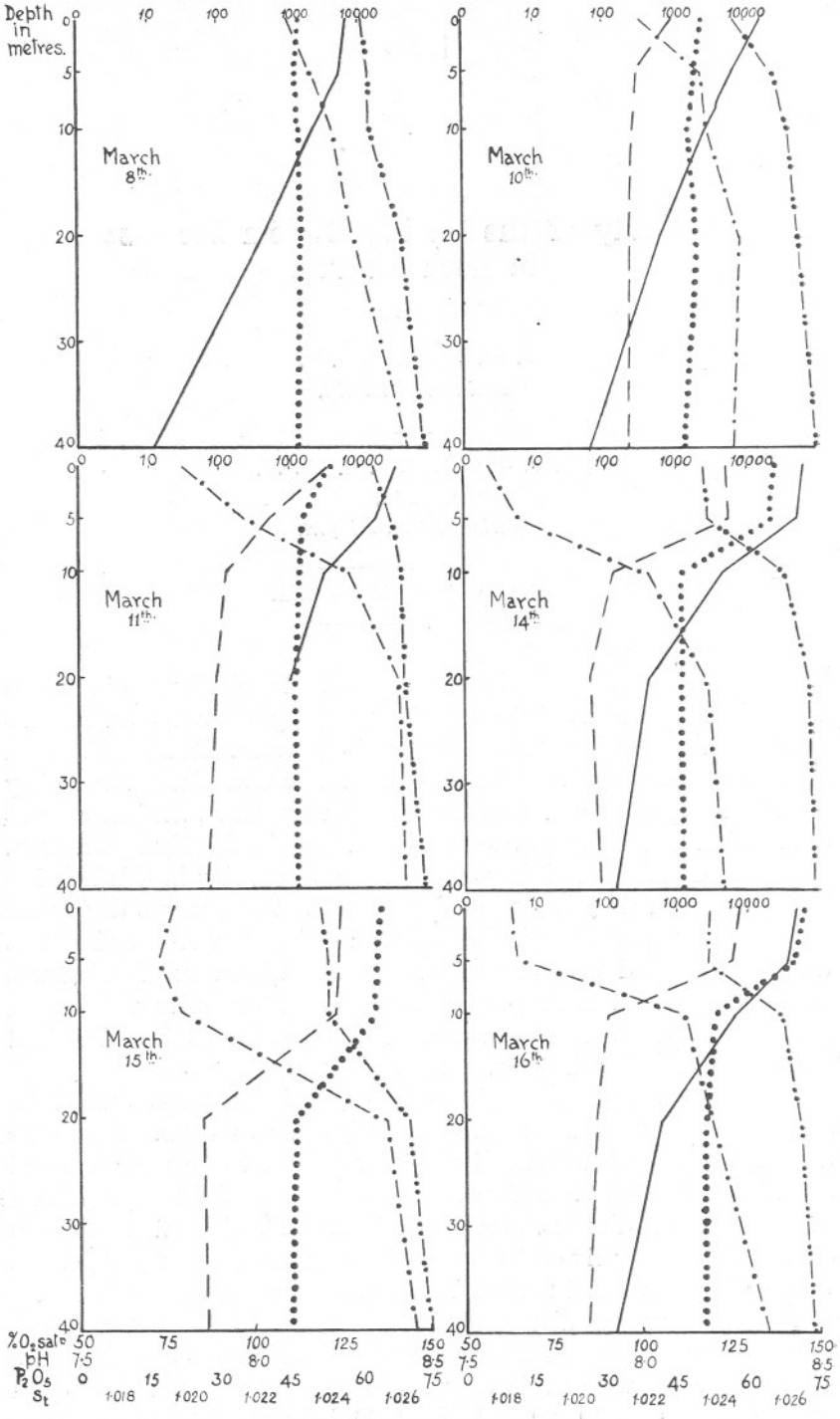


FIG. 1.—The spring increase in 1927.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — . . — . . S_t.

deeper water, so that the maximum at 5 fathoms occurred the week after the maximum at the surface, and the maximum at 10 fathoms a week later. After this the fall was rapid, showing that the diatoms had sunk below the depth to which photosynthesis was possible. Three weeks after the beginning of the increase the diatoms had almost disappeared from the loch. The chemical factors showed a similar series of changes, the pH value and oxygen content rising and the phosphate falling with an increase in diatom numbers.

In 1927 (see Figs. 1, 2, 3 and 8, and Table 1) the loch was visited more frequently and the depths worked were 0, 5, 10, 20 and 40 metres. The increase had started before the first visit was made on March 8th and there were more than 5000 diatom chains per 20 c.c. in both surface and 5-metre samples. This is an unusually early increase when compared with previous years. The diatoms had increased again on the 10th, and between the 10th and the 11th the numbers were doubled at the surface (16,700 to 33,100) and 5 metres (6900 to 16,400). This very rapid change was accompanied by a sharp rise in oxygen saturation (110% to 121%), a slight rise in pH value and a marked fall in dissolved phosphate. In the deeper water, however, there was also a considerable change, the phosphate and dissolved oxygen saturation values being different from that for the 10th. This leads one to suppose that the change was not due entirely to diatom growth, but that the water examined was not the same as on the previous day. That such an increase can take place naturally, however, is shown by Gran (1927).

At this time the surface density was lower than that of the other layers so that no vertical mixing was going on. On the 14th a fall in density at surface and 5 metres stabilised the loch still further and the chemical changes were correspondingly more marked. The diatoms also reached their maximum for the increase and were almost as numerous at 5 metres (51,000) as at the surface (62,700), but this is probably due to the mixing of the waters between these depths.

On the 15th there was a hard S.E. wind and the effect of this was similar to that described by Murray for some Scottish lochs (1888) and by Gran and Gaarder (1918) for the Oslo fiord. The surface waters were piled up in the loch so that the values found the previous day at surface and 5 metres were now found at surface, 5 and 10 metres. Diatoms were not counted this day, but it is almost certain that the high figures would have been found at 10 metres also. On the 16th and 17th conditions had returned to normal and were very much the same as on the 14th. By the 18th diatoms were very much more numerous at 5 metres than at the surface in spite of the fact that the density at these depths was much the same. This shows that the diatoms have begun to sink and this process had gone still further by the 22nd when the maximum numbers

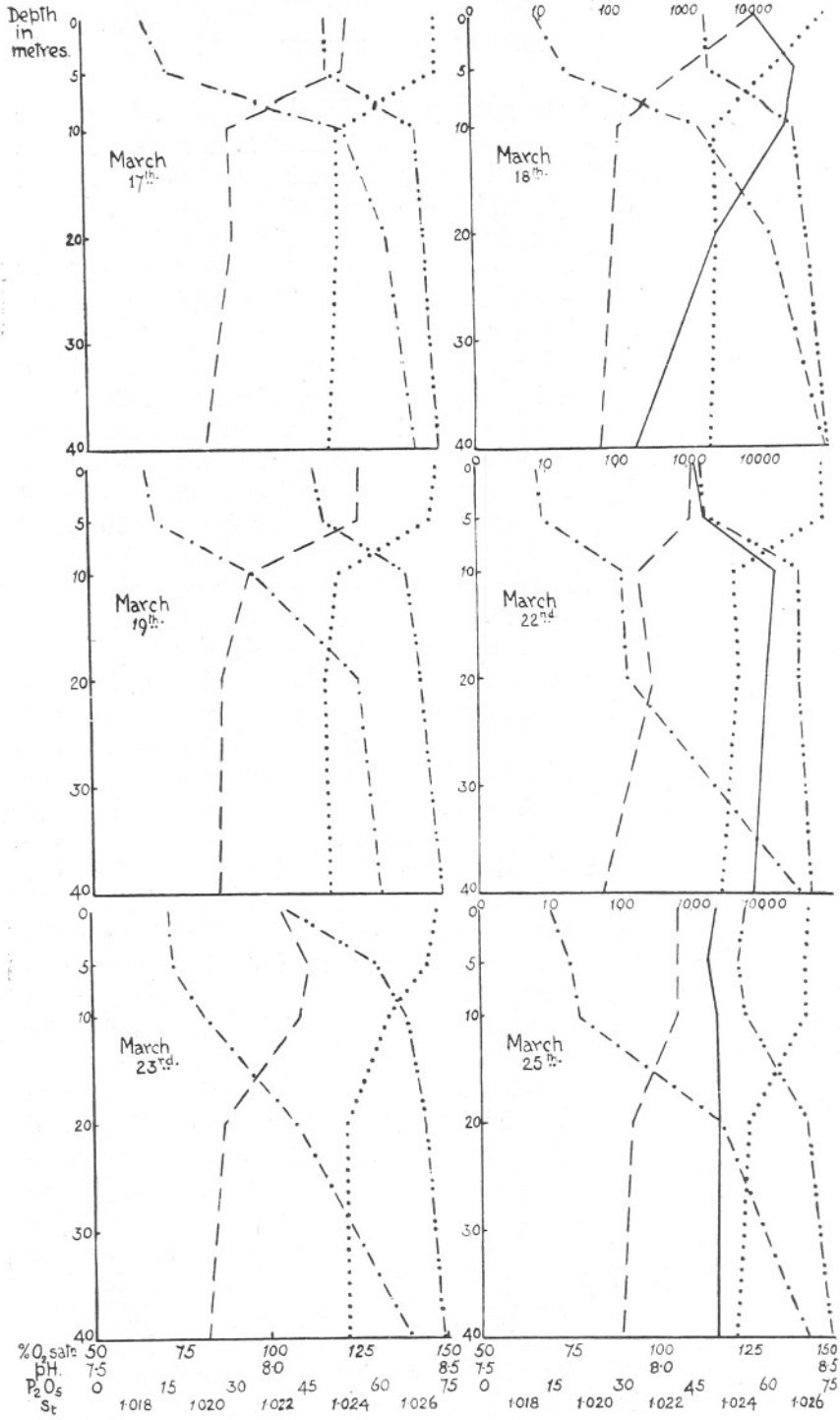


FIG. 2.—The spring increase in 1927 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were found from 10 to 40 metres. By the 25th numbers at all depths had fallen and the increase was over. There are no chemical changes corresponding to the high diatom numbers at and below 20 metres, which indicates that the diatoms are sinking passively and that no photosynthesis is going on there.

An examination of the loch at intervals of about two days shows that the regularity of the increase is not so marked as when the examination is made only once a week. These irregularities are partly because in an enclosed area the effect of wind and tide is much more marked than in the open sea. Another point of interest is that the increase falls off before all

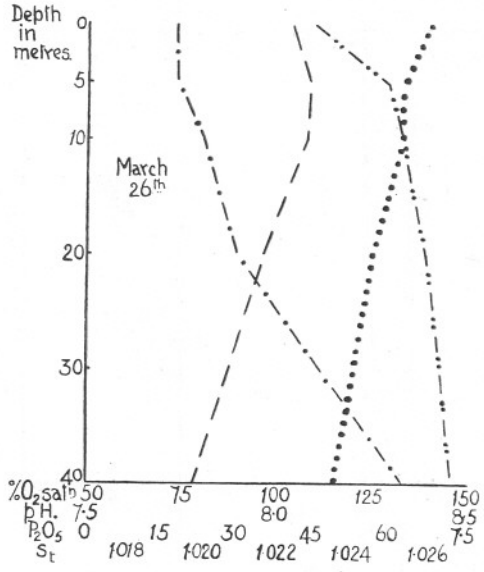


FIG. 3.—The spring increase in 1927 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

the phosphate is utilised, which is at variance with the results obtained in the open sea (Atkins, 1926), but is in agreement with the results obtained during the spring increase in the same loch in 1926. No other essential nutrient salts were estimated, however, and it is possible that one of these may have been limiting. There is, nevertheless, a definite relationship between the chemical factors and the diatoms. Estimation of small quantities of phosphate is not very exact when diatoms are very numerous, for they then give the sample a brownish tinge which interferes somewhat with the blue colour given by the phosphate reagent.

In 1928 (see Figs. 4, 5, 6 and 9, and Table 2) the number of diatoms was estimated by counting the cells and not the chains. Several counts

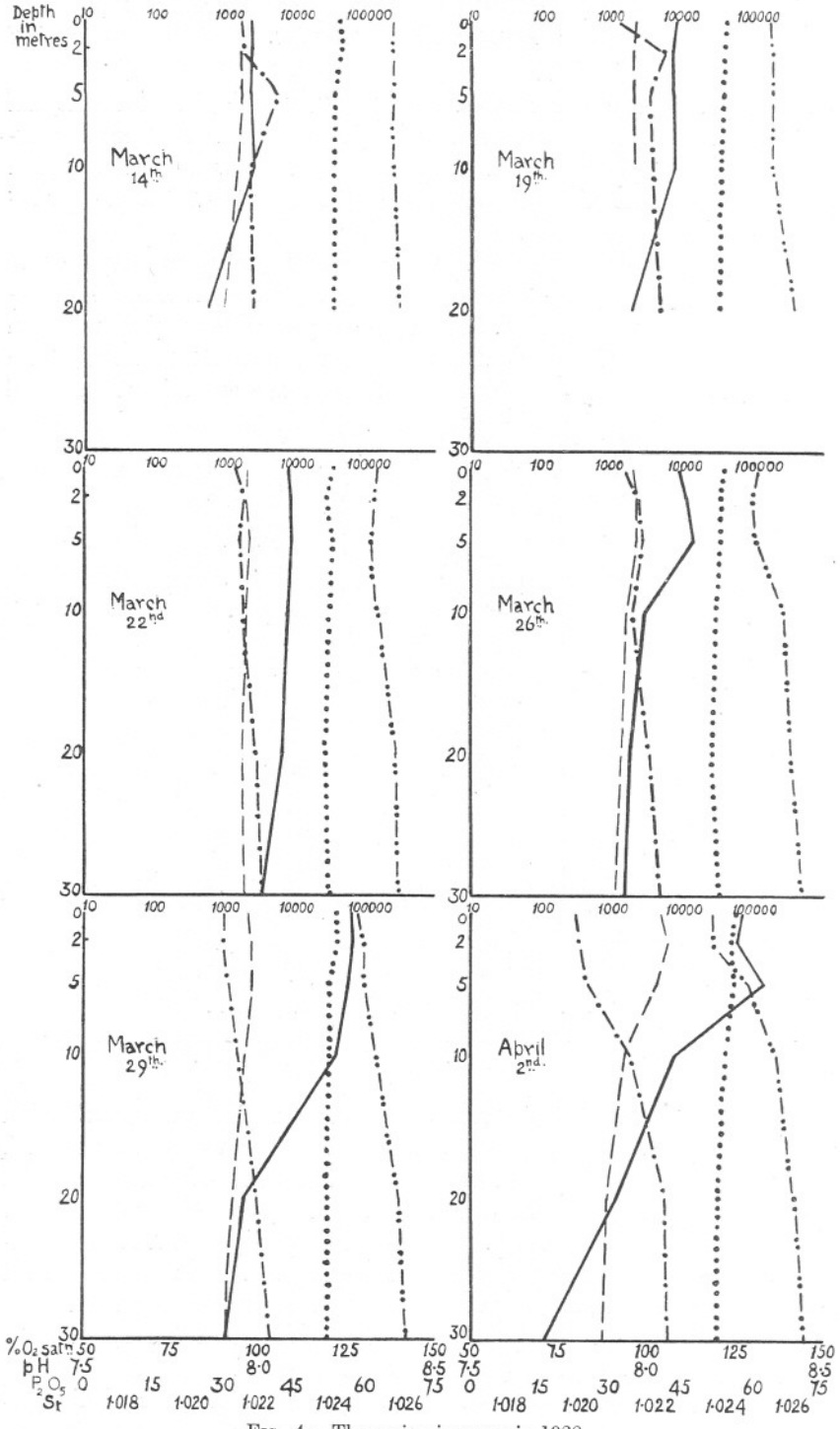


FIG. 4.—The spring increase in 1928.

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

gave an average of about 10 cells per chain and this figure held till the end of the increase when it fell somewhat. They were counted in this way to bring the work into line with that done elsewhere, and the comparison with 1926 and 1927 can be made by multiplying the figures for those years by 10. Gran (1929) estimates that the number of cells in a chain of *Skeletonema costatum* is 16 or more. The reason for the difference may be that our samples were centrifuged living and not after preserving. The depths worked were 0, 2, 5, 10 and 20 metres. The additional depth of 2 metres was chosen because the maximum amount of photosynthesis may not occur at the surface.

On March 14th there were already between two and three thousand cells per 20 c.c. down to a depth of 10 metres. This is higher than normal for winter, and a certain amount of growth must have been going on. The pH value was also higher than the normal winter value. By March 19th numbers had increased at all depths counted but were still much the same, 7000 to 8000 from 0 to 10 metres. Values for density, oxygen saturation, pH and phosphate show the same conditions. The temperature overturn had not yet taken place and the loch was therefore in an unstable condition in which vertical mixing was possible. Conditions were much the same on the 22nd, but mixing, and along with it, diatom numbers had spread deeper. The increase had progressed considerably by the 26th and diatoms were fairly rich (9000 cells at the surface, 11,300 at 2 metres, 13,500 at 5 metres). At the same time, however, density was almost uniform to 5 metres so that this distribution is apparently not due to a real sinking of the diatoms but to vertical mixing to this depth. The chemical changes also agreed with density. By the 29th the temperature had risen at the surface, the loch was in a more stable condition, and there was a great increase in the number of diatoms down to 10 metres. The values for the chemical factors, however, showed little alteration. On April 2nd the loch was supersaturated with oxygen down to 5 metres and the phosphate values had fallen as far as the same depth. The diatom distribution was irregular, rising as far as five metres, then falling sharply in the deeper water. Two days later, on April 4th, density had fallen again at the surface and there was a steep gradient from there down to 10 metres. Corresponding with this phosphate had fallen to zero at the surface, the oxygen saturation had risen to 115% and pH value had also risen, while the diatoms had multiplied still further and were richer in the 2-metre sample (248,000) than at the surface (180,000). Since the loch was now quite stable, this is probably a real sinking and not caused simply by mixing.

On April 6th the loch remained stable, the diatoms had fallen to 5 metres where they reached their maximum number for this increase (510,000 cells in 20 c.c.), the oxygen saturation had also reached its

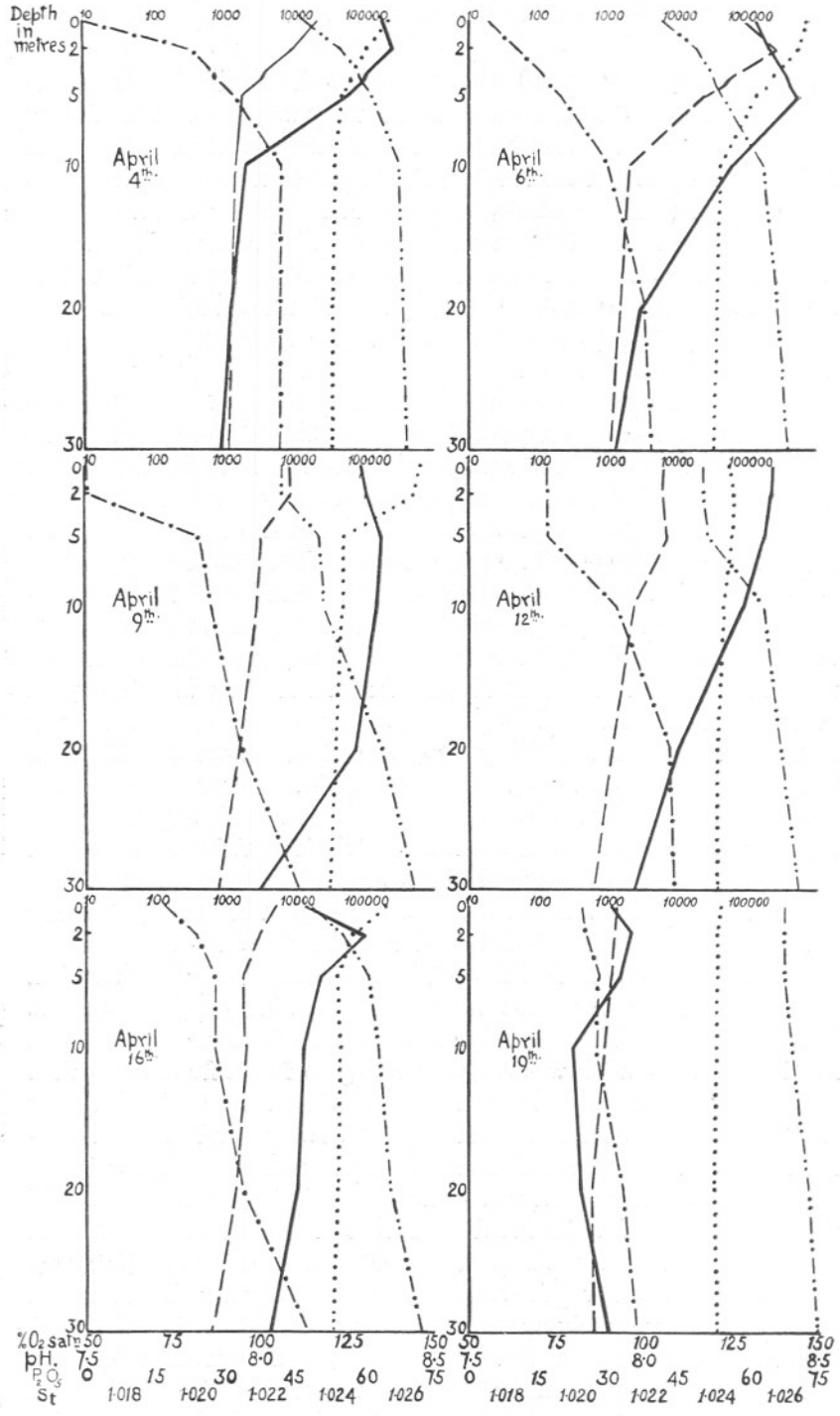


FIG. 5.—The spring increase in 1928 (contd.).

——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

maximum (138% at 2 metres), pH value had risen to 8·47, and phosphate had fallen at 2 and 5 metres. There are slight discrepancies in the phosphate results at surface and 2 metres on the 4th, 6th and 9th. These are due in part at least to the increased difficulty in matching colours when diatoms are very numerous.

It is curious that on the 6th, although the diatom present was as before, *Skeletonema costatum*, the type of cell was quite different from that of previous days, the cells being both larger and longer. This new type was found at surface and 2 metres while in all other samples they

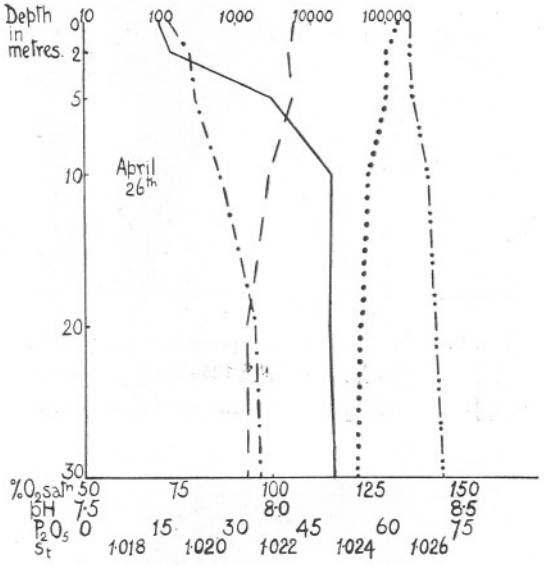


FIG. 6.—The spring increase in 1928 (contd.).
——— diatoms, ... pH, — — — O_2 satn.,
— . — . — . P_2O_5 mg. per cubic metre, — .. — .. S_t.

were of the usual form. On April 9th the diatoms were sinking and numbers had fallen except in the deeper water. The new type of Skeletonema cell was predominant at surface and 2 metres, at 5 metres the types were mixed and below this a few chains of the new type were present at each depth. Density conditions had altered again, so that there was vertical mixing between 0 and 2 metres, and between 5 and 10 metres. The chemical factors were correspondingly altered. By April 12th mixing had gone on to 5 metres and had brought up a fresh supply of phosphate into the surface water, at the same time lowering pH and oxygen saturation values. With the introduction of phosphate the diatoms had increased slightly again at the surface and 2 metres.

The new type of cell had disappeared and all samples contained only the old type.

By April 16th the loch was stable once more and the diatoms were sinking, their numbers having decreased again except in deeper water.

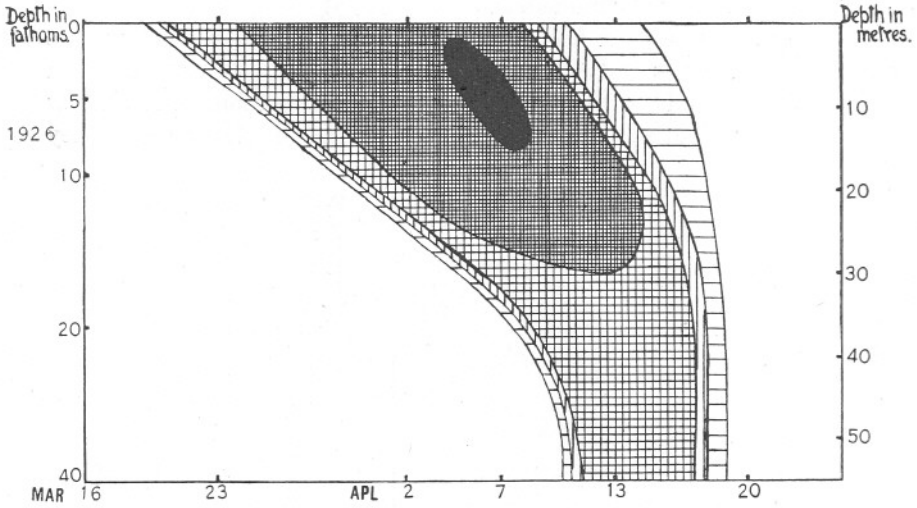


FIG. 7.—Diatom diagram. Spring increase of 1926.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

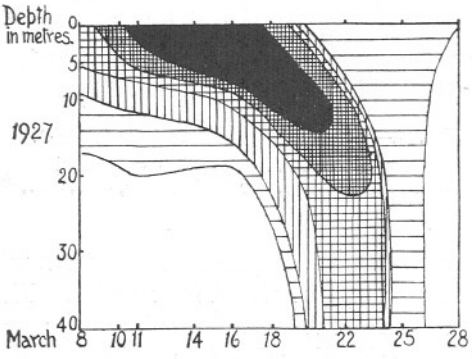


FIG. 8.—Diatom diagram. Spring increase of 1927.
□ under 50, ▭ 50–125, ▥ 125–250, ▦ 250–500,
▩ 500–1250, ■ over 1250 diatom chains per c.c.

There was still a fair amount of phosphate in the surface layers and it is difficult to understand why the diatoms stopped increasing at the surface. Diatom numbers were very low at all depths on the 19th and the distribution was irregular. The density gradient was only slight from top to

bottom and the loch appeared to be mixed. A week later it was visited again and there was evidence that another small increase of diatoms had taken place meanwhile, for the phosphate value had fallen a little, the pH value and oxygen saturation had risen and the diatoms increased in numbers down to 10 metres and then remained constant down to 30 metres.

The spring increase of 1928 was thus of a quite different type from that of 1926 and 1927, being much less regular. It began while vertical

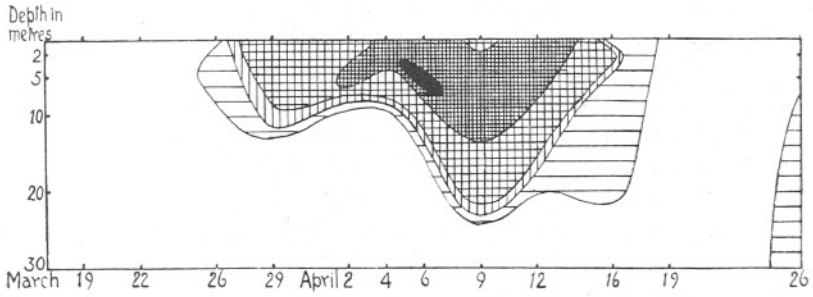


FIG 9.—Diatom diagram. Spring increase of 1928.
□ under 500, ▤ 500–1250, ||| 1250–2500,
▦ 2500–5000, ▩ 5000–12,500, ■ over 12,500 diatom cells per c.c.
The scales have been adjusted so that Figures 7, 8 and 9 are directly comparable.

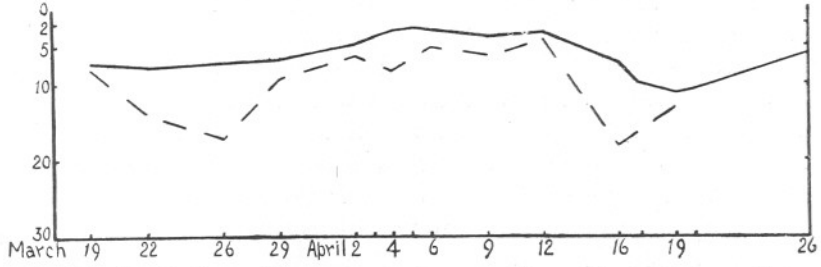


FIG. 10.—Secchi disc readings ———, and compensation-points for diatom cultures — — —, during the spring increase of 1928.

mixing was still going on and the diatoms increased in numbers simultaneously down to a considerable depth instead of only at the surface as usual. Since in deeper water there was not enough light for growth, the diatoms there sank as soon as mixing stopped and there was a great fluctuation in numbers at depths of 10 and 20 metres. When the temperature rose and stabilisation took place, the increase progressed much as in previous years, increasing rapidly at the surface and then sinking downwards. This process was interrupted, however, by further mixing, this time due to wind as well as temperature, and diatom numbers rose at the surface once more.

There are thus two factors responsible for the vertical distribution of the diatoms. First, there is the sinking of the diatoms which is strongly marked in the years 1926 and 1927 and is particularly clear in the late autumn of 1926 (Marshall and Orr, 1927). Second, there is the mixing of the diatoms which occurs when the sea-water itself is mixed by wind or temperature. This is recognisable by a uniform density at the depths mixed. This second factor was of considerable importance in 1928, but was found only on one occasion in 1927 (see p. 855). Another unusual event in the increase of 1928 was the change of diatom type for a short period, although the species remained unaltered. There was no apparent cause for either its arrival or its departure. Finally, as in the years 1926 and 1927, the end of the spring increase was not marked by a total lack of phosphate in the surface layers, but there was sufficient still in solution to supply another increase which in all probability followed after a short interval.

The spring increase starts at a time of year when the light for photosynthesis is comparatively poor, except at the surface, and the enormous number of diatoms present must decrease the light available still further. The figures for oxygen content are to some extent a measure of the amount of photosynthesis going on, but they are not reliable, partly because during the increase the water was often supersaturated and so gave too low an estimate of the oxygen produced, and partly because during the windy weather there was probably a good deal of movement among the different water layers. It was therefore thought of interest to estimate the amount of photosynthesis possible by sinking diatom cultures to different depths in the sea and measuring the amount of oxygen produced. Since the sea at that time was an almost pure culture of *Skeletonema costatum*, some samples of sea-water were tested in the same way. A culture of *Coscinosira polychorda* was used, while the sea-water samples used were taken from various depths (see Marshall and Orr, 1928). The most important external factor was, as might be expected, the number of diatoms present in the sea, and during the increase the total photosynthesis decreased from day to day as the cloud of diatoms in the water grew denser. Figure 11 and Tables 4 and 5 show two curves for diatom culture photosynthesis in the sea, the first taken before and the second during the spring increase of 1928. In the curve for March 22nd–23rd the oxygen production at 5 metres was considerable and the compensation-point lay between 10 and 20 metres. In the curve for April 6th–7th a steep fall occurred between $\frac{1}{2}$ and 2 metres and another between 2 and 5 metres, while the compensation-point lay between 2 and 5 metres. Since there was more sunshine on April 6th than on March 22nd, the smaller amount of photosynthesis going on at and below 2 metres must be ascribed to the effect of a thick screen of diatoms

in the surface water. The same type of result is seen in Figure 12 of which the curve for March 18th–19th was taken during, and that for March 28th–29th after the spring increase of 1927. After the diatoms had disappeared the photosynthesis at 5 metres increased again considerably. There was more sunshine on March 28th–29th than on March 18th–19th and the

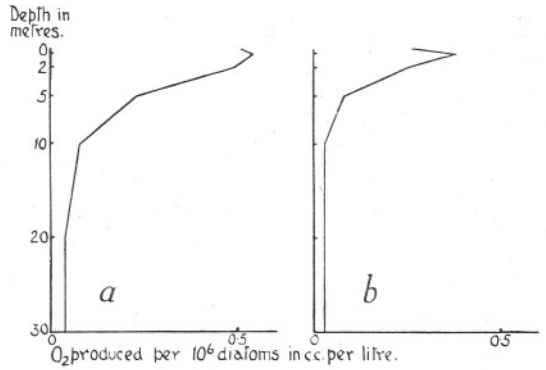


FIG. 11.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 22–23/3/28 (0·41 hours sunshine), (*b*) 6–7/4/28 (4·25 hours sunshine).

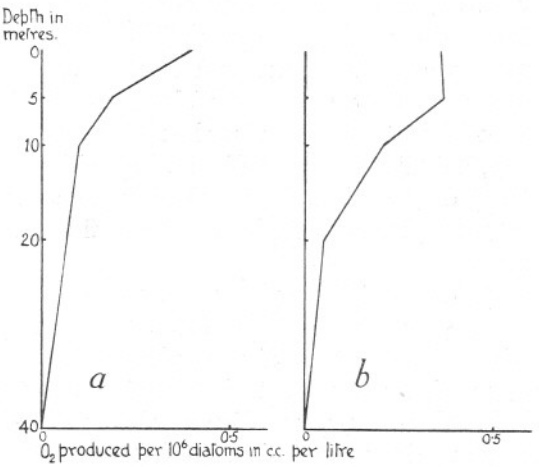


FIG. 12.—Oxygen production per 10^6 diatoms in Loch Striven, (*a*) 18–19/3/27 (no sunshine), (*b*) 28–29/3/27 (5 hours 50 minutes sunshine).

greater amount of photosynthesis at 5 metres may be due in part to this, but, as shown below, it is probable that it was also caused partly by the disappearance of the diatoms from the surface waters.

There is thus a relation between the type of curve and the number of diatoms present in the water. This is shown clearly in Figure 10 and Table 3,

where the compensation-points of eleven culture experiments carried out during the increase are plotted under the diatom increase diagram. The actual figures for compensation-points were arrived at by interpolation and are therefore only approximate. Before the increase began it was as deep as 17 metres, during the increase it rose as near the surface as 4 metres, and after the increase it sank again to 18 metres. This result is further confirmed by the Secchi disc readings which are plotted on the same figure. Before the increase the disc was seen to 7 metres and it disappeared at $2\frac{1}{2}$ metres during the height of the increase on April 5th. Diatoms were not counted on this day, but were at their recorded maximum on the 6th when the Secchi disc disappeared at 3 metres. After the increase was over, the reading was as deep as 11 metres. Confirmatory results were obtained with compensation-point figures in 1927, but Secchi disc readings were not taken. If allowance is made for the fact that the Secchi disc is not always seen as deep as the richest layer of diatoms, the correspondence becomes still more marked.

Poole and Atkins (1929) have found evidence of a decrease in the intensity of illumination due to the zoo-plankton, but did not find any effect produced by a diatom increase. While no data concerning the effect of the zoo-plankton are available for Loch Striven, the evidence quoted above seems to us conclusive concerning the obscuring effect of the phytoplankton. The results are not explicable either by rainfall or wind, the former by carrying down land detritus and the latter by agitation of the water. The much greater abundance of diatoms in the loch as compared with the open sea offers the most probable explanation of the discrepancy. The diatoms gave a distinct brownish tinge in columns of sea-water 15 cm. deep at the height of the increase and the quantity of detritus in centrifuged water samples was insignificant in comparison with the diatoms.

The experiments done with samples of sea-water taken during the course of the increase gave small and irregular results. The production was usually much less than that of a diatom culture and was often within, or very near to, experimental error. This is largely because the diatoms are so much smaller than the culture diatoms that twenty-four hours is hardly long enough to show production. Gaarder and Gran (1927) left samples of sea-water in flasks in the sea for periods of three days and got a considerable amount of oxygen produced. In our experiments the compensation-point was always found nearer the surface than in the case of culture diatoms. On an average the compensation-point for diatom cultures during the increase (7 experiments) was 8 metres, while that for sea-water experiments giving positive results (13 experiments) on the same dates as the above culture experiments was 3 metres. Since the sea diatoms do not produce so much as culture diatoms, it might be thought

that the illumination before the spring increase, although good enough for the latter (see Fig. 11a), was not good enough for the former to multiply. Proof that there is, at the surface at any rate, sufficient light for the growth of sea diatoms, was obtained in another way. Some weeks before the spring increase in 1928, a sample of sea-water was taken into the laboratory, filtered through a sterile sintered glass filter (see p. 868) and allowed to stand in an unheated room. After some days a good mixed culture of Skeletonema, Thalassiosira, Nitzschia and a few other small forms appeared. Similar results were obtained in December 1929 with both

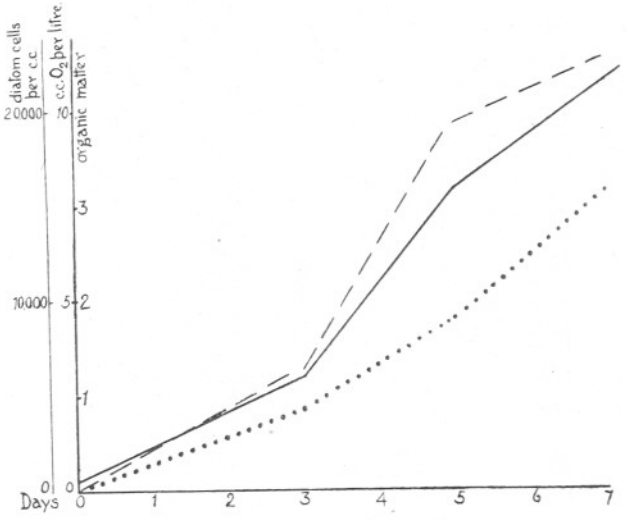


FIG. 13.—Curves showing relationship between ——— diatom numbers, — — — oxygen production, ... organic matter oxidisable by permanganate in a diatom culture in mg.O_2 per litre.

filtered and unfiltered water. It is apparent then that the sea diatoms themselves, as well as cultures, can grow in the ordinary illumination of the surface water before the date of the spring increase.

In view of the enormous production of diatoms during the spring increase, an attempt was made in 1928 to test whether there was a relationship between the organic matter oxidisable by permanganate in the sea (Ruppin, 1904) and diatom numbers. Because of the time required to complete the other work, the analyses for organic matter were not completed till two or three days after taking the samples. A disturbing factor is the inflow of water comparatively rich in dissolved organic matter from a burn at the head of the loch. This source of error was partially avoided by estimating the difference in organic matter between filtered and unfiltered samples. The filter used was a Jena sintered glass filter which

was found to be sufficiently fine in grain to stop practically all diatoms, although a few small forms were usually found on centrifuging the filtrate. The results were small but showed generally an increase with increasing diatom content. There was no good evidence that the organic matter in the filtered samples increased when the diatoms became richer, as would have been expected from the results obtained by Pütter (1924). He states that a large part of the organic matter produced by diatoms diffuses directly into the sea. Support was given to this work of Pütter's by Gran and Gaarder (1927), Gran and Ruud (1926), and Föyn and Gran

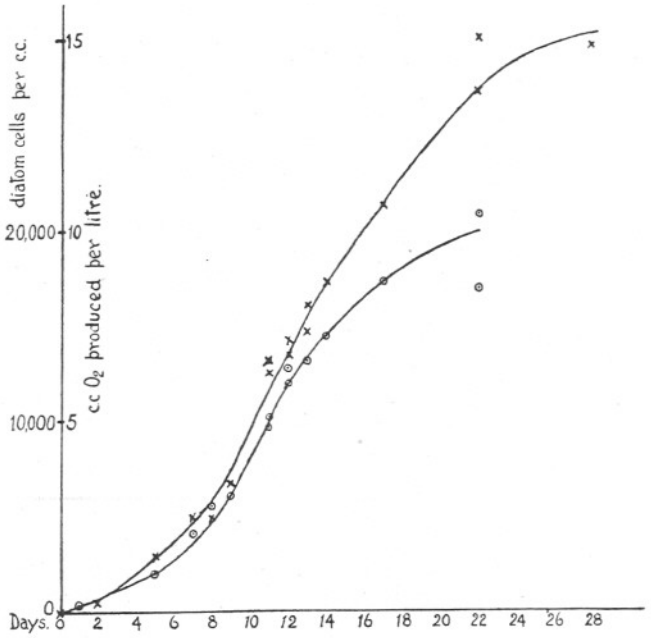


FIG. 14.—Diatom numbers (o) and oxygen production (x) in a diatom culture.

(1928) from results obtained in the Oslo fiord and later in the open sea. They used a biological method of estimating organic matter.

Since the results in sea-water are liable to error, some experiments were carried out with diatom culture, *Coscinosira polychorda* again being used. A few preliminary tests showed that while the total oxidisable organic matter was variable, the dissolved organic matter was higher in cultures old enough to have a fair number of dead cells. A culture was then started off by inoculating several litres of Miquel with a considerable amount of rich culture so that there were about 500 cells per c.c. This was then transferred to a large number of sterile stoppered bottles of about 120 c.c. capacity of which three were used for estimation of dissolved

oxygen content, diatom numbers and dissolved organic matter, filtered and unfiltered. The results obtained are shown in Figure 13 and Table 6. The difference in organic matter in the filtrate is negligible, showing that the dissolved organic matter does not increase along with the growth of diatoms but probably only when a number of the cells have died. The organic matter in the whole culture increases with the diatoms. At the end of the experiment the diatoms were very rich (21,300 cells per c.c.), so that, had diffusion of the organic matter taken place, the filtrate would have shown this clearly. Alkaline permanganate will, of course, only oxidise a portion of the organic matter present. In addition, though the analyses were made as described by Ruppin, it was found that, with diatom cultures, if the time of heating was increased the oxidation was also increased. It seems improbable, however, that any organic matter diffusing from the diatoms and so present in the filtered culture should have been entirely unaffected by it. While the above is true of a young culture, an old culture does show an increase in soluble organic matter, but this is more probably because the dead cells which are present are being attacked by bacteria.

The dissolved oxygen was estimated in the hope that it might be possible to find a factor by which the organic matter oxidisable by permanganate must be multiplied to give total organic matter. The increase of oxygen was so rapid and the degree of supersaturation so high that such a figure would be of doubtful significance. By the end of the experiment all the bottles had developed bubbles. The same type of growth was found in a similar experiment (Fig. 14) in which the slower rate of growth was probably due to the smaller amount of light in February than in May.

Discussion.

Of the many factors which might influence the beginning of the spring increase, there are several which can be excluded at once. The nutrient salts are probably present in abundance. Only one of these, phosphate, was actually estimated, but it does not seem likely that the mixing which led to the presence of phosphate did not bring up the other food salts also. Temperature also affects the spring increase only indirectly, since we find that on several occasions it started before the spring temperature overturn took place. We know, too, that Skeletonema can, and does, grow in waters both considerably warmer and considerably colder. It flourished at a temperature of 2–3° C. on the Norwegian coast in 1922 (Föyn, 1929), and at a temperature of 8–9° C. in Loch Striven in May, 1926 (Marshall and Orr, 1927), while it appears occasionally in the tropics (Karsten, 1907).

When we come to the question of light intensity the facts are more

complex. Diatom cultures grow well in winter, not only in the laboratory but also in the sea. The rate of growth is, of course, much slower than in summer and the growth in the sea shows that at the surface this effect is due chiefly to the shorter day. Below the surface the light intensity is suboptimal and growth is affected by both these factors. The result is that the compensation-point rises closer to the surface than in summer, to a depth of about 4 to 6 metres at midwinter (Marshall and Orr, 1928).

If we consider now the conditions for the sea diatoms themselves, we see that there is not only a sufficiency of food salts present in the sea throughout the winter, but the diatoms can grow in sea-water some time before the date of the spring increase if they are kept in a light approximately equal to that at the surface (see p. 867). Small diatom increases have been recorded after the autumnal temperature overturn has taken place. For example, in Loch Striven in November, 1926, there was a small increase of Skeletonema, and Atkins (1927*a*) has recorded an increase of Rhizosolenia in late autumn 1925 at Plymouth. In these cases food salts were present in sufficient quantity to have caused quite a large increase but did not do so. A probable explanation of this seems to be that the diatoms did not remain long enough in a sufficiently well-illuminated zone. In other words, the vertical mixing which takes place probably carries the diatoms below their compensation-point. Since the compensation-point in winter lies at 4 to 6 metres for culture diatoms and even nearer the surface for sea diatoms, it would need only a small vertical movement to bring the diatoms below their compensation-point. Such movements do occur in Loch Striven even in summer when the water is comparatively stable if there is a hard up-loch or down-loch wind and will be frequent in winter, during which time the loch is unstable. With the increasing light of the advancing spring, the compensation-point goes deeper and finally the diatoms will no longer be carried below it. Even after the increase has started, however, further mixing may modify its course considerably.

Gran (1929) has shown that on the Norwegian coast the spring increase near land is independent of the increase which occurs off the continental shelf. The former comes earlier and depends on the date of the melting of the snows. This fresh water lowers the salinity and adds large quantities of nutrient salts. In the Gulf of Maine also Bigelow (1924) believes that the spring increase depends on the nutrient salts added by the melting snows. This explanation will not hold for any area which has not a permanent covering of snow in winter, for the salts brought down by land drainage are being added all through the winter and are not held up to be added in a comparatively short time during the spring thaw.

On the other hand, Atkins (1928), among others, considers that the most important factor is the amount of spring sunshine. Figure 15 shows

the amount of sunshine daily during the spring months 1924–29, along with the date on which the number of diatom chains reached 20 per c.c. (or 200 in the case of diatom cells).* This is, of course, a purely arbitrary figure, but since the numbers usually increase very rapidly within a few days, the actual figure chosen makes little difference. It will be seen that the date of the spring increase is approximately constant, on about March 20th. In 1924 it was a little later and in 1927 a little earlier than usual, and it is interesting to notice that off the Norwegian coast in 1927

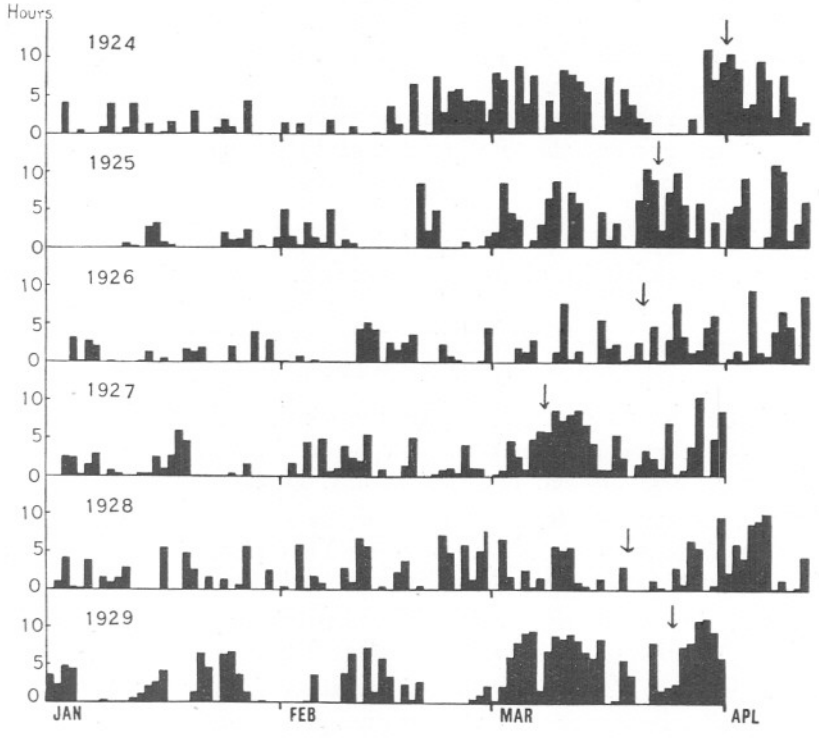


FIG. 15.—Daily sunshine during spring months of 1924–1929. The arrows show the beginning of the spring diatom increase.

it began exceptionally early too (Föyn, 1929). This was not a year with much early sunshine. At Plymouth the spring increase began earlier in 1924 than in 1925 (Atkins, 1927*b*), whereas the reverse was the case in the Clyde.

In Loch Striven, then, it appears that the date of the spring increase is decided chiefly by the total light which depends both on length of day and brightness. Only such a comparatively constant external factor could account for the narrow limits of time within which the increase

* The observations on diatoms in 1929 were made by Mr. Elmhirst.

begins. Vertical mixing may alter this date a little, but the increasing light gradually overcomes this factor and allows the spring increase to begin. As soon as the loch becomes stabilised the increase runs its normal course.

SUMMARY AND CONCLUSIONS.

1. The spring increase in Loch Striven is described in detail for three consecutive years. Contemporaneous experiments with diatom cultures and sea-water samples helped to elucidate the changes which occurred. Vertical mixing of the water layers was found to have an important effect on the form of the increase.

2. Although there is a relationship between organic matter oxidisable by permanganate and the total number of diatoms present, there is no relationship between *dissolved* organic matter oxidisable by permanganate and diatoms.

We wish to thank Mr. Elmhirst and members of the staff for their help throughout the work.

REFERENCES.

1926. Atkins, W. R. G. A quantitative consideration of some factors concerned in plant growth in water. Part 2. Some chemical factors. Journal du Conseil, Vol. I, No. 3.

1927 (*a*). Atkins, W. R. G. Seasonal changes in the Silica Content of Natural Waters in Relation to the Phytoplankton. Journ. Mar. Biol. Assoc., N.S., Vol. XIV.

1927 (*b*). Atkins, W. R. G. The Phosphate Content of Sea-Water in Relation to the Growth of the Algal Plankton. *Ibid.*, Vol. XIV.

1928. Atkins, W. R. G. Seasonal variations in the phosphate and silicate content of sea-water during 1926 and 1927 in relation to the phytoplankton crop. *Ibid.*, Vol. XV, No. 1.

1924. Bigelow, H. B. Plankton of the Offshore waters of the Gulf of Maine. Bulletin of the Bureau of Fisheries, Vol. XL, Part 2.

1929. Föyn, Birgithe Ruud. Investigations of the Phytoplankton at Lofoten, March–April, 1922–1927. Skrifter utgitt av Det Videnskaps-Akademi i Oslo. I. Matem.-Naturv. Klasse, 1928, No. 10.

1928. Föyn, B., and Gran, H. H. Über Oxydation von organischen Stoffen im Meerwasser durch Bacterien. Avhandlinger utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matem.-Naturv. Klasse, No. 3.

1927. GAARDER, T., AND GRAN, H. H. Investigations of the Production of Plankton in the Oslofjord. Rapports et Procès-verbaux des Réunions, Vol. XLII.

1927. GRAN, H. H. The Production of Plankton in coastal waters off Bergen, March–April, 1922. Report on Norwegian Fishery and Marine Investigations, Vol. III, No. 8

1929. GRAN, H. H. Investigation of the Production of Plankton outside the Romsdal-fjord, 1926–1927. Rapports et Procès-verbaux des Réunions, Vol. LVI.

1918. GRAN, H. H., AND GAARDER, T. Über die Einfluss des atmosphärischen veränderungen Nordeuropas auf die hydrographischen Verhältnisse des Kristianiafjord bei Dröbak im Marz, 1916. Publications de Circonstance, No. 71.

1926. GRAN, H. H., AND RUUD, B. Untersuchungen uber die im Meerwasser gelösten organischen Stoffe und ihr Verhältnis zur Planktonproduktion. Avhandlinger utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matem.-Naturv. Klasse, No. 6.

1907. KARSTEN, G. Das Indische Phytoplankton nach dem Material der deutschen Tiefsee Expedition, 1898–99. Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition, Zweiter Band, Zweiter Teil.

1927. MARSHALL, S. M., AND ORR, A. P. The Relation of the Plankton to some Chemical and Physical Factors in the Clyde Sea Area. Journ. Mar. Biol. Assoc., N.S., Vol. XIII, No. 4.

1928. MARSHALL, S. M., AND ORR, A. P. The Photosynthesis of Diatom Cultures in the Sea. Journ. Mar. Biol. Assoc., N.S., Vol. XV, No. 1.

1888. MURRAY, JOHN. On the effects of winds on the distribution of temperature in the sea- and fresh-water lochs of the West of Scotland. Scottish Geographical Magazine.

1929. POOLE, H. H., AND ATKINS, W. R. G. Photoelectric measurements of submarine illumination throughout the year. Journ. Mar. Biol. Assoc., N.S., Vol. XVI, No. 1.

1924. PÜTTER, AUGUST. Der Umfang der Kohlensäurereduktion durch die Planktonalgen. Pflügers Archiv. für die gesamte Physiologie, Bd. 205.

1904. RUPPIN, E. Ueber die Oxydierbarkeit des Meereswasser durch Kaliumpermanganat. Publications de Circonstance, No. 20.

TABLE 1.

1927.

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c.
8–3–27.								
0	6·79	31·97	1·0251			8·13	45	6,400
5	6·87	32·11	1·0253			8·12	50	5,400
10	7·18	32·30	1·0253			8·13	55	2,280
20	7·30	34·01	1·0262			8·14	59	423
40	7·38	34·43	1·0269			8·13	70	12
10–3–27.								
0	7·09	31·54	1·0247	7·60	109·6	8·18	38	16,700
5	7·22	33·02	1·0258	6·72	99·5	8·16	50	6,900
10	7·21	33·39	1·0262	6·33	98·4	8·14	52	2,800
20	7·30	33·78	1·0265	5·97	97·4	8·17	59	670
40	7·39	34·49	1·0270	5·85	97·1	8·13	58	65
11–3–27.								
0	7·11	32·41	1·0254	8·35	120·7	8·22	22	33,100
5	7·25	33·09	1·0259	7·16	104·2	8·14	36	16,400
10	7·21	33·39	1·0262	6·33	92·1	8·13	58	3,200
20	7·26	33·56	1·0263	6·12	89·5	8·12	69	1,050
40	7·29	34·39	1·0269	5·92	87·2	8·13	70	.....
14–3–27.								
0	6·27	30·21	1·0238	8·99	124·4	8·38	5	62,700
5	6·28	30·34	1·0239	8·98	125·2	8·37	13	51,000
10	7·22	33·30	1·0261	6·35	92·3	8·12	39	4,350
20	7·35	34·21	1·0268	5·89	85·9	8·12	52	402
40	7·38	34·39	1·0269	6·04	88·8	8·12	55	141
15–3–27.								
0	6·12	30·34	1·0239	8·96	124·5	8·36	20	
5	6·12	30·58	1·0241	8·92	123·9	8·35	17	
10	6·12	30·60	1·0241	8·88	123·3	8·35	22	
20	7·30	33·74	1·0264	5·82	85·2	8·12	66	
40	7·38	34·47	1·0270	5·88	86·7	8·10	72	
16–3–27.								
0	6·24	30·41	1·0239	9·18	127·6	8·46	10	47,500
5	7·17	30·55	1·0239	8·82	125·7	8·43	13	36,300
10	7·19	33·26	1·0260	6·23	90·6	8·21	47	6,300
20	7·28	33·82	1·0265	5·97	87·4	8·18	52	600
40	7·37	34·41	1·0269	5·81	85·6	8·18	64	138
17–3–27.								
0	6·18	30·33	1·0239	8·98	125·1	8·50	12	
5	6·14	30·31	1·0239	8·91	123·8	8·50	18	
10	7·19	33·73	1·0264	6·25	91·2	8·22	55	
20	7·13	33·88	1·0266	6·29	91·8	8·22	64	
40	7·38	34·46	1·0270	5·77	85·1	8·19	70	
18–3–27.								
0	6·49	30·07	1·0236	9·44	131·0	8·51	14	11,000
5	6·48	30·16	1·0237	7·91	110·6	8·35	20	39,600
10	7·11	33·30	1·0261	6·37	92·5	8·19	48	26,400
20	7·21	33·72	1·0264	6·17	90·1	8·19	63	2,740
40	7·35	34·48	1·0270	5·83	86·0	8·17	74	212

TABLE 1 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom chains in 20 c.c
19–3–27.								
0	6·79	29·83	1·0234	9·00	127·0	8·49	12	
5	6·51	30·21	1·0237	9·07	126·9	8·47	14	
10	6·99	33·12	1·0260	6·66	96·5	8·21	35	
20	7·25	33·72	1·0264	6·00	88·1	8·17	57	
40	7·35	34·49	1·0270	5·87	86·6	8·18	62	
22–3–27.								
0	7·50	29·87	1·0233	7·75	110·7	8·48	13	1,280
5	7·53	30·05	1·0235	7·75	110·7	8·48	14	1,700
10	7·00	33·26	1·0261	6·61	95·7	8·23	31	16,100
20	6·92	33·24	1·0261	6·91	100·2	8·24	32	12,000
40	7·25	33·72	1·0264	5·91	86·4	8·19	68	7,400
23–3–27.								
0	7·57	28·79	1·0225	7·33	104·4	8·48	16	
5	7·47	31·92	1·0250	7·76	112·3	8·45	17	
10	7·12	32·99	1·0259	7·51	108·9	8·34	24	
20	7·17	33·70	1·0264	5·95	86·9	8·22	43	
40	7·33	34·41	1·0269	5·61	82·5	8·22	67	
25–3–27.								
0	7·20	31·24	1·0245	7·42	106·4	8·43	15	2,200
5	7·21	30·98	1·0243	7·42	105·9	8·42	19	1,700
10	7·20	31·24	1·0245	7.39	105·7	8·42	21	2,200
20	7·03	33·37	1·0262	6·40	92·6	8·26	51	2,300
40	7·32	34·26	1·0268	6·15	90·3	8·22	69	2,200
26–3–27.								
0	7·17	29·32	1·0230	7·38	104·2	8·41	18	1,090
5	7·20	31·97	1·0250	7·55	108·6	8·34	18	67
10	7·18	32·40	1·0254	7·51	108·3	8·34	23	143
20	7.02	33·14	1·0260	6·70	97·0	8·26	30	688
40	7·30	34·10	1·0267	5·36	78·6	8·16	63	192

TABLE 2.

1928.

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
14–3–28.								
0	5·56	32·66	1·0258	6·75	94·5	8·22	33	2,182
2	5·50	32·65	1·0258	6·75	94·1	8·22	34	2,246
5	5·50	32·65	1·0258	6·79	94·6	8·21	41	2,191
10	5·52	32·65	1·0258	6·76	94·3	8·21	35	2,607
20	6·24	33·02	1·0260	6·31	89·5	8·21	36	579
19–3–28.								
0	5·55	32·38	1·0255	6·95	96·9	8·23	32	8,100
2	5·51	32·38	1·0256	6·92	96·3	8·22	42	7,300
5	5·50	32·34	1·0255	6·90	96·0	8·22	38	7,300
10	5·50	32·38	1·0256	6·91	96·2	8·21	39	7,600
20	6·17	33·30	1·0262	....	....	8·21	40	1,900

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
22–3–28.								
0	5·63	32·01	1·0253	6·91	96·2	8·21	32	7,600
2	5·50	32·01	1·0253	6·90	95·7	8·19	34	8,300
5	5·58	31·87	1·0252	6·95	96·5	8·21	33	8,800
10	5·67	32·25	1·0254	6·87	95·9	8·20	34	7,800
20	5·94	32·89	1·0259	6·77	95·4	8·19	37	6,800
30	5·99	33·04	1·0260	6·78	95·9	8·20	38	3,400
26–3–28.								
0	5·93	31·85	1·0251	6·85	95·7	8·22	33	9,000
2	5·97	31·75	1·0250	6·92	97·0	8·21	36	11,300
5	5·85	31·87	1·0251	6·93	96·8	8·21	37	13,500
10	5·90	32·83	1·0259	6·64	93·5	8·20	35	2,900
20	6·02	33·15	1·0261	6·55	92·8	8·19	38	1,800
30	6·19	33·49	1·0264	6·37	90·7	8·21	40	1,500
29–3–28.								
0	5·95	31·52	1·0248	6·95	97·2	8·22	30	64,000
2	5·95	31·70	1·0250	7·01	98·1	8·22	30	68,000
5	5·97	31·75	1·0250	7·00	98·0	8·20	31	57,000
10	5·95	32·21	1·0254	6·83	96·0	8·20	33	41,000
20	6·02	33·02	1·0260	6·57	93·0	8·20	37	2,000
30	6·09	33·27	1·0262	6·42	91·2	8·20	40	1,050
2–4–28.								
0	6·62	30·36	1·0239	7·43	104·2	8·25	23	73,000
2	6·50	30·44	1·0239	7·53	105·6	8·24	24	61,000
5	6·09	31·62	1·0249	7·32	102·7	8·25	26	133,000
10	6·08	32·63	1·0257	6·65	93·9	8·22	34	8,000
20	6·22	33·34	1·0262	6·25	89·0	8·20	41	1,200
30	6·36	33·68	1·0265	6·18	88·4	8·20	42	115
4–4–28.								
0	6·55	29·54	1·0232	8·37	117·1	8·37	0	180,000
2	6·48	30·98	1·0243	7·79	109·7	8·31	22	248,000
5	6·18	31·99	1·0252	6·73	94·8	8·24	32	60,000
10	6·12	33·02	1·0260	6·56	93·1	8·22	42	2,100
20	6·12	33·15	1·0261	6·53	92·7	8·21	42	1,250
30	6·15	33·25	1·0262	6·37	90·6	8·21	42	890
6–4–28.								
0	6·49	28·56	1·0225	9·33	129·2	8·47	5	128,000
2	6·96	29·93	1·0235	9·77	138·0	8·44	10	199,000
5	6·56	30·76	1·0242	8·28	116·6	8·32	19	510,000
10	6·19	32·24	1·0254	6·81	96·1	8·22	30	56,000
20	6·11	32·81	1·0258	6·55	92·8	8·21	37	3,100
30	6·11	33·19	1·0261	6·41	91·2	8·20	39	1,280
9–4–28.								
0	7·00	28·83	1·0226	7·77	109·0	8·46	0	90,000
2	7·00	28·81	1·0226	7.76	108·8	8·44	0	106,000
5	6·77	30·21	1·0237	7·05	99·5	8·24	24	176,000
10	6·73	30·27	1·0238	7·04	99·1	8·24	27	152,000
20	6·27	32·45	1·0255	6·60	93·6	8·22	34	77,000
30	6·28	33·54	1·0264	6·15	88·0	8·20	46	3,500
12–4–28.								
0	7·15	30·32	1·0237	7·47	106·3	8·24	17	225,000
2	7·14	30·21	1·0237	7·47	106·0	8·26	17	220,000
5	7·13	30·32	1·0238	7·51	106·7	8·25	17	169,000
10	6·40	32·31	1·0254	6·83	96·8	8·23	32	83,000
20	6·17	32·89	1·0259	6·43	91·2	8·21	43	10,000
30	6·30	33·55	1·0264	6·04	86·3	8·21	44	2,400

TABLE 2 (*continued*).

Depth in m.	Temperature °C.	Salinity ‰	Density.	Oxygen c.c. per l.	O_2 Saturation %.	pH.	P_2O_5 mg. per c.m.	Diatom cells in 20 c.c.
16–4–28.								
0	7·20	29·88	1·0234	7·43	105·4	8·36	17	14,200
2	6·70	30·97	1·0243	7·06	99·7	8·26	24	99,000
5	6·50	31·97	1·0251	6·71	95·1	8·22	28	24,000
10	6·50	32·30	1·0254	6·72	95·6	8·23	28	13,800
20	6·36	32·72	1·0257	6·57	93·4	8·22	34	10,900
30	6·26	33·76	1·0266	6·00	85·8	8·21	48	4,700
19–4–28.								
0	6·32	33·03	1·0260	6·47	92·1	8·22	24	1,120
2	6·32	33·09	1·0260	6·45	91·9	8·21	25	2,015
5	6·29	33·09	1·0260	6·41	91·3	8·21	28	1,400
10	6·29	33·27	1·0262	6·25	89·0	8·21	28	306
20	6·40	33·94	1·0267	5·90	84·7	8·20	33	400
30	6·40	34·20	1·0269	6·06	87·1	8·21	36	1,008
26–4–28.								
0	7·52	32·74	1·0256	7·19	104·7	8·33	17	101
2	7·43	32·77	1·0256	7·18	104·4	8·30	21	138
5	7·18	32·77	1·0257	7·22	104·6	8·30	22	3,072
10	6·67	33·30	1·0261	6·88	98·8	8·25	27	18,400
20	6·50	33·47	1·0263	6·50	93·1	8·23	34	17,800
30	6·47	33·65	1·0265	6·47	92·7	8·22	35	19,600

TABLE 3.

Date	March 19	22	26	29	April 2	3	4	5	6	9	12	16	17	19	20
Compensation-point of culture in metres.	8	14	17	9	6	–	8	–	5	6	4	18	—	13	—
Secchi disc reading in metres.	7	7½	—	6½	4½	3½	2¾	2⅝	2¾	3½	3	7	9½	11	10½

TABLE 4.

Loch Striven. 22–23/3/28. 0·41 hours sunshine.
Diatom culture of Feb. 20th—7,400 cells per c.c.
12.20 p.m.–11.45 a.m. Initial O_2 content 1. 8·21, 2. 8·18, 3. 8·22 } 8·20

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	11·26 11·65	11·46	7·70	7·73	3·74	0·51
½	11·64 11·88	11·76	7·75	7·73	4·03	0·54
2	11·34 11·41	11·38	7·74	7·73	3·65	0·49
5	9·51 9·55	9·53	7·71	7·73	1·80	0·23
10	8·37 8·29	8·33	—	7·73	0·60	0·08
20	8·01 8·04	8·02	7·79	7·73	0·29	0·04
30	7·95 8·03	7·99	7·68	7·73	0·26	0·04

TABLE 5.

Loch Striven. 6–7/4/28. 4·25 hours sunshine.
Diatom culture of March 7th—8,300 cells per c.c.
11.35 a.m.–11.15 a.m. Initial O_2 content $\left.\begin{matrix}7{\cdot}71\\7{\cdot}72\end{matrix}\right\}$ 7·72

Depth in metres.	Light.		Dark.	Av.	Total O_2 produced.	O_2 produced by 10^6 diatoms.
0	$\left.\begin{matrix}9{\cdot}11\\9{\cdot}04\end{matrix}\right\}$	9·08	6·86	6·89	2·19	0·26
½	$\left.\begin{matrix}10{\cdot}21\\9{\cdot}84\end{matrix}\right\}$	10·02	6·92	6·89	3·13	0·38
2	$\left.\begin{matrix}8{\cdot}98\\9{\cdot}01\end{matrix}\right\}$	8·99	Lost	6·89	2·10	0·25
5	7·56	7·56	6·86	6·89	0·67	0·08
10	7·15	7·15	6·91	6·89	0·26	0·03
20	Lost		6·94	6·89	——	——
30	$\left.\begin{matrix}7{\cdot}10\\7{\cdot}14\end{matrix}\right\}$	7·12	Lost	6·89	0·23	0·03

TABLE 6.

Date.	Diatom cells per c.c.	Oxygen c.c. per litre.	Oxygen produced.	Oxidisable Organic Matter. Total mg. O_2 per litre.	Production mg. O_2 per litre.	In filtered samples mg. O_2 per l.
4–5–28	575	5·89	0	1·36	0	1·24
7–5–28	6,000	9·07	3·18	2·22	0·86	—
9–5–28	15,700	15.48	9·59	3·15	1·79	—
11–5–28	21,300	17·13	11·24	4·46	3·10	1·22

Bacteria of the Clyde Sea Area: A Quantitative Investigation.

By

Blodwen Lloyd, M.Sc., Ph.D.,

From the Dept. of Bacteriology and Botany, Royal Technical College, Glasgow, and the Marine Biological Station, Millport.

With 7 Figures in the Text.

CONTENTS.

Introduction.

The importance of bacterial action in the seas has long been recognised, but investigation in marine bacteriology lags behind that of corresponding terrestrial problems. Such general information about marine bacteria as is now available is derived mainly from bacteriological work of some decades ago. At that time the technique of the science was not fully developed, but at the present day it has become so specialised that it lies outside the province of the marine biologist, although he alone is able to appreciate the significance of bacteria in the general economy of the sea.

Whilst the part played by bacteria in the food-cycle of the sea depends partly upon special features in the metabolism of the various bacterial species, it obviously depends chiefly upon the abundance of such organisms. Now in an investigation of the numbers of bacteria in any sample, it is extremely important that due regard be paid to the conditions under which the work is performed. In much of the early work on marine bacteria the experimental methods are not described. Where such

information is available, one finds that there is lack of uniformity in the experimental methods adopted, and that therefore the results of different workers are not readily comparable with one another. Standard routine methods are needed for the bacteriological examination of sea-water, such as are customary for the routine analysis of fresh water. It is significant that among the various bacteriological handbooks on the technique of water-examination, none that has come to the writer's notice gives consideration to the special aspects of marine bacteriology.

It is the purpose of this paper to present a quantitative report on the marine bacteria of the Clyde Sea Area. This report is based on observations carried out over a period of 18 months, standardised routine methods having been devised for taking the samples and for laboratory technique.

Historical.

The earliest numerical record of marine bacteria appears to be that of Sanfelice (see Bertel, **5**), who found in 1889 that the number of organisms in the sea decreased as the distance from the shore increased. From this he deduced that bacteria in the sea were not native to it, but terrigenous, " apportées à la mer avec les ordures." This prompted de Giaxa (**11**) to investigate the viability of pathogenic organisms in sea-water. He found that they flourished in sterile sea-water but did not survive competition with other forms in unsterilised sea-water—a finding that has been confirmed in more recent years by the Royal Sewage Commission (**16**). Russel (**21**), who analysed samples from the Gulf of Naples and the Atlantic, observed that the number of bacteria decreased from the surface down to 200 metres ; he also noted that marine mud contained many more bacteria than the water immediately above. Schmidt-Nielsen (**23**), however, found the reverse to hold, obtaining for northern waters an average of 26 bacteria per c.c. at the surface and 420 per c.c. at 25 metres.

Fischer's report (**10**), which is based on samples taken by the German Plankton Expedition of 1889, is the most comprehensive account of marine bacteria. He gave full accounts of technique employed and furnished descriptive and statistical analyses of the water samples obtained. His results vary very much, but in general he found that there were fewer bacteria at greater depths than at the surface. He noted also that the numbers were greater at sunrise than in the afternoon.

The Prince of Monaco made some analyses of the Atlantic sea-water, and found the bacterial content to be extremely high between the Azores and Portugal (see Bertel, **5**) ; this he attributed to the existence of a submarine ridge with very rich fauna.

In 1911 Bertel (**5**) investigated the bacteria of the sea-water off Monaco,

and found (1) that the number of bacteria diminished progressively from coastal areas outwards, (2) that the number of bacteria increased from the surface downwards, and (3) that the number at the surface increased during the night, and diminished during the early hours of the morning.

Experimental Technique.

Sampling Stations.

Regular monthly samples were taken at three stations which were selected as likely to be different yet characteristic areas; in addition, samples were taken at less regular intervals at other places.

The regular stations were :—

1. *Loch Striven.* This loch is notably free from steamer traffic, and the adjoining land is sparsely populated. It thus represents an area remarkably free, in view of its proximity to land, from industrial or other human contamination.

2. *Loch Long* (*Thornbank Station*). This station is moderately free from land contamination, but there are habitations along the shores of the loch, and there is a certain amount of boat traffic. Terrestrial influences are thus more marked here than in Loch Striven.

3. *Greenock.* Here the water is estuarine in character, and highly polluted with sewage, with waste from sugar refineries and with industrial effluents generally, which are emptied into the River Clyde. This area was chosen in order to determine to what extent the true water bacteria would be outnumbered by those species present as a result of contamination. A detailed account of the Clyde Sea Area is given by Mill (**19**); a map of the area and a summary are also given by Marshall and Orr (**17**).

Sampling Technique.

Vertical series of samples were taken periodically at the above-mentioned stations. It was necessary to employ an apparatus capable of collecting water at the desired depth without taking in water from other depths when being hauled up. The closing water-bottles generally employed in marine work are not suitable for the collecting of sea-water destined for bacteriological analysis. The following are the principal objections :—(i.) Such bottles are made of metal, and most metals have a marked bactericidal effect. This objection is not a cogent one if the sample is in the bottle for only a short time (**3**). (ii.) When a series of samples has to be taken with one bottle, each sample has to be siphoned into a sterile container for transport ashore, and while this operation is being carried out there is a risk of contamination. (iii.) Between the taking of successive samples it would be necessary to sterilise the bottle,

and these water-bottles are usually so unwieldy that it is laborious to accomplish this effectively.

Several bacteriological samplers have been described, notably those by Bertel (**4**), Russel (**21**), Portier and Richard (**20**), Drew (**8, 9**), Matthews (**18**), Birge (**6**) and Sclavo-Czaplewski (**14**). The simplest type consists essentially of a stoppered bottle, the stopper being pulled out at the required depth. The chief disadvantage of the method is that the removal of the stopper requires a second line which is apt to foul the lowering wire. The second type consists of a glass container with a drawn-out sealed tip ; this tip can be broken by a messenger when the apparatus is at the required depth. Matthews has described a deep-sea bacteriological water-sampler of more complicated design than the foregoing.

For the work described in the following pages a comparatively simple apparatus was required, capable of use to a depth of 60 fathoms. Eventually a sampling apparatus similar to that described by Birge (**6**) and Wilson (**24**) was selected.

It consists of (i.) a glass sampling tube and (ii.) a metal tube-holder. The tube is an ordinary combustion tube 15 cm. $\times$ 3 cm., fitted with a one-holed rubber cork. Through this projects a glass tube bent at a right angle, having the end drawn out and sealed at about 12 cm. from the bend. The right-angle tubes are fitted into the corks, and together with the combustion tubes sterilised by steam. These are then fitted together, due precautions being taken to avoid contamination of the parts.

The tube-holder consists of a plate-sinker A (Fig. 1), with a spring clamp B to hold the sampling tube in position. At the top of the sinker is a projecting arm at the free end of which is a small brass breaking pin C. There is also a lever arm D so placed that when the sampling tube is in position the tip of the inlet tube lies immediately above the end of the lever arm and immediately under the breaking pin. When the apparatus reaches the required depth a messenger is sent down the connecting wire to operate the lever arm ; in this manner the tip of the capillary tube is broken.

The above apparatus was modified by Wilson from the sampler used by Russel (**21**) and was designed for limnological work in shallow waters down to 23 metres ; Wilson evacuated his sampling tubes, but the author found experimentally that at a depth of 10 fathoms a tube filled with air at atmospheric pressure would take a sample whose volume would be about half that of the whole tube ; at greater depths, the increased pressure caused proportionally greater filling of the tube. Most of the samples were taken at depths greater than this, and it was necessary to evacuate only those tubes destined to take surface samples.

The apparatus was sent down on a Kelvin sounding wire worked from a sounding machine recording in fathoms.

Evacuation of the surface sampling tubes was accomplished in the following manner :—sterile glass tubing was prepared as shown in Figure 2 and attached to a sterile sampling tube. This was evacuated to a pressure

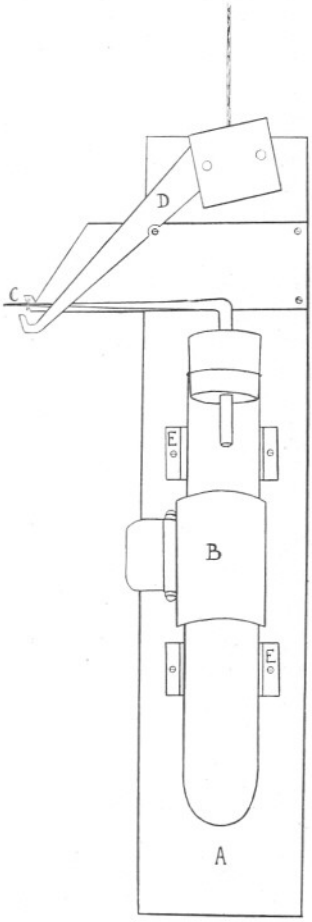


FIG. 1.—Wilson's bacteriological water-sampler, showing sampling tube in position and lever arm open. A, plate-sinker; B, spring clamp; C, breaking pin; D, lever arm; E, rubber cushion.

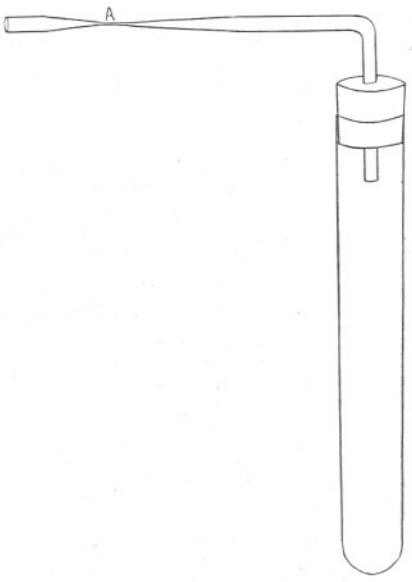


FIG. 2.—Surface sampling tube prepared for evacuation. The tube is attached to a filter pump, and sealed off at A.

of 30–60 mm. and sealed off at A. The connections at the rubber were made air-tight with paraffin wax.

The advantages of this apparatus lie chiefly in its simplicity, the extreme rapidity with which a series of samples can be taken at any one station, and the circumstance that the same tube serves both for taking the sample and for transporting it to the laboratory. The rubber cork is

liable to be forced inwards as the sampler descends; if this occurs the tube breaks at the right-angle bend. In practice this can be avoided by selecting well-tapered corks, though for constant deep-water work it would be necessary to have the sampling tube and the inlet arm blown in one piece after the retort-shaped type used by Drew (**8**) for depths greater than 70 fathoms.

While the sampler is being hauled up, the tip of the tube is of course open, but there is no admixture with water from the upper layers through which it is passing, for as the apparatus is being raised the pressure in the tube is being continuously reduced and the compressed air is flowing out of the tube at the narrow orifice. An inflow of water is therefore prevented.

For the quantitative work described below, samples were taken in vertical series at intervals of 10 fathoms from the surface downwards. For transit ashore the open tips of the tubes were sealed off in the flame of a spirit lamp, and packed in sterilised cotton-wool.

Transport of Samples.

In making total counts of the bacterial content of water the following are significant factors :—

(i.) The time interval which elapses between the taking of the sample and its examination in the laboratory, because during that period the bacteria present in the sample may be actively dividing. In the course of this work, the samples at any one station were always taken at the same time of day, and dealt with in the laboratory after approximately the same time interval. In this way uniformity of treatment was ensured, and the numerical results so obtained at any one station for different dates are comparable with one another.

	Time of Sampling.	Time of Inoculating.
Loch Striven	12.30 p.m.	5.0 p.m.
Loch Long	1.0 p.m.	5.30 p.m.
Greenock	4.0 p.m.	6.0 p.m.

(ii.) The temperature at which the samples are kept during transport. It is advisable to inhibit bacterial reproduction by keeping the samples on ice until they are examined in the laboratory. It was found that when samples were transported in a padded box, the temperature of the water on arrival at the laboratory was not raised more than 2° C.; the rate of multiplication of the bacteria would thus not be appreciably increased.

Laboratory Technique.

The technique adopted for routine work followed as nearly as possible the procedure recommended by the American Society of Bacteriologists

(1) for the standard examination of water. The regular bacteriological examination of sea-water does not appear to have called for special attention in their schedule.

The following culture media were used :—

Standard Agar.

Tap-Water	1000 gm.
Lab-Lemco	3 gm.
Peptone (Witte's)	10 gm.
Agar	15 gm.
NaCl	5 gm.

The medium was prepared in the usual way, cleared with 10 gm. egg-albumen dissolved in 100 c.c. of water, and adjusted with NaOH to neutral, using phenolphthalein as an indicator. The agar was sterilised by autoclaving for 30 minutes at a pressure of 2 atmospheres (Giltner, **12**. p. 40).

The following modifications were tried experimentally :—

(i.) Tap water and NaCl were replaced by filtered sea-water.
(ii.) NaCl was replaced by 34 grams of evaporated sea salt.
(iii.) Tap water and Lab-Lemco were replaced by fish extract. The fish extract was prepared by slowly heating 1 kilog. of cod in 1 litre of sea-water for about 4 hours ; it was then filtered and made up to 1 litre with tap water.

These media all favoured growth, but they were not found to be markedly superior to the ordinary bacteriological media, and therefore they were not used for routine quantitative work.

Standard Gelatine. This was prepared in the same manner as the foregoing, using 150 grams of gelatine per litre instead of the agar (**12**, p. 35).

Conradi-Drigalski Agar.

(*a*)	Water	2 litres.
	Agar	60 gm.
	NaCl	10 gm.
	Nutrose	20 gm.
	Peptone	20 gm.
	Lab-Lemco	6 gm.
(*b*)	Azolitmin (2·5%)	40 c.c.
	Lactose	30 gm. in 100 c.c. water.
	Na_2CO_3 (10%)	4 c.c.
	Crystal Violet (0·1 gm. in 100 c.c.)	20 c.c.

The agar (*a*) is prepared in the usual way and sterilised. The ingredients (*b*) are sterilised separately and added to the hot agar (**12**, p. 387).

On this medium the growth of non-intestinal organisms is inhibited. The presence of colonies is presumptive evidence of fæcal contamination ; the coliform lactose-fermenting species appear as red colonies, and the typhoid-dysentery group as white or blue colonies.

McConkey Agar.

Water	500 c.c.
Peptone	10 gm.
Agar	7·5 gm.
Neutral Red (1%)	1·25 c.c.
Sodium taurocholate	2·5 gm.
Lactose	5 gm.

The lactose is added to the hot agar after filtration. This medium also inhibits the growth of non-intestinal species.

Litmus-lactose-bile-salt Broth.

Tap Water	1000 gm.
Sodium taurocholate	5 gm.
Peptone	20 gm.
Lactose	10 gm.
Azolitmin (2%)	20 c.c.

The peptone and sodium taurocholate are boiled and the lactose and azolitmin added afterwards. Fermentation of the lactose is presumptive evidence of the presence of intestinal organisms (**12**, p. 382).

Of the above media, the first two were used for ordinary quantitative work, and the last three for the detection of pollution.

Plate cultures were made by adding measured volumes of the sample to the nutrient media. The inoculations were made at as low a temperature as possible, i.e. above 35° C. for agar, and above 25° C. for gelatine. At this temperature the medium is still liquid, and is not so hot as to kill the ordinary micro-organisms.

From each water sample the following cultures were made :—

(*a*) Agar : 1·0 c.c., 1·0 c.c. (duplicate), 0·5 c.c., 0·1 c.c., and a control plate, not inoculated.

(*b*) Gelatine : as for agar.

(*c*) Conradi-Drigalski agar : 1·0 c.c.

(*d*) McConkey agar : 1·0 c.c.

(*e*) Litmus-lactose-bile-salt broth : one tube culture.

Quantitative Work. Cultures (*a*) and (*b*) were incubated in dark containers at room temperature. At the fifth day after inoculation the number of colonies was counted with the naked eye; after this period of incubation the number was fairly constant.

Some departures were made from the accepted routine for the bacteriological examination of water. Firstly, the incubation temperature was some six to twelve degrees lower than that usually employed. This was done for two reasons: (i.) to encourage the growth of the true water bacteria, which appear to thrive better at a temperature lower than that which favours soil bacteria; freshwater bacteria, and presumably marine bacteria also, are extremely sensitive to high temperatures both during plating and during incubation. (ii.) to discourage the growth of any organisms present which grow best at higher temperatures, as, for example, coliform bacteria. In this way the colonies which grew on the agar and the gelatine plates were representative chiefly of the true water bacteria.

A second departure from the usual routine was that the dilution method not being necessary was not employed. It had been ascertained by preliminary tests that the number of colonies obtained from an inoculum of 1·0 c.c. could easily be counted. In the Greenock area the total number of bacteria was very high, but this was due largely to putrefactive and intestinal organisms, and since their growth was discouraged by the low incubation temperature employed, the numbers obtained on agar and gelatine plates represent the approximate number of true water bacteria and not the total number of bacteria present.

A third point of difference from ordinary routine lay in the method of recording results. The American Society of Bacteriologists (**1**) recommend that, in order to avoid fictitious accuracy, the numbers obtained from bacterial counts should be approximated as under :—

1– 50 recorded as enumerated.
51– 100 recorded to the nearest 5.
101– 250 recorded to the nearest 10.
251– 500 recorded to the nearest 25.
501–1000 recorded to the nearest 50.

This recommended procedure is, however, intended for use in reports based on the evidence of one sample only for any one locality. This plan was not adopted in this work, but the actual figures obtained are given, since a number of plates was made for each sample and a number of samples was taken for each place at intervals throughout a year.

Detection of Pollution. Conradi-Drigalski and McConkey plates (*c*) and (*d*) and broth tube (*d*) were incubated at 37° C. for 24 hours. Any

colonies which appeared by the end of that period were presumptive coliform organisms, the red colonies being of course lactose fermenters. When the numbers so obtained were compared with the gelatine and agar counts for the same sample, it was possible to estimate the proportion of high-temperature intestinal organisms to low-temperature free-living organisms. This indicated not only whether the water sampled was polluted or not, but also the degree of pollution of the sample.

Results.

Loch Striven. This is the type area of natural sea-water, with minimal contamination despite its proximity to land. The numerical results of the plate cultures made from the samples taken each month are given in

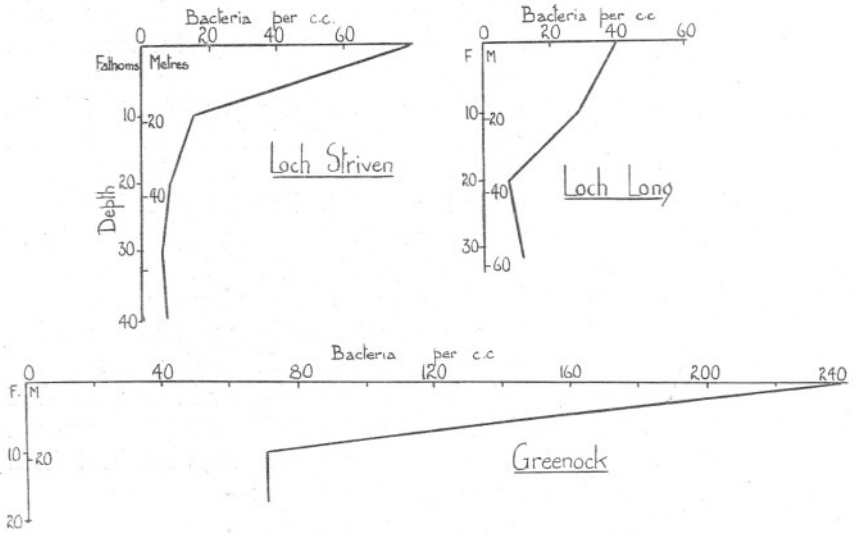


Fig. 3.—Average number of bacteria per c.c. for the year, May, 1928–April, 1929.

Table I. The average number of bacteria per c.c. is estimated for each sample from the total volume of water-sample plated out (usually 5·2 c.c.) ; these averages are given in the last column.

Samples were taken at the surface, and at intervals of 10 fathoms down to the bottom ; the bottom sample was taken immediately above the mud, in approximately the same place, but as the sides of the loch were steep, the depth at which the bottom sample was taken varied from 37 to 40 fathoms.

The following results are noted :—

Vertical Variation. 1. The number of bacteria per c.c. is low compared with that of other stations in the Clyde Sea Area.

2. The number of bacteria is greater at the surface than at lower levels (Fig. 3).

3. At the surface, the bacterial content of the water fluctuates much more than in deep waters, where it is more nearly constant.

4. At and below 10 fathoms, the number of micro-organisms does not exceed 30 per c.c. at any season.

5. Bottom samples show a rather lower bacterial content than the water at higher levels. This is an unusual feature, which will be discussed in the following section.

Seasonal Variation. 1. The numbers of bacteria per unit volume vary only little throughout the course of a year. Any variations outside the limits of accuracy of the experimental methods adopted appear to be erratic and therefore cannot be correlated with any factor varying seasonally. Such fluctuations may be due to external factors which operate only intermittently. This is particularly applicable to the surface waters, whose composition varies so much with conditions affecting drainage from the land (**17**).

2. At the surface and below, the bacterial content is relatively high in August.

Diurnal Variation. The samples just described were taken at intervals of several weeks, so they do not show short-period variations due to such factors as tide, sunshine, and perhaps diatom increases. Accordingly, samples were taken in vertical series quarterly at 3-hour intervals over a period of 24 hours. The experimental conditions differed from those under which the other periodical samples were examined. Plating was done on the boat immediately after sampling; two agar plates were made from each sample, using 1·0 c.c. as inoculum. Gelatine plates were not employed, as the lower solidifying point of gelatine made it unsuitable for plating work carried out on a boat. Four such 24-hour series were made. The results are given in Tables IIA, IIB, IIC and IID.

Winter Series, December 19/20, 1928. The following results were observed :—

1. The general vertical distribution over the 24 hours agrees with that of the monthly samples, i.e. there is a progressive decrease in the bacterial content from the surface to the bottom and the surface samples show wider fluctuations.

2. The number of surface bacteria is unusually high : this may be correlated with the fact that the herring fishing was in progress at the time.

3. At any given depth the numbers were higher at night, with a tendency to decrease from 7 p.m. till the early hours of the morning

(Fig. 4). With increasing depth the maximum occurs at a later hour, but this may be due to chance variations.

Spring Series, March 7/8, 1929. From Table IIB the following observations were made :—

1. The number of surface bacteria is unusually low. This may have been due to the low temperature then prevailing, and to the fact that the herring fishing had ceased some weeks earlier. These possible causes are discussed in the following section.

2. There is an increase in the number of bacteria during the night hours, the highest numbers being attained at 3 a.m. in all except the bottom samples (Fig. 5).

Summer Series, July 23/24, 1929. From Table IIC the following observations were made :—

1. In this series, the number of surface bacteria is again relatively high and fluctuates very much between the 3-hour samplings.

2. The lowest surface numbers are at noon and the highest at 5 p.m.

3. Below the surface the numbers were fairly constant, but at 10 and at 20 fathoms there were increases after midnight (Fig. 6).

Autumn Series, October 24/25, 1929. These samples confirmed the findings of the three previous series. The following conclusions were drawn (Table IID) :—

1. The number of surface bacteria fluctuates very much, but on this occasion there were relatively few organisms in the surface water.

2. At lower levels there was in general an increase in numbers during the night, so that the bacterial content tends to be highest in the early morning hours (Fig. 7).

In summing up the results of these series of bacteriological analyses spread over a period of a year, it is seen that (i.) the number of surface organisms is usually relatively high, and is much subject to short-period variations, (ii.) in deeper water layers the bacterial content is very much lower and remains almost constant throughout the year, and (iii.) during the hours of darkness the numbers tend to increase slightly.

Results of Pollution Tests.

Conradi-Drigalski agar and McConkey agar were used as routine media for the detection of pollution. Both these media inhibit, or at least retard, the growth of all but intestinal bacteria, so that the presence of colonies on a plate inoculated from a water sample is presumptive evidence of the contamination of that water. Most of such colonies will appear red and will be the lactose-fermenting *B. coli* or its congeners. This can be confirmed by a lactose-broth culture made from the same

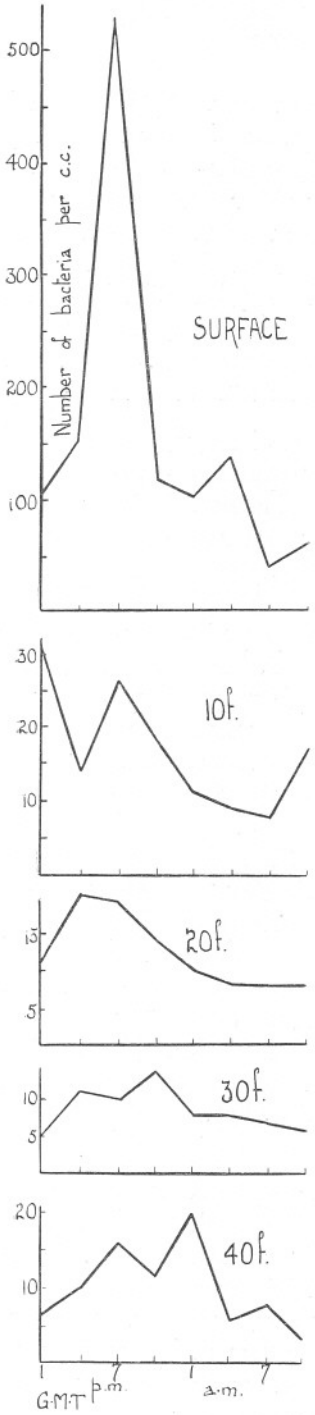


FIG. 4.—Diurnal variation in the numbers of bacteria at different depths. Samples taken 19/20.xii.29. Loch Striven.

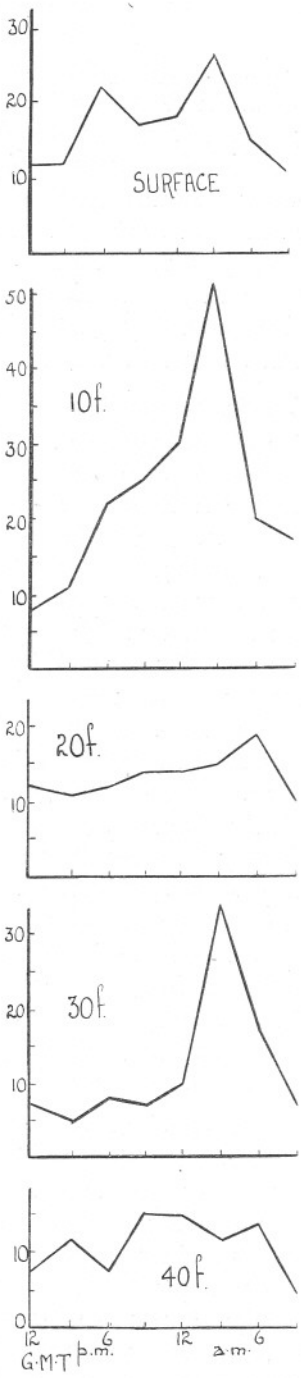


FIG. 5.—Samples taken 7/8.iii.29. Loch Striven.

water sample. The intestinal organisms, e.g. *B. typhosus*, Morgan's bacillus, which do not ferment lactose, are less common in polluted water; on the above media they appear as blue-white colonies.

It was found that bacteriologically the Loch Striven waters were remarkably pure throughout the greater part of the year. During the winter months, however, when the herring fishing was in progress, the surface samples showed an increase in the total bacterial content, and this was due in part to an increase in the numbers of presumptive coliform organisms, when they formed about 20% of the total. When the herring season was over, however, the water became free from these organisms.

Loch Long. The results given in Table III show that at Loch Long the vertical distribution of bacteria is very similar to that of Loch Striven, though the bacterial content is in general higher. This is possibly to be connected with the greater accessibility of this loch to steamer traffic.

Here again there is little evidence of regular seasonal variation (Fig. 3). Table III shows that the bacterial content of the surface water varies widely and apparently erratically. The samples taken at other levels show a midsummer minimum, an autumn increase and a minimum in the months of January and February. Very few bacteria were present in the January samples; at this time the temperature was so low that the waters at the head of the adjoining branch, Loch Goil, were frozen. This seems to bear out the opinion generally held that water bacteria are specially sensitive to changes in temperature.

Normally there are more bacteria at the surface than at other levels; there is only one exception, namely, the May series of samples taken in Loch Long. Here a much higher bacterial content is found at 10 fathoms. For this there does not appear to be a suitable explanation, unless we have regard to the fact that the number of presumptive coliform organisms obtained on McConkey plates on that date was specially high and that 3 out of 4 lactose-broth cultures produced gas. This points to some special circumstances causing localised subsurface contamination of the water at the spot where the samples were taken.

Greenock. In this area the samples were taken at the deepest part of the river channel off Greenock, where the water is much polluted with sewage and with industrial effluents. The effect of such pollution will of course be more marked near the shore-line. Between the coast and mid-channel there is a certain amount of self-purification of the water; nevertheless, the bacterial content of the open water is affected. The number of organisms per c.c. is considerably higher than in the lochs (see Table IV and Fig. 3); further, the number of colonies on McConkey plates is many times more than the number on gelatine and agar plates, so that it is not possible to estimate the number of coliforms without dilution of the

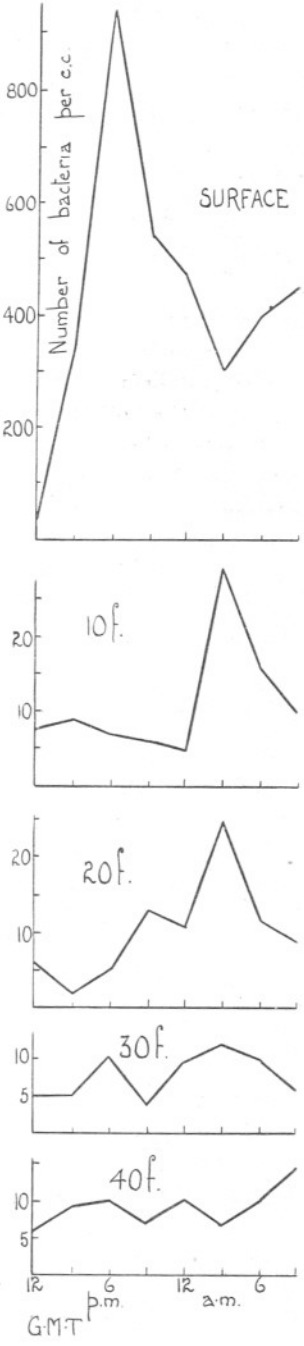


FIG. 6.—Diurnal variation in the numbers of bacteria at different depths. Samples taken 23/24.vii.29. Loch Striven.

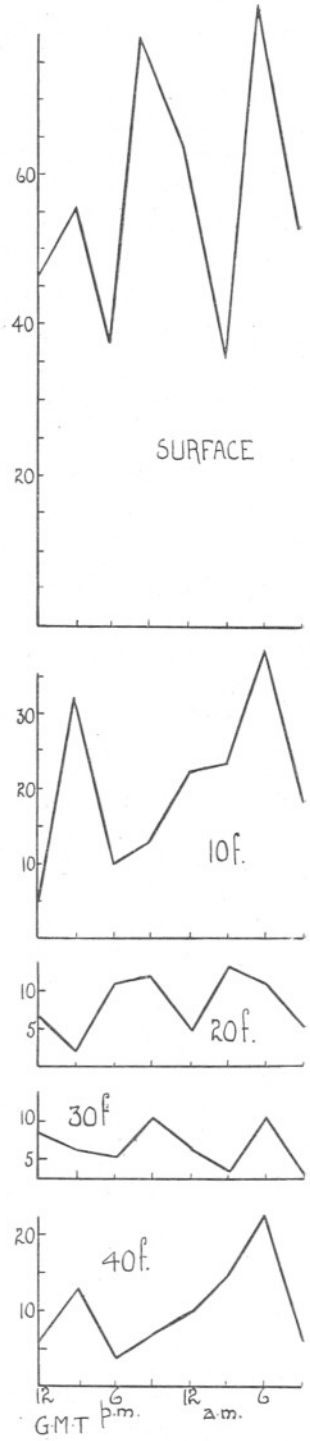


FIG. 7.—Samples taken 24/25.x.29. Loch Striven.

sample before plating. In this area then a high proportion of the constituent organisms are of the intestinal type.

The surface samples again showed by far the highest numbers; at 10 fathoms it was found always that there were fewer organisms; at the bottom, however, there was an increase. In none of these was any regular seasonal quantitative variation found.

Cumbrae Deep. At the above-mentioned stations samples could not be obtained at great depths, the deepest being 40 fathoms in Loch Striven. At Cumbrae Deep, however, there is a depth of 62 fathoms. The results from one series of samples (Table V) show that the vertical distribution is similar to those of the lochs, namely, that the surface waters have a relatively higher bacterial content, that the numbers decrease with increasing depth and that they increase again near the bottom.

It is interesting to note that the number of bacteria here is higher than it is in the lochs, but Cumbrae Deep is not typical of the Clyde Sea Area, since it is used as a dumping-ground for the Glasgow sewage treated by the activated sludge process at the Shieldhall Sewage Disposal Works. Buchanan states that such activated sludge, like crude sewage, has a bacterial flora of largely intestinal species (see **13**, p. 2); this sludge therefore appears to affect the bacterial content of the sea-water into which it is discharged.

Millport. The foregoing samples were taken in open water. For purposes of comparison, samples were taken (*a*) in the intertidal zone and (*b*) in a high-water rock pool, and the bacterial content investigated. From the results given in Tables VI and VII it is seen that the numbers of bacteria are very much higher than in the open water—a fact to be correlated with the congestion of other living organisms in the strip of water bordering the land.

Factors Affecting Distribution of Bacteria.

The foregoing work deals only with the free-living bacteria; these may be differentiated by their mode of nutrition into prototrophic and metatrophic species. It is not yet definitely established to what extent the prototrophic forms, as for example, the nitrogen-fixing bacteria, are found free-living in the sea. Ordinary marine conditions are not always favourable for their growth, so their existence is problematic. Experimental proof of their activity is available, but much of the work done on the subject is contradictory.

The majority of free-living bacteria are metatrophic, deriving their organised food-stuffs directly or indirectly from other organisms. In the sea two classes may be conveniently distinguished :—

(i.) The saprophytes living on and attached to particles of an organic nature, such as decaying seaweed, dead plankton and terrigenous detritus. This group will include the putrefactive bacteria ; they will be common where suspended matter is common and will be particularly abundant where such particles will accumulate, as for instance at the sea-bottom.

(ii.) The true planktonic bacteria, which have a simple metabolic cycle, and whose source of food is the dissolved organic material—amino-acids, proteins, and carbohydrates,—present in the sea, particularly in the surface waters near the coast-line.

(*a*) *Sunlight.* Among the physical factors affecting bacteria, sunlight is well-known to have a deleterious action on the growth of micro-organisms. This is due to the bactericidal action of ultra-violet light, and is to be distinguished from the ordinary retarding effect of light on growth. If the insolation is sufficiently intense, it would be expected that this effect would be most marked at the surface. The foregoing results for the Clyde Sea Area, however, show a greater number of bacteria at the surface, even when the samples were taken on sunny days, so that the bactericidal effect of light was apparently negligible. Schmidt-Neilsen (**23**), on the other hand, records finding at Dröbak 26 bacteria per c.c. at the surface and 420 per c.c. at a depth of 25 metres, and states that this progressive increase with depth is possibly due to the influence of sunlight. Similarly Bertel (**5**) found that off the coast of Monaco the numbers increased with depth. From two series of samples he found that the numbers increased from 1 per c.c. at the surface, (*a*) to 30 at a depth of 200 metres, (*b*) to 36 at a depth of 400 metres ; these results were obtained during the months of May and June, when insolation is intense.

In the same way, the bactericidal effect of sunlight would be expected to be more marked during the summer months, and, if it were the limiting factor, the numbers of bacteria would be lower in the summer than in the winter months. For the Clyde Sea Area, the bacterial content of the water on the whole is lower in the period from June to August, but it is not possible at this stage to correlate such seasonal variations with definite variations in the intensity of light. There do not appear to be other seasonal records with which these results may be compared.

The diurnal variation in the bacterial content may be due in part to the effect of sunlight. Tables IIA, B, C, and D show that in general there is an increase during the hours of darkness. This confirms the findings of Fischer (**10**), that more bacteria are to be found at sunrise than in the afternoon. Bertel (**5**) also states that there is a night-time bacterial increase which persists even to the early hours of the morning. He bases his conclusions, however, on the evidence of three series of samples taken

on different dates, so that it is possible that other factors came into play during the intervals. From his experimental work Bertel deduces that the night-time is more favourable for reproduction by bacteria ; but the fact that bacteria are more numerous at night does not prove that they necessarily reproduce more rapidly at night, since other factors such as the vertical mixing of water may cause movement of particles supporting bacteria from one water level to another.

(*b*) *Temperature.* An increase of temperature within certain limits favours the growth of micro-organisms in general. Sudden and marked changes in temperature may, however, have an unfavourable effect on bacteria, particularly on those species which do not form spores and which have not a highly resistant cell-membrane. Water bacteria are in general small non-sporing bacilli, notoriously sensitive to sudden changes in temperature (**2**).

Ordinarily, in the Clyde Sea Area the range of temperature variation is not sufficiently wide to show its effect on the bacterial content of sea-water. An examination of the results of the January samples taken in Loch Long shows the number to be very low ; these samples were taken during an extremely cold spell when the head waters of the adjoining loch were frozen.

(*c*) *Movements of Water.* In a still body of water it would be reasonable to expect a greater number of micro-organisms at the surface and at the bottom than in the intervening layers. However, any movements which cause vertical mixing from one layer to another may cause short-period variations in the bacterial content of the water at any depth. In view of this, it is remarkable that for the Clyde Sea Area the vertical progressive diminution in the number of bacteria is so constant.

Near land masses, especially off the steep western coast of Scotland, there is a tendency for vertical upwelling of water from the bottom and a surface flow away from the land. Foodstuffs are thus brought up to the surface, and become available for aerobic marine bacteria. At the same time, land drainage contributes its quota of detritus and soluble organic compounds, the less dense fresh water tending at first to distribute itself over the surface (**17**). Thus the surface waters appear to be best furnished with foodstuffs for the support of a more numerous bacterial population than is found at lower water levels. Almost all the samples taken illustrate this.

Tidal movements, similarly, may affect the bacterial content of the water. The results of the German Plankton Expedition (**10**) show that the number is higher during the ebb than during the flood tide. This influence is more marked when there is a slightly shelving coast-line with a comparatively broad intertidal zone which supports much plant and animal life, the number of bacteria being correspondingly high. In

the lochs investigated, however, the steeply sloping sides afforded only a narrow intertidal zone, and the tidal variations do not appear to have much effect on the bacterial content of the water. This is best shown in Tables IIA, B, C and D, where samples were taken at 3-hour intervals over periods of 24 hours at various seasons of the year.

(*d*) *Sedimentation of Organic Particles.* Attention has already been drawn to the fact that the saprophytic bacteria are not truly planktonic, but are attached to suspended organic particles of various origins. Any factor which determines the distribution of these particles will affect also the number of saprophytic bacteria. In water where there are no currents and no vertical mixing, it would be reasonable to expect at the surface an accumulation of such organic matter as has lower density than sea-water, with a corresponding accumulation of bacterial saprophytes. Similarly, the deposits at the bottom induce a high number of bacteria. In the intervening layers, however, through which suspended matter, as for example, the "plankton rain," tends to sink slowly, the number of bacteria also decreases progressively with depth.

Almost all the vertical series of samples taken in the Clyde Sea Area show this, viz., a relatively high bacterial content at the surface, with a gradual decrease till the bottom is reached, when the numbers again rise. Probably the increase at the bottom is due to the proximity of the mud which exists at all the stations. Some work now in progress has shown that the number of bacteria in the mud itself far exceeds that of the water immediately above it.

(*e*) *Biological Factors.* Since most water bacteria are heterotrophic, they will enter into competition for foodstuffs with the simpler animal forms, and will in turn be preyed upon by protozoa. It is well known that in the soil the numbers of protozoa and bacteria bear a numerical relationship to one another, namely, that when one group is abundant, the other is scarce and vice versa. It is highly probable that a similar state of affairs exists in the sea, though experimental evidence is lacking as yet.

After a period of great activity in the development of any group of organisms, there will be a glut of dead organisms and bacteria may thereafter multiply very rapidly. After the spring diatom increase in 1929, the bacterial content of the water was high, especially at the surface. There was a comparable increase during the autumn of 1928, when the herring season was in progress in Loch Striven, but not at the other stations sampled. In Loch Striven there was a great increase in the numbers of bacteria at the surface, with no corresponding increase at the other stations.

The following table shows the average number of bacteria at the surface in Loch Striven, compared with the herring catches for the season. The

latter figures are available through the courtesy of the Fishery Board for Scotland.

	1928								1929			
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Ap.
Quantity of herrings taken monthly (crans)	0	0	40	0	0	4,644	16,841	14,075	4,727	–	–	–
No. of bacteria taken at surface in one sample per month	43	5	–	39	–	17	136	26	44	120	12	1

Thus it appears that the surface maximum in November coincides with the maximum herring catch ; this is followed by a decrease in numbers during December, and a second increase in February.

The writer wishes to make acknowledgments to the Scottish Marine Biological Association for permitting the frequent use of their boat, the *Nautilus ;* to Mr. Elmhirst, the Superintendent of their Laboratory at Millport, for readily affording facilities for work there ; to Professor D. Ellis and to Dr. J. A. Cranston of the Royal Technical College, Glasgow, for much helpful criticism and advice ; and to Mr. R. J. Nairn for frequently deputising for the writer in the collecting of samples.

SUMMARY.

1. A bacteriological survey of the Clyde Sea Area has been made over a period of a year. Water samples have been taken monthly at three stations, and also less frequently at other places. A uniform routine technique has been adopted for studying their bacterial content.

2. *Vertical Variation.* The surface waters were found to have the highest bacterial content. With increased depth until near the bottom, there was a progressive decrease in numbers. At the bottom there was usually a slight increase.

3. *Seasonal Variation.* Throughout the year the numbers were found to be remarkably constant for all layers except the surface, with only slight evidence of rhythmic seasonal variation. At the surface, the bacterial content fluctuated widely, apparently in relation to factors which are not seasonal but irregular.

4. *Diurnal Variation.* At the surface the bacterial content is irregular throughout the day ; at lower levels, there is a slight increase during the hours of darkness, the maximum occurring in the evening hours in December, and at 3–6 a.m. in March, July and October.

5. *Purity of the Water.* The waters of both Loch Striven and Loch Long were found to be remarkably free from pollution. In Cumbrae

Deep, however, and in the estuary off Greenock, the numbers of bacteria were high, and a large proportion of these were found to be presumptive coliform organisms.

LITERATURE.

1. American Public Health Association. Standard Methods for the Examination of Water and Sewage. New York, 1923.
2. Bergey, H. A Manual of Determinative Bacteriology. Baltimore, 1923.
3. Berkeley, C. A Study of Marine Bacteria. Trans. Roy. Soc. Canada, XII, 3rd series, 1919.
4. Bertel, R. Ein einfacher Apparat zur Wasserentnahme aus beliebigen Meerestiefen für bakteriologische Untersuchungen Biol. Centralbl., XXXI, 1911.
5. ——. Sur la distribution quantitative des Bactéries planctoniques des côtes de Monaco. Bull. de l'Inst. Ocean. Monaco, No. 224, 1912.
6. Birge, E. A second report on limnological apparatus. Trans. Wisconsin Acad. Sci., XX, 1922.
7. Bohart, R. M. Bibliography of Marine Bacteria. Publ. Puget Sound Biol. Stat., Vol. V, p. 309, 1928.
8. Drew, G. H. Preliminary investigations on the marine denitrifying bacteria. Year Book, No. 10, Carnegie Inst., Washington, 1911.
9. ——. Investigations on marine bacteria at Andros Island, Bahamas. *Ibid.*, No. 11, 1912.
10. Fischer, B. Die bakterien des Meeres. Ergebnisse Plankton Expedition, Bd. IV, 1894.
11. de Giaxa. Verhalten pathogener Mikro-organismen im Meerwasser. Zeitschr. f. Hygiene, VI, 1889.
12. Giltner, W. Laboratory Manual in General Microbiology. New York, 3rd edition, 1926.
13. Harris, F. W., Cockburn, T., and Anderson, T. Biological and physical properties of activated sludge. Corporation of Glasgow, Sewage Purification Dept., 1926.
14. Janke, A. u. Zikes, H. Arbeitsmethoden der Mikrobiologie, Dresden, 1928.
15. Johnstone, J. Conditions of Life in the Sea. Camb. Univ. Press.
16. Letts. Report of the Royal Commission on Sewage Disposal, No. 3, Vol. II, 1903.

17. Marshall, S. M., and Orr, A. P. The relation of the Plankton to some chemical and physical factors in the Clyde Sea Area. Journ. Mar. Biol. Assoc., N.S., XIV, 1927.

18. Matthews, D. A deep-sea bacteriological water-bottle. Journ. Mar. Biol. Assoc., N.S., IX, 1911.

19. Mill, H. R. The Clyde Sea Area. Trans. Roy. Soc. Edin., XXXVI–XXXVIII, 1891.

20. Portier et Richards. Sur une methode de prélèvement de l'eau de mer destinée aux études bactériologiques. Bull. de l'Inst. Oceanog. Monaco, No. 97, 1907.

21. Russel, H. Untersuchungen uber in Golf von Neapel lebende Bakterien. Zeitschr. f. Hyg., XI, 1892.

22. ——. The bacterial flora of the Atlantic Ocean. Bot. Gaz., XVIII, 1903.

23. Schmidt-Nielsen, S. Beitrag zur Biologie der marinen Bakterien. Biol. Centralbl., XXI, 1901.

24. Wilson, F. Description of an apparatus for obtaining samples of water at different depths for bacteriological analysis. Journ. Bacteriol., V, 1920.

TABLE I.

Loch Striven.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
18/5/28										
Surface	28	34	31	36	26	–	–	–	155	43
10 fathoms	8	47	1	1	17	–	–	–	74	20
20 fathoms	4	4	0	0	3	–	–	–	11	3
30 fathoms	6	2	0	1	10	–	–	–	19	5
Bottom	1	3	1	0	2	–	–	–	7	2
15/6/28										
Surface	8	3	0	–	2	11	–	–	26	5
10 fathoms	5	3	6	–	10	13	6	–	43	8
20 fathoms	1	2	0	–	4	8	6	–	21	4
30 fathoms	0	0	0	–	6	7	5	–	18	3
Bottom	2	2	2	–	13	11	3	–	33	6
24/8/28										
Surface	43	30	28	16	36	31	7	13	204	59
10 fathoms	31	43	1	4	1	5	4	5	94	18
20 fathoms	9	9	6	1	9	11	1	5	51	10
30 fathoms	15	21	18	0	6	12	11	4	87	17
Bottom	20	16	4	4	19	22	29	7	121	23

TABLE I (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
5/10/28										
Surface	15	24	2	0	21	17	7	1	87	17
10 fathoms	4	6	5	0	7	9	2	0	33	6
20 fathoms	9	8	–	–	3	2	–	–	22	5
30 fathoms	0	0	2	0	2	0	0	0	4	1
Bottom	0	1	0	2	2	3	1	0	9	2
2/11/28										
Surface	73	118	63	23	113	185	89	47	711	136
10 fathoms	9	18	6	1	11	5	3	1	54	10
20 fathoms	1	8	3	0	4	4	0	0	20	4
30 fathoms	6	2	1	1	3	3	0	0	16	3
Bottom	3	8	5	0	4	4	2	0	26	5
1/12/28										
Surface	27	29	5	0	33	27	12	1	134	26
10 fathoms	11	1	3	0	15	12	5	1	48	9
20 fathoms	3	8	1	0	3	1	1	1	18	3
30 fathoms	2	2	0	0	0	3	0	0	7	1
Bottom	4	7	2	0	0	1	4	0	18	3
18/1/29										
Surface	17	21	4	2	90	81	12	1	228	44
10 fathoms	2	8	4	1	10	13	7	0	45	9
20 fathoms	3	5	3	0	2	7	1	1	22	4
30 fathoms	6	6	7	0	0	7	0	0	26	5
Bottom	7	6	1	3	2	5	1	0	25	5
15/2/29										
Surface	117	159	22	15	109	161	41	5	629	120
10 fathoms	40	42	20	3	29	9	6	4	153	29
20 fathoms	12	15	8	2	0	15	13	11	76	15
30 fathoms	8	7	5	3	6	11	2	0	42	8
Bottom	5	9	1	1	10	3	3	0	32	6
7/3/29										
Surface	24	1	–	–	–	–	–	–	25	12
10 fathoms	10	7	–	–	–	–	–	–	17	8
20 fathoms	12	13	–	–	–	–	–	–	25	12
30 fathoms	7	7	–	–	–	–	–	–	14	7
Bottom	7	10	–	–	–	–	–	–	17	8
12/4/29										
Surface	0	1	0	0	1	1	0	0	3	1
10 fathoms	1	0	1	0	1	0	1	0	4	1
20 fathoms	3	–	2	0	1	0	2	3	11	2
30 fathoms	1	1	0	0	–	1	0	1	4	1
Bottom	4	4	2	2	1	0	0	0	13	3

Summary of Tables I and II. Loch Striven.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	4565	80
10 fathoms	825	15
20 fathoms	433	8
30 fathoms	361	7
Bottom	417	8

TABLE IIa.

Loch Striven.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Winter Series, 19/12/28–20/12/28.

Depth.	1 p.m.	4 p.m.	7 p.m.	10 p.m.	1 a.m.	4 a.m.	7 a.m.	10 a.m.
Surface	79	131	493	123	106	97	45	53
	123	172	560	112	103	181	38	75
(Average)	101	151	526	117	104	139	41	64
10 fathoms	43	1	23	19	9	10	8	19
	18	27	29	18	13	9	9	16
(Average)	30	14	26	18	11	9	8	17
20 fathoms	13	19	17	11	12	4	9	8
	10	22	21	18	9	12	7	–
(Average)	11	20	19	14	10	8	8	8
30 fathoms	9	13	12	14	11	6	2	2
	1	10	9	14	6	11	12	10
(Average)	5	11	10	14	8	8	7	6
Bottom	9	3	15	13	–	5	8	4
	3	18	18	11	20	8	8	2
(Average)	6	10	16	12	20	6	8	3

Table IIb.

Loch Striven.

Spring Series, 7/3/29–8/3/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	24	14	24	18	12	22	14	7
	1	10	21	17	26	29	17	16
(Average)	12	12	22	17	18	26	15	11
10 fathoms	10	20	11	22	29	45	22	23
	7	3	33	28	31	57	19	12
(Average)	8	11	22	25	30	51	20	17
20 fathoms	12	12	11	13	16	10	17	12
	13	11	13	15	12	20	22	9
(Average)	12	11	12	14	14	15	19	10
30 fathoms	7	3	10	4	9	33	17	6
	7	7	6	11	11	35	17	9
(Average)	7	5	8	7	10	34	17	7
Bottom	7	9	7	15	21	14	11	4
	10	15	9	15	10	9	18	6
(Average)]	8	12	8	15	15	12	14	5

TABLE IIc.

Loch Striven.

Summer Series, 23/7/29–24/7/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	91	*300	*1100	*690	537	403	307	*400
	9	*400	*800	*400	409	209	494	*500
(Average)	50	350	950	545	473	306	400	450
10 fathoms	16	6	6	9	7	31	19	12
	1	13	8	3	4	27	13	8
(Average)	8	9	7	6	5	29	16	10
20 fathoms	6	1	4	18	6	11	9	11
	6	3	6	8	17	39	16	8
(Average)	6	2	5	13	11	25	12	9
30 fathoms	6	6	8	3	9	11	9	3
	4	5	12	6	6	14	11	9
(Average)	5	5	10	4	7	12	10	6
Bottom	9	2	19	2	3	9	5	20
	3	16	1	13	18	6	15	9
(Average)	6	9	10	7	10	7	10	14

* Approximate numbers only.

TABLE IId.

Loch Striven.

Autumn Series, 24/10/29–25/10/29.

Depth.	Noon.	3 p.m.	6 p.m.	9 p.m.	Midnt.	3 a.m.	6 a.m.	9 a.m.
Surface	41	59	41	66	49	32	101	61
	53	54	35	91	79	41	63	45
(Average)	47	56	38	78	64	36	82	53
10 fathoms	6	36	7	18	21	24	35	8
	4	29	13	9	23	22	42	29
(Average)	5	32	10	13	22	23	38	18
20 fathoms	6	0	14	15	6	14	7	7
	3	4	9	9	4	13	16	3
(Average)	4	2	11	12	5	13	11	5
30 fathoms	5	4	4	8	5	2	10	1
	8	5	3	8	4	0	6	1
(Average)	6	4	3	8	4	1	8	1
Bottom	7	15	4	11	8	11	12	12
	5	11	5	4	12	20	34	1
(Average)	6	13	4	7	10	15	23	6

TABLE III.

Loch Long.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
23/5/28										
Surface	39	37	8	–	40	–	18	–	142	36
10 fathoms	157	216	143	–	184	–	76	–	776	194
20 fathoms	1	0	1	–	3	–	3	–	8	2
Bottom	3	7	2	–	0	–	1	–	13	3
22/6/28										
Surface	39	10	0	–	53	48	37	–	187	37
10 fathoms	21	10	2	–	40	18	14	–	105	21
20 fathoms	5	7	0	–	9	6	4	–	31	6
Bottom	1	0	1	–	8	6	6	–	22	4
27/8/28										
Surface	35	49	0	4	10	0	1	3	102	20
10 fathoms	16	6	1	1	11	15	0	3	53	10
20 fathoms	0	1	0	0	1	4	1	0	7	1
Bottom	1	3	0	1	4	4	4	5	22	4
21/9/28										
Surface	38	70	33	8	123	89	83	5	449	86
10 fathoms	9	7	5	1	23	20	4	3	72	14
20 fathoms	9	11	3	3	1	12	6	11	56	11
Bottom	19	11	4	1	34	19	11	1	100	19
12/10/28										
Surface	39	46	33	1	41	43	3	5	211	40
10 fathoms	1	3	3	1	7	4	0	0	19	4
20 fathoms	1	5	1	0	2	3	4	0	16	3
Bottom	28	59	3	0	1	1	0	0	92	18
16/11/28										
Surface	129	107	51	5	50	43	14	12	411	79
10 fathoms	20	21	7	6	19	17	2	0	92	18
20 fathoms	3	13	4	1	0	2	5	1	29	6
Bottom	27	24	15	2	12	10	1	1	92	18
17/12/28										
Surface	90	21	8	0	29	15	7	11	181	35
10 fathoms	17	3	2	0	12	11	12	1	58	11
20 fathoms	11	13	1	2	19	18	8	1	73	14
Bottom	5	11	1	1	17	4	0	0	39	8
25/1/29										
Surface	3	3	0	0	0	4	1	1	12	2
10 fathoms	1	0	1	0	5	2	1	0	10	2
20 fathoms	3	2	0	0	8	2	2	0	17	3
Bottom	6	2	8	1	5	2	1	0	25	5
22/2/29										
Surface	81	32	41	30	33	30	3	4	254	48
10 fathoms	7	2	0	0	1	0	0	0	10	2
20 fathoms	13	12	2	6	2	9	0	0	44	8
Bottom	17	24	4	1	23	19	1	0	89	17

TABLE III (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
1/3/29										
Surface	7	24	5	4	2	3	0	0	45	9
10 fathoms	3	1	7	1	1	0	0	0	13	2
20 fathoms	5	4	7	0	5	9	2	1	27	5
Bottom	10	9	4	2	11	5	1	1	43	8
15/4/29										
Surface	11	3	3	7	0	2	0	0	26	5
10 fathoms	9	9	9	11	3	1	1	5	48	9
20 fathoms	10	3	9	0	0	1	0	7	30	6
Bottom	8	11	1	18	1	8	1	0	48	9

Summary of Table III. Loch Long.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	1740	39
10 fathoms	1198	27
20 fathoms	264	6
Bottom	448	10

TABLE IV.

Greenock.

No. of bacteria present, determined by colony counts of plate cultures incubated 5 days at room temperature.

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
8/6/28										
Surface	103	189	–	5	409	261	–	1	968	230
10 fathoms	71	13	–	0	77	50	–	0	211	50
Bottom	12	40	–	10	56	72	–	1	191	45
28/8/28										
Surface	123	80	6	28	119	71	31	63	521	100
10 fathoms	8	17	3	6	88	93	25	34	274	52
Bottom	153	61	6	5	113	51	35	17	441	85
22/9/28										
Surface	274	502	197	112	637	531	345	149	2747	530
10 fathoms	62	33	11	2	102	73	12	2	297	57
Bottom	36	48	63	3	110	143	79	51	533	103
12/10/28										
Surface	544	476	207	90	341	191	132	103	2084	400
10 fathoms	71	112	89	13	29	41	67	20	442	85
Bottom	51	107	28	11	18	28	13	6	262	50
16/11/28										
Surface	206	217	120	49	273	233	191	53	1342	257
10 fathoms	39	20	24	13	29	35	12	3	173	33
Bottom	38	31	31	2	44	47	16	4	213	41

TABLE IV (*continued*).

Depth.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
17/12/28										
Surface	121	70	51	12	326	131	49	21	781	150
10 fathoms	67	51	21	5	47	41	33	4	269	52
Bottom	113	70	51	9	71	29	12	11	367	71
25/1/29										
Surface	49	46	36	5	88	139	29	1	393	75
10 fathoms	69	119	69	19	63	130	39	13	521	100
Bottom	18	17	4	0	8	11	6	0	64	12
22/2/29										
Surface	401	317	91	35	177	210	23	7	1261	243
10 fathoms	79	91	40	9	154	115	70	0	558	130
Bottom	94	61	24	10	81	207	73	9	559	130
1/3/29										
Surface	76	201	153	71	89	331	71	41	1033	198
10 fathoms	36	119	139	25	18	17	101	24	480	92
Bottom	101	91	28	2	30	27	91	141	511	98
15/4/29										
Surface	229	89	23	8	109	6	0	0	464	90
10 fathoms	123	41	29	7	110	11	0	3	324	62
Bottom	207	22	9	17	140	2	3	0	400	77

Summary of Table IV. Greenock.

Depth.	Total No. of bacteria counted.	Average per c.c.
Surface	10,626	240
10 fathoms	3,338	71
Bottom	3,340	71

TABLE V.

Cumbrae Deep.

Depth.	Agar Cultures. 1·0 c.c.	0·5 c.c.	0·1 c.c.	Gelatine Cultures. 1·0 c.c.	0·5 c.c.	0·1 c.c.	Total.	Average per c.c.
1/9/28								
Surface	204	56	22	193	103	29	607	100
10 fathoms	11	10	1	6	0	0	28	9
20 fathoms	40	5	3	–	1	0	49	23
30 fathoms	20	5	2	2	0	1	30	9
40 fathoms	6	3	0	3	1	0	13	4
50 fathoms	11	1	0	3	0	0	15	5
62 f. (bottom)	21	13	0	–	0	0	34	16

TABLE VI.

QUANTITATIVE BACTERIAL ANALYSES OF LITTORAL SURFACE SAMPLES TAKEN IN THE FUCUS ZONE, CRAN BIGHT, OUTSIDE THE MILLPORT MARINE BIOLOGICAL STATION.

Date of Sample.	Agar Cultures. 1·0 c.c.	1·0 c.c.	0·1 c.c.	0·01 c.c.	Total.	Average per c.c.
31/3/28	442	457	91	0	990	470
2/4/28	∞	227	181	227	408	> 500
3/4/28	238	104	101	8	451	210
4/4/28	201	–	15	5	221	220
5/4/28	130	–	44	0	174	170
6/4/28	521	479	71	1	1072	550
7/4/28	89	198	21	0	308	150
8/4/28	514	347	66	–	927	440
9/4/28	193	85	10	10	298	140
10/4/28	503	200	–	–	703	350
11/4/28	371	366	–	–	737	370

Approximate mean average number of bacteria per c.c. = 500.

TABLE VII

QUANTITATIVE BACTERIAL ANALYSES OF SURFACE SAMPLES TAKEN FROM AN ENTEROMORPHA POOL OUTSIDE THE MILLPORT MARINE BIOLOGICAL STATION.

Date of Sample.	Agar Cultures. 0·1 c.c.	0·1 c.c.	0·01 c.c.	0·01 c.c.	Total.	Average per c.c.
31/3/28	494	593	61	27	1175	5300
2/4/28	731	448	59	73	1311	6000
3/4/28	728	568	81	35	1412	6400
4/4/28	381	473	51	92	997	4600
5/4/28	640	341	49	50	1080	4900
6/4/28	760	451	60	81	1352	6100
7/4/28	331	307	52	70	760	3500
8/4/28	800	488	60	23	1371	6200
9/4/28	411	571	21	82	1085	4900
10/4/28	566	498	20	27	1111	5000
11/4/28	470	403	21	72	966	4400

Approximate mean average number of bacteria per c.c. = 5200.

Note on the Distribution of *Lichina confinis* and *L. pygmœa* in the Plymouth District.

By

Gladys L. Naylor, B.Sc.

With one Chart.

Introduction.

Very little work has as yet been done on the occurrence and distribution of marine lichens in the Plymouth district. The present investigation of the genus Lichina was undertaken at the suggestion of Dr. J. H. Orton, who, having noticed the two Lichina species at New Train Bay near Padstow, North Cornwall, thought it might be of interest to determine their distribution in the Plymouth area.

The characteristic appearance of the Lichina vegetation is too well known to require more than a brief mention (**10**). Both are small fruticose lichens with densely branched, dark-coloured thallus. *L. confinis*, the smaller of the two, has rounded branchlets barely 3 mm. long, and forms small patches 2–4 cm. across, while *L. pygmœa* has slightly longer branches, up to 10 mm. in length, with flattened lobes, and may form circular patches varying from a few inches to a foot or more in diameter. In colour *L. confinis* is black or very dark brown, but *L. pygmœa*, though usually very dark, may occasionally be light brown or greenish in colour.

The definite zones occupied by these two lichens on the shore are also well known, and have been recorded by Nylander (**7**), Joubin (**4**, p. 13), Cotton (**2**, p. 26), and Knowles (**6**, p. 105). On most rocky coasts the zone immediately above mean high water is colonised by the black crustaceous lichen *Verrucaria maura*, the lower limit of which is bounded by the brown alga *Pelvetia canaliculata*. *L. confinis* occurs at the upper limit of the *V. maura* zone where this overlaps the belt of orange lichens (for detailed account see Knowles [**6**, p. 101]), and is not strictly marine, though exposed to spray and probably to occasional immersion by very high tides. The vertical width of the *L. confinis* zone varies with the exposure, being greatest where there is a wide spray zone. *L. pygmœa*, on the other hand, never occurs above the Pelvetia zone, but is usually most abundant a little below it, though it may be present down to low neap-tide level (**2**), (**6**). This lichen is truly marine, and is incapable of surviving the desiccation to which *L. confinis* is often exposed.

The rocks round Plymouth Sound are chiefly Devonian (**13**), consisting for the most part of slates, grits and shales, the strata running at various angles but often nearly vertical; volcanic rocks occur at Rum Bay and Drake's Island, felsite at Kingsand; the shore below the Hoe, Tinside to Devil's Point, is limestone, this rock also occurring at Mount Batten and the north-west end of Drake's Island, while there are two further exposures, one at Cremyll and a small one below Mount Edgcumbe.

Localities Investigated.

The localities investigated include all the shores skirting the Sound itself, from Reny Rocks to Batten Breakwater, Tinside to Devil's Point, Cremyll to Penlee Point, as well as Drake's Island and the Breakwater, and outside the Sound as far as the mouth of the River Yealm to the east and from Penlee Point to Rame Head and Whitsand Bay (Polhawn Cove) to the west (see Chart). These localities will be considered briefly below, working from east to west, with the exception of the calcareous rocks which will be taken together at the end.

River Yealm to Ram's Cliff. Both species of Lichina occur all along this part of the coast, the width of the zones varying chiefly with the slope of the foreshore. Where the rocks are steep, as to the east of Wembury Church, and at Staddon Point, the lichen zones are well developed, but where the foreshore is flatter the zoning is not so marked, and with the restriction of the spray zone *L. confinis* is less abundant, as for example between Wembury Church and Reny Rocks. Both species are necessarily absent from the sandy bays at Wembury and Bovisand, and *L. pygmæa* is also absent from the protected part of the south bank of the River Yealm. Throughout the area both species are usually found on the south and west faces of the rocks, these being the sides exposed to greatest wave action and insolation.

Ram's Cliff to Mount Batten (Jennycliff Bay). This area is interesting because of the entire absence of *L. pygmæa* between Ram's Cliff and a point just south of Batten Breakwater. The disappearance of *L. confinis* is not complete, but this species becomes steadily less common to the north of the Bay. The coast here is much less exposed than the part previously considered, lying as it does well within the Breakwater and facing west. The central part of the Bay is rather flat, with some sandy beaches, but numerous steep rocks also occur, especially towards Ram's Cliff. Owing to the decreased exposure and more level foreshore, the less steeply inclined rocks are covered with a dense growth of seaweeds, the different zones of which overlap; this would effectually prevent the establishment of *L. pygmæa* which seems to require a good supply of light and air.

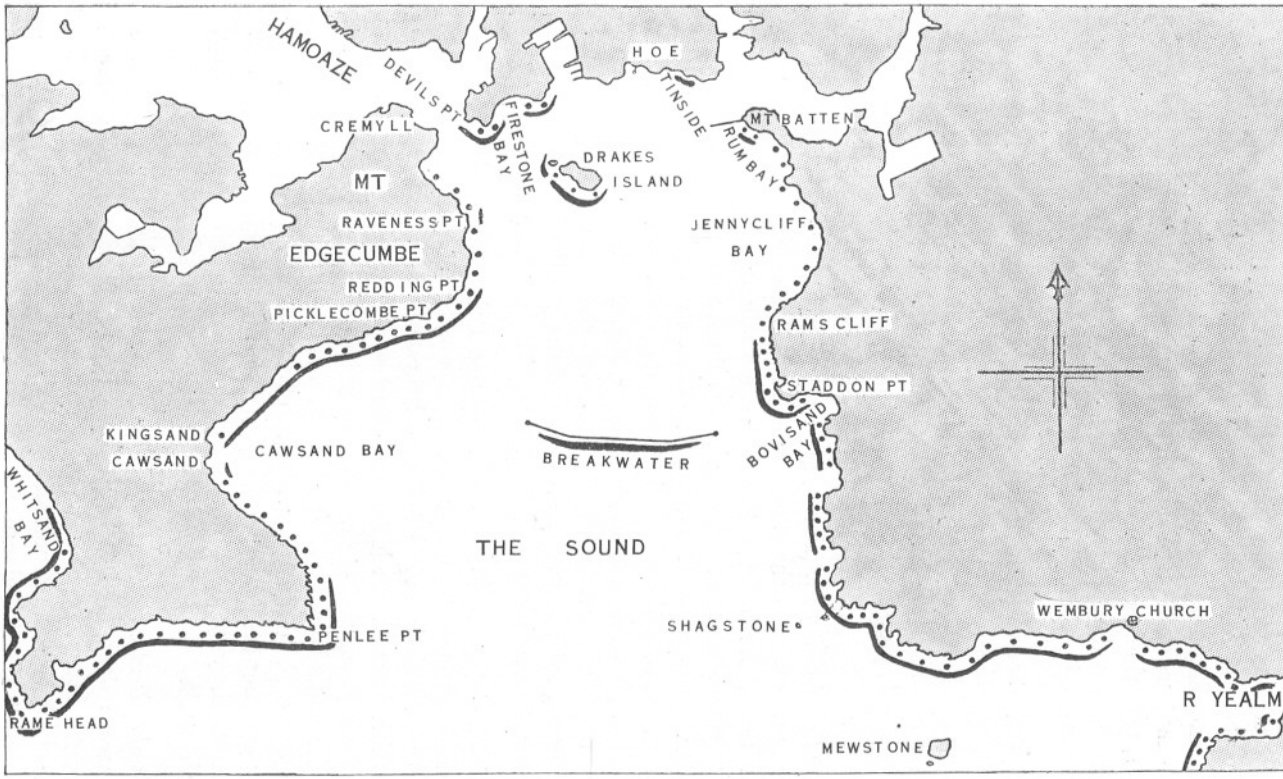


Chart of the Plymouth District showing the distribution of *Lichina confinis* and *L. pygmœa*.

Continuous line —— *L. pygmœa*
Dots . . . *L. confinis*.

There are many rocks, however, especially towards Ram's Cliff, which appear to be eminently suitable for the growth of this lichen, having steep faces, barnacle-covered, but bare of fucoids, the competition factor being thus removed. The small red seaweed, *Catenella opuntia*, which normally occupies the same zone as *L. pygmæa* but on the shady sides of the rocks, is abundant here even on the less shady surfaces, and this would indicate, however, that the insolation of this part of the shore is less intense than might be supposed, and possibly this, combined with decreased exposure to wave action, is enough to account for the absence of the lichen.

The Cattewater and the Hamoaze. Neither of these areas was investigated in detail, but *L. pygmæa* is certainly absent from the Cattewater ; both this area and the Hamoaze are sheltered from direct wave action, and as the latter also offers few if any rocky situations such as are necessary for the growth of *L. pygmæa*, it is probable that this lichen is absent from here also.

Cremyll to Redding Pt. (Mt. Edgcumbe). Both species of Lichina are rare along this part of the shore, which, like Jennycliff Bay opposite, is very sheltered. From Cremyll to Raveness Point the foreshore consists chiefly of pebble beaches, but at Raveness Point the cliffs jut out into the water, and at this point only does *L. pygmæa* occur as two or three small patches on a limestone rock. Between Raveness and Redding Points the Staddon grits which form the bulk of Mount Edgcumbe, and which reappear at Picklecombe Point, give place to river gravel, which forms a boulder beach from which *L. pygmæa* is entirely absent, though *L. confinis* appears occasionally.

Redding Point to Cawsand. From Redding Point the coast bears away west and is exposed to much more direct wave action. About halfway between Picklecombe Point and Kingsand the grits give place to felsite which forms a much flatter, less dissected foreshore. *L. confinis*, though locally very abundant on the grits, hardly occurs along the felsite, the rocks being too low to form a suitable spray zone, and the lichen does not, in this district, make use of occasional immersion by spring tides by growing at a lower level than usual (**2**, p. 28). *L. pygmæa* is abundant all the way along and shows a decided preference for the sunny side of the rocks.

Cawsand to Penlee Point. This stretch is again marked by the absence of *L. pygmæa* although *L. confinis* occurs quite abundantly. The coast faces north-east, and the wooded cliffs dip very steeply to the water. Exposure both to wave action and insolation is therefore low, and this is emphasized by the abundance of *Catenella opuntia* even on the exposed surfaces of the rocks.

Penlee Point to Whitsand Bay. All along this part of the coast the Lichina vegetation is very well developed. The rocks, which consist of Dartmouth slates, form steeply inclined surfaces, barnacle-covered, and the exposure is too great to allow the growth of seaweed to any great extent. *L. pygmæa* forms a well-marked zone, 4–5 ft. wide vertically, the individual patches sometimes occupying an area of two or three square feet—as at Polhawn Cove, Whitsand Bay. *L. confinis* shows a vertical range of 2–3 ft. between Penlee and Rame Head, but is less abundant in Whitsand Bay. Although the exposure of this part of the coast is great, the actual cliff face is low, and therefore the spray zone is comparatively narrow, and this possibly accounts for the restricted vertical range of *L. confinis* in this district as compared with its range at Clare Island (**2**) and Howth (**6**).

Drake's Island. The rock here is mostly volcanic, but at the north-west end is a small mass of limestone. On the sheltered north shore there are two or three small sand and pebble beaches, but with these exceptions the foreshore is short and the rocks rugged. *L. pygmæa* is entirely absent from the north and north-east sides, but appears on the east and is abundant all along the southern shore. On the limestone mass, the more or less level top of which about corresponds to the Pelvetia zone, *L. pygmæa* occurs occasionally on the edges of small sunny pools. *L. confinis* is comparatively rare on the island, though it appears at intervals along the southern side. It seldom grows on flat surfaces, but prefers cracks and hollows on the seaward side of the rocks.

The Breakwater. The upper level of the Breakwater is below the *L. confinis* zone, and this lichen is therefore absent, but *L. pygmæa* is well represented on the sloping seaward face, the exposure of which is too great to permit a dense growth of seaweed. *L. pygmæa* shows a vertical range of about 4–5 ft., the region of greatest abundance being in the upper middle part of the zone : it is especially frequent along the upper and lower edges of the limestone blocks of which the Breakwater is built, but where the surface of these is very rough it may cover them more or less entirely. It is usually associated with a good deal of Enteromorpha and Porphyra. It is entirely absent from the two ends of the Breakwater which are built up with a horizontal surface in the *Fucus platycarpus* zone—that is, just below the Pelvetia level ; neither does it occur at all along the inner north-facing side of the Breakwater, which, though more steeply inclined than the outer face, is protected, and along which the brown seaweeds form a more or less continuous covering.

Calcareous rocks. The calcareous rock of the district takes the form

of hard limestone, on which the lichen flora is thin and poorly developed in most places, with fewer orange forms, while the *Verrucaria maura* belt is ill-defined or lacking (**6**, p. 116). The calcareous areas investigated include Mount Batten, Tinside, Firestone Bay, and Devil's Point.

Mount Batten. Neither species of Lichina occurs on Batten Breakwater itself, and indeed they are but poorly represented in this locality. *L. confinis* grows thinly in the crevices of rocks exposed to spray, but is never common; *L. pygmæa* is present for a few yards on the south-west face at the limit of the main limestone mass, and a few patches of this species also occur among the Pelvetia plants on the seaward side of some high rocks further down the beach. *V. maura* is similarly scanty, and favours shady places, also growing rather lower on the rocks than usual.

Tinside. The lichen vegetation of this area is very scarce altogether: *L. confinis* does not occur at all, *V. maura* is scanty, being present in the more shady and sheltered places only, and *L. pygmæa* is only found here and there. The limestone of this part is worn into innumerable small pockets, and it is chiefly in these, at a level corresponding to the upper Pelvetia zone, that *L. pygmæa* occurs. The pockets probably remain moist for a considerable time, but it is noticeable that the situations are usually exposed to the sun.

Firestone Bay and Devil's Point. *L. confinis* is comparatively rare throughout this area, only appearing on the rocks most exposed to spray, and even on these it is confined to a very narrow zone. *L. pygmæa*, however, is quite common, its zone of occurrence ranging from the upper Pelvetia to the upper *Ascophyllum nodosum* zones, i.e. about 3 ft. vertically. It is most abundant where the algal vegetation is not well developed, that is, on the more exposed rocks, but it may also be present in rather more shady situations, as around the bases of the Pelvetia or *Fucus platycarpus* plants. The centre of Firestone Bay consists of an artificial frontage of large limestone blocks, from which both species of Lichina are absent, although *V. maura*, and the brown seaweeds grow well on the sides of the stones.

Discussion.

Both species of Lichina are to be found abundantly in many parts of the Plymouth district, and their absence from others can probably be accounted for by a consideration of environmental conditions more especially with regard to exposure both to wave action and insolation.

Lichina confinis is the more generally distributed of the two species, occurring more or less all round the shore wherever there are rocks exposed

to spray. An exception might be noted in the limestone area of Tinside where *L. confinis* does not appear to be present. No part of the area investigated, with the possible exception of Rame Head, is subjected to very great exposure, and in all parts the actual cliff face is low, the spray zone being therefore restricted. It is probably due to this that, though so widely distributed through the whole locality, the vertical range of this lichen here is so narrow, rarely exceeding 2–3 ft., and often less than this, as compared with 12–15 ft. at Clare Island (**2**), and 50 ft. or more at Howth (**6**). Another point which might be noted is that as Plymouth is further south than these Irish localities, the desiccation to which the lichen is subjected during the summer months is probably greater in the former district. The absence of the species from the limestone of Tinside, which receives little spray in the summer, and its but scanty growth in the other limestone areas, also its comparative abundance along the tree-shaded rocks between Cawsand and Penlee, seem to emphasize that moisture is a limiting factor in the distribution of this lichen in the Plymouth district.

Lichina pygmæa. The occurrence and distribution of this lichen at Plymouth are similar in many particulars to those at Clare Island and Howth, but differ slightly in detail, more especially with regard to extent of vertical range. The chief points which correspond in all three areas are summarised below :—

1. *L. pygmæa* is most abundant on rocks which have steeply inclined faces, though it may occur on horizontal surfaces in certain situations.

2. It prefers rough surfaces and is abundant on barnacles.

3. It grows best in exposed and semi-exposed positions, the action of breaking waves seeming to be of special importance since the lichen is absent from protected situations.

The vertical range of *L. pygmæa* as seen on the Plymouth shores would appear to be more restricted than in the Irish localities, although there is no great difference in the vertical range of the tides at the three places, the smallest being at Howth with a 12 ft. spring-tide range as compared with 16 ft. at Plymouth and Clare Island. *L. pygmæa*, in the Plymouth district, extends from the upper Pelvetia zone to half-tide level only, but never as low as low neap tide, with its area of greatest abundance corresponding approximately to Mean High Water Neaps—that is, just below the *Fucus platycarpus* zone. It never occurs as undergrowth to *F. vesiculosus* or *A. nodosum*, though in some parts, as at Devil's Point, it grows around the base of *P. canaliculata* and *F. platycarpus* where these do not form a dense covering. In the places where *L. pygmæa* is most abundant there is little or no growth of the larger seaweeds, the steep rock surfaces being presumably too exposed for these plants to survive the action of the waves. Even Pelvetia and *F. platycarpus*, the least affected by exposure (**2**, p. 24), are sometimes absent, *L. pygmæa* forming the only macroscopic

vegetation, as at certain parts of Drake's Island and between Penlee and Rame Head.

Of the factors affecting the growth and distribution of the lichen considered, exposure to wave action is probably of greatest importance, though insolation, foulness of water, and salinity may also play a part. It is not easy in this district to get any clear idea of the effect of insolation, since it is only the southern shores which are directly exposed to breaking waves, and hence the absence of *L. pygmæa* from less highly insolated parts facing northwards may be due rather to the protection from wind and wave action than to decreased light intensity. This is supported by the observations of Joubin (**4**, p. 13) at the Ile de Bas, off the north coast of Finistère, where *L. pygmæa* grows freely on the exposed north and west shores, but is absent from the sheltered south side. He does not, however, give any details as to the aspect favoured by the lichen in the more exposed situations. On the west coast of Inverness-shire *L. pygmæa* is absent from the shores of sheltered sea lochs, but occurs abundantly along the coast outside, and in these exposed situations it is certainly not confined to the most highly insolated aspects so long as the surface is exposed to breaking water. Whether it is the actual mechanical stimulus of the moving water, or the high aeration—the water being not only fully saturated with dissolved oxygen as are all the surface waters of the sea, but having also a high content of air bubbles—it is certain that exposure to wave action plays a very important part in the distribution of *L. pygmæa*. The significance of light in the economy of the lichen, apart from its direct effect in photosynthesis, may lie rather in the need for a certain degree of drying-out of the thallus between tides, which could only be obtained on the better-lighted, bare rock surfaces. Such periodic drying-out is certainly essential in the case of many of the seaweeds of the foreshore. The effects of foulness of water, and salinity, have not been investigated ; the degree of exposure demanded by this lichen makes its absence from such sheltered areas as the Cattewater and the Hamoaze easily accountable without supposing any inhibition due to foulness of water or low salinity, although these may have some secondary effects.

Fruiting of *L. pygmæa* occurs freely throughout most of the district, but is less common among the Tinside and Mount Batten specimens.

SUMMARY.

The occurrence and distribution of the lichens *Lichina confinis* and *L. pygmæa* have been investigated for the Plymouth district. Both species occur frequently throughout the area. *L. confinis* is the more generally distributed, being present, though sometimes scantily, on most of the coast with the exception of Tinside ; on the exposed shores

outside the Sound itself it forms a zone 2–3 ft. wide, being especially common between Penlee Point and Rame Head. *L. pygmœa*, though very abundant on the open coast, is scanty or entirely absent along the sheltered parts of the Sound, as from Cawsand to Penlee, Cremyll to Redding Point, Jennycliff Bay, etc.

The distribution of the two species of Lichina in this district emphasizes the importance to both of the degree of exposure to wave action to which the situation is subjected. The importance to *L. confinis* lies in the height to which the spray is flung up the rocks, since occasional wetting by salt water is essential to this species. In the case of *L. pygmœa*, mechanical stimulus, aeration of water, and probably the removal of the competition factor—the larger fucoids being unable to maintain a footing on steep exposed rock surfaces—all play a part. The effect of light would appear to be secondary, and is probably of importance as connected with the desiccation of the lichen thallus between periods of immersion.

I should like to take this opportunity of expressing my gratitude to the Council of the Marine Biological Association for allowing me to work at the Plymouth Laboratory, and also to thank Dr. E. J. Allen and the members of the Staff for their kindness. I am especially indebted to Dr. J. H. Orton and Dr. W. R. G. Atkins for advice and criticism.

REFERENCES.

1. Batten, L. Note on the occurrence of *Arthopyrenia foveolata* at Plymouth. Journ. Mar. Biol. Ass., N.S., Vol. XII, No. 3., p. 557, 1921.

2. Cotton, A. D. Marine Algæ. Clare Island Survey, Pt. XV. Proc. Roy. Irish Acad., Vol. XXXI, 1908.

3. Hartley, J. W., and Wheldon, J. A. Lichens of the Isle of Man. Supplement. North-Western Naturalist, Vol. 2, pp. 1–12, 1927.

4. Joubin, L. Recherches sur la distribution océanographique des végétaux marins . . . de Roscoff. Ann. de l'Institut Océanographique. Tome I, fasc. 1, pp. 1–17, 1909.

5. Knowles, M. C. Notes on West Galway Lichens. Irish Naturalist, Vol. XXI, 1912.

6. Knowles, M. C. The Maritime and Marine Lichens of Howth. Sci. Proc. Roy. Dublin Soc., Vol. XIV, pp. 79–143, 1913.

7. Nylander, W. Circa Lichenes Armoricæ et Alpium Delfinatus. Actæ Societatis Scientiarum Fennicæ, Tome VII, 1863.

8. Orton, J. H. Observations on *Patella vulgata*. Pt. III. Habitat and Habits. Journ. Mar. Biol. Ass., N.S., Vol. XVI, No. 1, pp. 277–288, 1929.

9. Smith, A. Lorrain. Lichenes, Clare Island Survey, Pt. XIV. Proc. Roy. Irish Acad., Vol. XXXI, pp. 1–14, 1908.

10. Smith, A. Lorrain. Monograph of British Lichens, Pt. II. 1911.

11. Smith, A. Lorrain. Lichens. Cambridge Botanical Handbooks, 1921.

12. Smith, A. Lorrain. Recent work on Lichens. Trans. Brit. Mycol. Soc., Vol. 10, pp. 133–152, 1925, and Vol. 12, pp. 231–275, 1927.

13. Ussher, W. A. E. The Geology of the Country around Plymouth and Liskeard. Mem. of the Geol. Survey, Eng. and Wales, Sheet 348. 1907.

14. Weddell, H. A. Excursion Lichénologique dans l'Ile d'Yeu sur la côte de la Vendée. Mem. de la Soc. Nat. des Sci. Naturelles de Cherbourg, Tome XIX, 1875.

On Abnormal Conditions of the Gills in *Mytilus edulis*. Part I. On Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

By

D. Atkins, B.Sc.,

Amy, Lady Tate Scholar of Bedford College.

With 35 Figures in the Text.

CONTENTS.

Introduction.

A HEAVY percentage of the mussels obtained from various parts of the Fal Estuary, during October and November, 1927, had the gills in an exceedingly abnormal condition (31·8% among 1488 recorded). Occasional mussels from other localities (Padstow, Teignmouth, Yealm, Saltash) have been observed to have slightly abnormal gills, though perhaps in the majority of these the condition was due to the presence of a large female pea-crab, *Pinnotheres pisum*. In the Fal Estuary mussels the abnormal conditions were doubtless correlated with some factor in the environment, the percentage of pea-crabs in these being so low (4·8%) that their presence could have no relation to the abnormal condition of the gills.

These abnormal conditions will be described in some detail as they are thought to be of considerable general interest for experimental work.

The present paper will be restricted to a description of the permanent reversal of the frontal cilia on the gill filaments. In a further paper it is hoped to deal with: (1) folding over of the free edge of the gill with concrescence, (2) fusion of filaments side by side, and (3) enlargement of filaments.

The Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

Perhaps the most interesting of the abnormal conditions for experimental work is the occurrence of supernumerary food grooves on the surface of the gill (see Fig. 2, p. 921), accompanied in most cases by a permanent reversal of the frontal cilia, generally on that part of the lamella between the main and secondary grooves. The supernumerary

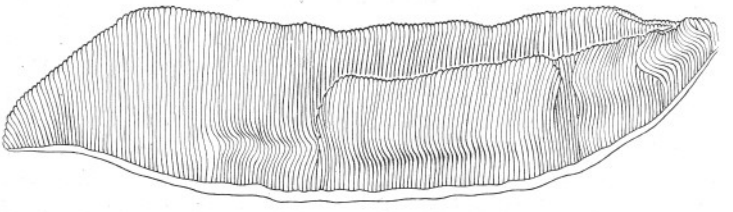


Fig. 1.—Sketch of the right inner gill of an uninfected* *Mytilus edulis* from Trelissick Reach, Fal River, showing a large fold—composed of three folds in series—on the ascending lamella. From preserved material. ×3.

groove may be set directly on the frontal surface of the lamella, as in Fig. 7, III, p. 930, or may be raised on a slight projection (Fig. 23, p. 948), or the lamella may be produced into a tiny fold (Fig. 35, II, p. 963), passing in some cases into a pocket (Fig. 30, II, p. 954). Food collected in any of these secondary grooves is passed eventually into the main grooves without interfering with the normal functioning of the gill.

These conditions were of rather rare occurrence among the Falmouth mussels, and—when found in mussels from other localities—are undoubtedly in most cases, as will be shown later, due to injury caused by the presence of a large female *Pinnotheres pisum*.

There is considerable range of variation in the size of the folds or pockets. The greatest development of pockets—indeed they are so large as almost to merit the term secondary gills—occurred on the gills of a small uninfected* mussel, 5·1 cm. long, from Trelissick Reach, Fal River. The gills were roughly 33 mm. long and 8 mm. deep; the secondary gills occurred on the ascending or reflected lamellæ of the inner

* "Infected" and "uninfected" means infected and uninfected with *P. pisum*.

gills,* that on the left gill was about 24 mm. long and 4 mm. deep ; that on the right about 18 mm. long and 4 mm. deep was composed of three pockets in series (Fig. 1). The descending or direct lamellæ of these gills were nearly normal, only a very little fusion of filaments side by side occurring. (The nomenclature employed for the gill filaments is that figured on p. 226, *Treatise of Zoology*, Vol. V, Mollusca, edited by E. Ray Lankester.) The ascending lamella of the left outer gill had a pocket about 7 mm. long and 3 mm. deep near the posterior end, and near the anterior end a simple secondary groove about 9 mm. long running into the main groove very near the mouth. A pocket about 10 mm. long and

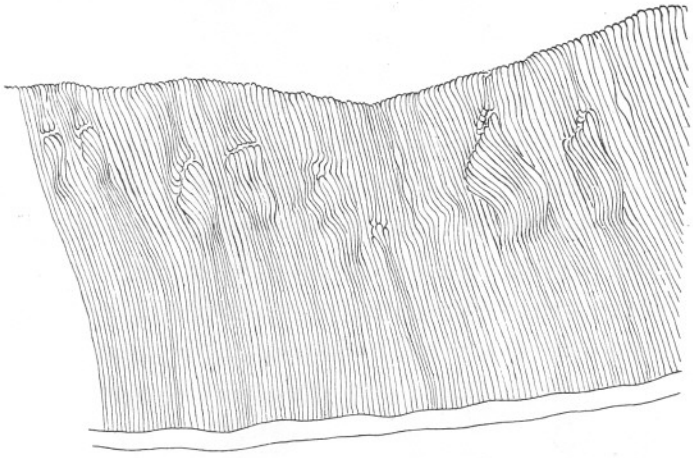


FIG. 2.—Sketch of part of a gill of an uninfected Mytilus from Trelissick Reach, Fal River, showing a series of small folds or pockets on the ascending lamella. From preserved material. ×4.

5 mm. deep, and a simple secondary groove about 13 mm. long occurred on the right outer gill in similar positions to those on the left. The descending lamellæ of both gills were nearly normal, a very little fusion only occurring. The supernumerary pockets and grooves were arranged in such a symmetrical manner as to make it appear doubtful whether they were due to abnormal conditions in the environment.

Figure 2 is a sketch of a series of small pockets on the gill of another mussel from Trelissick Reach, Fal River, which again did not contain a pea-crab.

The gills of a Padstow mussel harbouring a female *P. pisum* (12 mm. carapace width), had numerous secondary grooves, which were almost entirely restricted, in an unusual manner, to the descending lamellæ of all four gills, as though the crab had been scrambling between the two gills of each side (Fig. 3).

* For convenience in description the two demibranchs on each side of the body are considered as two gills.

Possible Cause of Formation of Secondary Grooves and Folds.

Owing to pressure of other work at the time the Falmouth mussels were received they were preserved after no more than a cursory examination. The following observations on the structure of secondary grooves and folds and their ciliation have been made on those which may occur exceedingly rarely on gills of normal, healthy, uninfected mussels, but

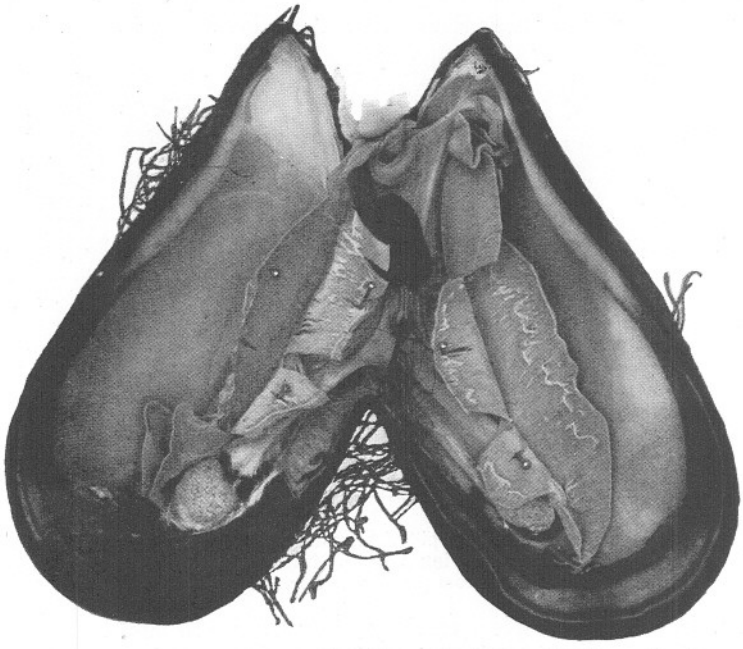


Fig. 3.—Photograph of a mussel (10·0 cm. long) from Padstow, showing numerous secondary food grooves on the descending lamellæ of the gills. In some places the free edge of the two right gills is permanently folded over. From preserved material.

more frequently on the gills of mussels which harbour a large female *P. pisum*.

In working on Pinnotheres since October, 1927, a look out had been kept for any possible direct harmful effect of the crab on its host, and it had been noticed that the gills of mussels containing large specimens were sometimes injured, though it has not been found so far that the pea-crab injures the mantle causing the nacreous layer to be dissolved away, as described by Wright (**43**, p. 145). Mussels with injured gills and containing crabs, have been obtained from the River Yealm, the estuaries of the Hamoaze (Saltash), Padstow, and Teignmouth ;

those from the Fal were so commonly abnormal that it was impossible to distinguish abnormality possibly due to the presence of a pea-crab. No careful record of the frequency of injury, however, had been kept until the last two batches of mussels from Padstow were examined. These gave the following results :—

Date. 1929	Total number of mussels.	(a) No. of mussels with large pea-crabs.	No. of gills of (a) affected.	(b) No. of mussels with small pea-crabs.	No. of gills of (b) affected.	Gills abnormal, no crabs present.
June 6	944	88 (crabs with carapace width 9·0–14·0 mm.; eight were accompanied by males)	65 (73·86 %)	85 (crabs with carapace width 1·45–7·25 mm.)	0 (0·0 %)	12 (1·56 %)
Aug. 9	508	34 (crabs with carapace width 8·0–13·0 mm.; three were accompanied by males)	29 (85·29 %)	86 (crabs with carapace width 2·0–7·0 mm.	4 (4·65 %)	3 (·77 %)

Included under gills affected are mussels with (1) gills simply short, (2) gills folded over slightly at the free edge, (3) fusion of filaments, and (4) secondary grooves and folds. It may be pointed out that where gills are abnormal in mussels containing only a small pea-crab or none, there is the possibility that the injury may be due to a previous infection.

A large *Modiolus modiolus* from the Salstone, Salcombe, containing a female *P. pisum*, about 13 mm. carapace width, had not only the gills of both sides injured but also the mantle of one side. In Modiolus, however, the mantle is much thinner than is usual in healthy *Mytilus edulis*, for it appears that in the former the gonad does not encroach on the mantle.

Judging by the usually restricted area of injury—it is extremely rare for the gills of both sides to be damaged—it would seem that large pea-crabs move about very little in a mussel. On opening a mussel they are generally found on one of the inner gills mostly near the base of the foot, but just beyond the reach of the outstretched palps, and backing on the visceral mass. Beneath the crab the inner gill of the infected mussel is often considerably narrower than normal ; sometimes the outer one may also be slightly narrow in this region. The shortness may be restricted to a small semicircular area (Figs. 13, I, p. 937, and 17, I, p. 943), or may extend for almost the entire length of the inner gill (Figs. 7, I, p. 930 ; 20, I, p. 946 ; 22, I, p. 947). In some cases, except for the shortness, the gill appears normal, in others the food groove is very irregular, and a slight folding over of the edge may occur with some fusion to the lamella (Fig. 4) ; in some places a food groove may be entirely absent for a short distance so that food collected posterior

to the break will not reach the oral end of that gill, possibly however at the break food strings will be carried on to the deeper outer gill and reach the palps that way.

In connection with the shortening of the gill there are, in perhaps the majority of cases, to be found small secondary grooves and folds or pockets. They may occur on the inner much shortened gill and on the inner face (descending lamella) of the outer gill, where it is exposed to possible injury by the pea-crab, owing to the shortness of the inner gill (Figs. 12, I, p. 936 ; 17, I, p. 943), but are not always restricted to these areas and may occur on gills of normal depth (Fig. 14, I, p. 938). The secondary grooves vary much in length, a tiny one involving only one grooved filament is shown in Figure 13, II (p. 937), while one 16 mm. long has been seen.

It is thought that these secondary grooves arise in some way as the

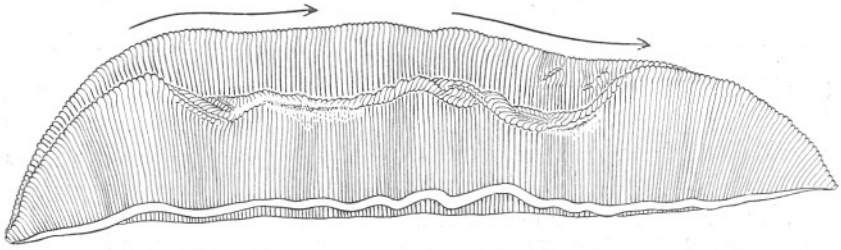


FIG. 4.—View of gills of the right side of a Padstow mussel, which harboured a large ♀ *Pinnotheres pisum*. The inner gill is short for most of its length, the free edge is in part folded over ; in one place a food groove is wanting and considerable fusion of the filaments has occurred, while elsewhere secondary food grooves are present. Three short secondary grooves are present on the descending lamella of the outer gill. The arrows indicate the direction of the current in the main food grooves at the free edges of the gills. Drawn from life. ×2.

result of injury caused by the presence of the pea-crab. A pea-crab is often very difficult to remove from a gill without injury to itself or the gill, as when disturbed it hooks the pointed claw-like tips of its legs well into the gill. Whether the pockets are caused by the pea-crab hooking its claws into the gill and drawing it up into folds, which become permanent, or whether the folds grow as the result of wound stimulus, following a simple tear, can only be determined by experiment. The pockets or folds, however, are permanent. In all those examined it has been found that only the lamella on which the groove occurs is involved in the groove or fold : in some of the folds there is a bend in the non-groove-bearing filament (Figs. 23, p. 948 ; 35, II, p. 963) which seems to point to the possibility that the filaments on which the pocket occurs have been mechanically pulled into a fold, or that growth of the filament in its normal

direction has been restricted or has ceased, while that of the uninjured filament has proceeded normally. In connection with pockets and secondary grooves there is often considerable growth of inter-filamentar junctions, which of course does not occur normally in *Mytilus edulis*. (Cf. *Margaritifera vulgaris* **20**, p. 227, and *Avicula argentea* **38**, p. 155, with ciliated discs and inter-filamentar junctions.) This makes the stripping of such pockets, filament by filament, impossible without careful micro-dissection, which was not attempted, only those with little inter-filamentar growth being examined thoroughly. The two filaments of a fold are not only often strongly connected with each other, but a filament may be connected with one in the opposite lamella other than its pair ; also there may be fusion of filaments side by side. In fact, wherever there is a fold or secondary groove on a gill there is a strong tendency for fusion and inter-filamentar, as well as inter-lamellar, growth to occur, especially in pockets the filaments of which are somewhat askew.

In some instances it would seem that originally deep pockets have become fused with the main lamella, little more than the secondary groove remaining, along with a greater width of the filaments and a greater number of ciliated discs for a certain distance dorsal to the secondary groove, to indicate what has occurred. Stages in this possible process are shown in Figures 5, I–II ; 26 (p. 950) ; and 5, III. In Figure 5, I, the pocket is distinct, in Figure 5, II, the two contiguous filaments, one belonging to the main lamella and the inner one of the secondary pocket, have fused for a certain distance so that it appears that there are three filaments. In Figure 26 (p. 950) the fusion has gone a step further, and in Figure 5, III, there are only two filaments, except for a short distance, but by the structure it may be seen that the part of the filament which is dorsal to the secondary groove is formed by the fusion of filaments. This type of pocket will be referred to again in connection with its ciliation.

The cavity of pockets has always been found to face toward the free edge of the gill, but when the secondary groove is carried on only a slight elevation of the lamella it has been noticed, once or twice, that there may be a slight tendency for the process to slope dorsally (Figs. 3, p. 922) ; 22, II, p. 947).

When a secondary groove occurs very near the main groove it is often found joining the latter at one end, and that most usually the anterior end. In Figure 35, I (p. 963), however, a secondary groove is shown which joined the main groove and then diverged. Secondary grooves near the main groove may very occasionally join the latter at both ends.

In secondary grooves on the surface of the gill one or two filaments at either end of the groove are usually raised into a projection in continuation of the groove (Fig. 10, II, p. 934), though rarely the secondary groove

FIG. 5.—Lateral views of living filaments, bearing secondary grooves and folds, from four specimens of Mytilus from Padstow. The direction of beat of the frontal cilia is shown by arrows; heavier arrows are used when the direction is the reverse of normal. × ca. 9.

I. Filament from a deep fold or pocket on the ascending lamella of a left inner gill. The fold was near the posterior end of the gill, near the posterior adductor muscle.

II. Filament from a fold on the ascending lamella, inner gill of a Mytilus, which did not harbour a pea-crab. The fusion of adjacent parts of the filament has caused partial obliteration of the fold.

III. Filament from an outer left gill with secondary food grooves on the descending and ascending portions of the filament. That on the ascending filament (to the right) was apparently originally at the edge of a deep fold, but almost complete fusion of the filaments forming the fold has taken place.

IV. Filament from a left inner gill with secondary folds on the descending and ascending parts of the filament.

begins and ends abruptly, the preceding and following filaments being perfectly normal.

Gills have very occasionally been found with secondary grooves on the descending and ascending lamellæ of the same gill, a certain number of filaments being common to both (Fig. 5, III–IV, p. 926). Two secondary grooves one above the other on the same lamella are shown in Figures 20 (p. 946) and 22 (p. 947), while in Figure 3 (p. 922) several occur in series across the depth of the gill.

General Ciliation of Filaments Bearing Secondary Grooves.

Gills bearing a secondary groove show, over a certain area of the lamella between the main and the secondary groove, in the majority of cases, a reversal in the direction of food transportation caused by a reversal of the frontal cilia. Food particles drawn on to the gill surface instead of passing in the normal direction towards the main groove at the ventral edge of the gill, for a certain distance ventral to the secondary groove pass in a reversed direction into the secondary groove (see Fig. 9, I, p. 932). (For the ciliation and currents on the gill of *Mytilus edulis* see Orton, **29**.)

In the secondary groove the food current is always in the same direction as that of the main groove, that is towards the oral end of the gill. In secondary grooves, which do not join the main groove at their anterior end, particles debouching on the first filament with normal ciliation are carried along it into the main groove. Secondary food grooves on a gill therefore interfere little, if at all, with the efficient working of the gill.

There is not the slightest doubt of the fact of the permanent reversal of the frontal cilia. In all cases stripped filaments were examined at a magnification of 280 or 506 diameters and in many cases the reversal of the current was also demonstrated by carmine particles.

The frontal cilia on the gill filaments of Mytilus are brought to rest at the beginning of their preparatory stroke by increase in osmotic pressure (see Gray, **18**, **19**, p. 54). Presumably owing to increase in osmotic pressure, due to increasing salinity in a preparation by evaporation on a slide, the frontal cilia were found to come to rest at the beginning of their preparatory stroke; it was then seen very clearly that those on either side of the line at which reversal occurs were lying in opposite directions. This would appear to be evidence in favour of the effective stroke being reversed. Gray (**19**, p. 63) remarks that: "It is difficult to imagine how the frontal cilia of *Mytilus*, . . ., could perform any appreciable amount of work during their recovery strokes; but if a cilium is of such a type that there is not much difference between the form of the two strokes it is conceivable that the nett effect of the beat could be reversed

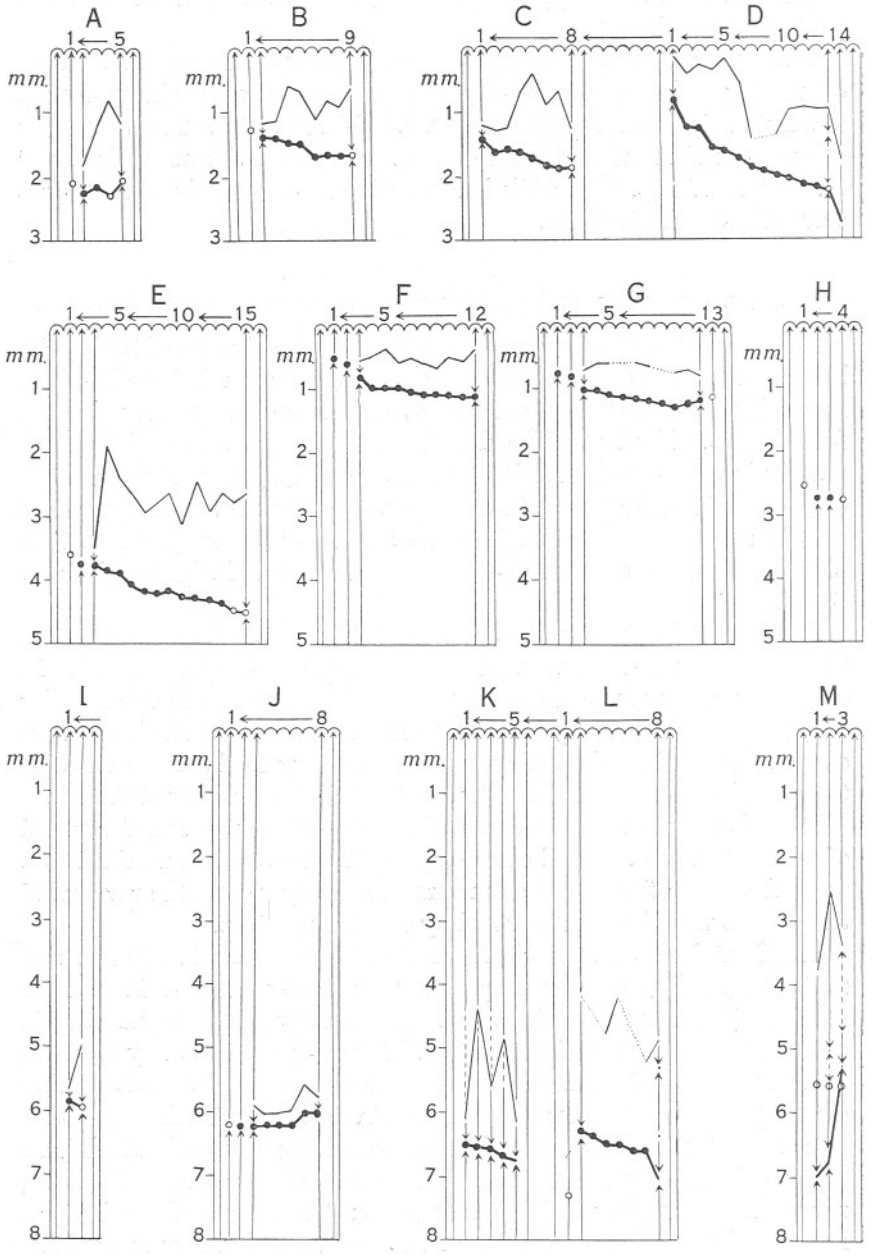


FIG. 6 (description opposite).

by quickening the recovery stroke and slowing the effective stroke as appears to be the case in some protozoa." Parker (**31**, p. 12) suggested that the reversal of Metridium cilia was effected by a system of flexor and extensor elements, placed on the opposite sides of a supporting axis, and his view was elaborated by Williams (**42**).

In *Mytilus edulis*, as in Metridium (**31**, p. 9), the metachronal wave is reversed with the reversal of beat of the frontal cilia.

When the surface of a gill bearing a secondary groove was supplied with carmine particles it was seen that the point of division was by no means always at the same level, or nearly the same level, on adjacent filaments, but as it was thought at first that there might be a simple or direct relation between the influence of the main and the secondary groove, it was decided to strip parts of gills bearing secondary grooves of as many types as possible, to measure the distance from the main groove at which reversal of the beat of the frontals occurred, and to plot the results as a graph.* The results show that if there is a relation between the influence of the main and the secondary groove it is by no means simple : it also appears as though the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella, rather than that the ciliation of each filament is effected only by its own supernumerary groove.

LEGEND FOR FIGURE 6.

FIG. 6.—Graphs showing the relation of the distance of a secondary groove—set directly on the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The filaments are numbered antero-posteriorly ; arrows between the numbers show the direction of the current in the main groove. Distance from the main groove is shown in mm. Semicircles ⌒ denote the main food groove at the free edge of the gill. Filled-in circles ● denote a well-formed secondary groove on a filament. Circles o denote a slight groove or a projection of the frontal surface of a filament. When a projection bears cilia beating anteriorly, the arrow showing the direction of beat of the frontal cilia stops dorsal to the projection and begins again ventral to it ; when the projection is clothed with short frontal cilia beating ventrally, there is no break.

A broken arrow — — —> is used in those instances where the direction of beat of the frontals was somewhat erratic, but the direction of the current was mainly as indicated. A double-headed and broken arrow <— — —> is used when particles at different times passed in opposite directions.

Inner right or left direct or descending lamella = R2 or L2.
Inner right or left reflected or ascending lamella = R1 or L1.
Outer right or left direct or descending lamella = R3 or L3.
Outer right or left reflected or ascending lamella = R4 or L4.

A was on R3, B „ R3, C „ R3, D „ R3 } of one Mytilus.

E was on L3, F „ L3, G „ L3, H „ L3 } of different specimens of Mytilus.

F „ L3, G „ L3, H „ L3 } of one Mytilus.

I was on R1, J „ R1 } of a *Modiolus modiolus*.

K was on R1, L „ R1, M „ R1 } of one Mytilus.

* The measurements were made with a Leitz eye-piece micrometer, No. 2 eye-piece, and a No. 3 objective.

The basis of these observations is given in the following detailed description :—

Ciliation of Filaments Bearing Secondary Grooves Set Directly on the Face of the Lamella.

Graphs of the change of ciliary current on the filaments comprising a series of short secondary grooves, in which the groove is set directly on

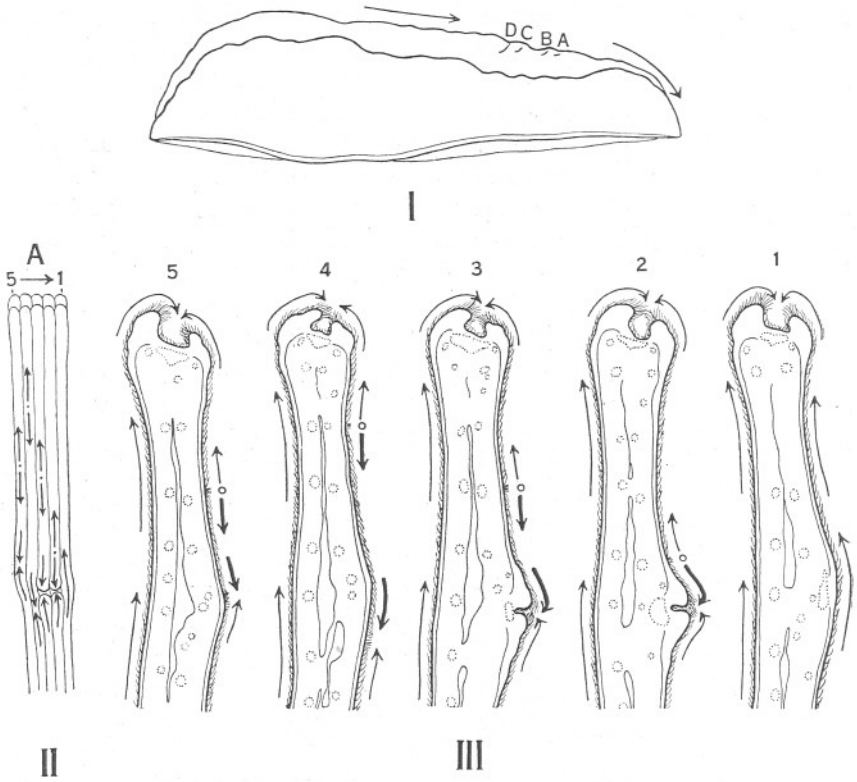


Fig. 7.—I. Sketch of gills of the right side of an infected Mytilus to show the position of the secondary food grooves A–D. The arrows indicate the direction of the current in the main food groves. From life, natural size.

II. Surface view of filaments composing secondary groove A with arrows showing the direction of beat of the frontal cilia. The filaments involved are numbered antero-posteriorly—this order is adhered to in all the figures—and the arrows between the numbers show the direction of the current in the main groove. All figures of surface views, unless otherwise stated, have been constructed from sketches and measurements.

III. Lateral views of single living filaments composing secondary groove A, showing the direction of beat of the frontal cilia. The outline of the filaments, in this and all figures, was traced by the aid of camera lucida. The fine inner line indicates the distribution of the latero-frontal and lateral cilia. The arrows show the direction of beat of the frontal cilia ; heavier arrows are used when the direction is the reverse of normal. I–II × 18¼.

the frontal face of the filament, are shown in Figure 6 (p. 928). The filaments are numbered antero-posteriorly, and where necessary have been so arranged that the first filament is always on the left (in the graphs) from which it follows that the direction of the current in the main and secondary grooves is from right to left.

The graphs in Figure 6, A, B, C and D, are of secondary grooves forming a series on the descending lamella of the right, outer gill of one mussel (Fig. 7, I) where the shortness of the inner gill exposed it to injury by the pea-crab. They were near the main food groove—within 3·0 mm.—and towards the anterior end of the gill.

The secondary groove A (Fig. 7, II), that nearest the anterior end of the

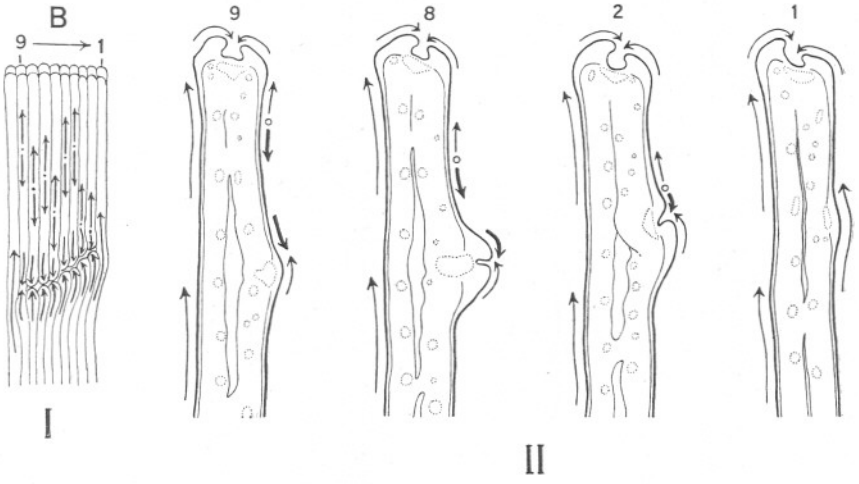


FIG. 8.—I. Surface view of filaments composing the secondary groove B (see Fig. 7, I).
II. Lateral views of representative living filaments. I–II × 18¼.

gill, was composed of only two grooved filaments and all the filaments involved in the abnormality have been drawn (Fig. 7, III). The filament (Fig. 7, III, filament 1) preceding the first grooved filament was nearly normal, there was a break in the rows of latero-frontal and lateral cilia where there was a large elongated ciliated disc, but the length and direction of beat of the frontals was normal. The first grooved filament (Fig. 7, III, filament 2) had a change of ciliary current very near the secondary groove ; in the second grooved filament the change occurred further from the secondary groove. The following filament though practically normal in structure had a change in the direction of the beat of the frontals which was here only 0·82 mm. from the main groove : filament 5 was similar, but the change was 1·2 mm. from the main groove. On both these filaments the cilia at the point of meeting of the currents

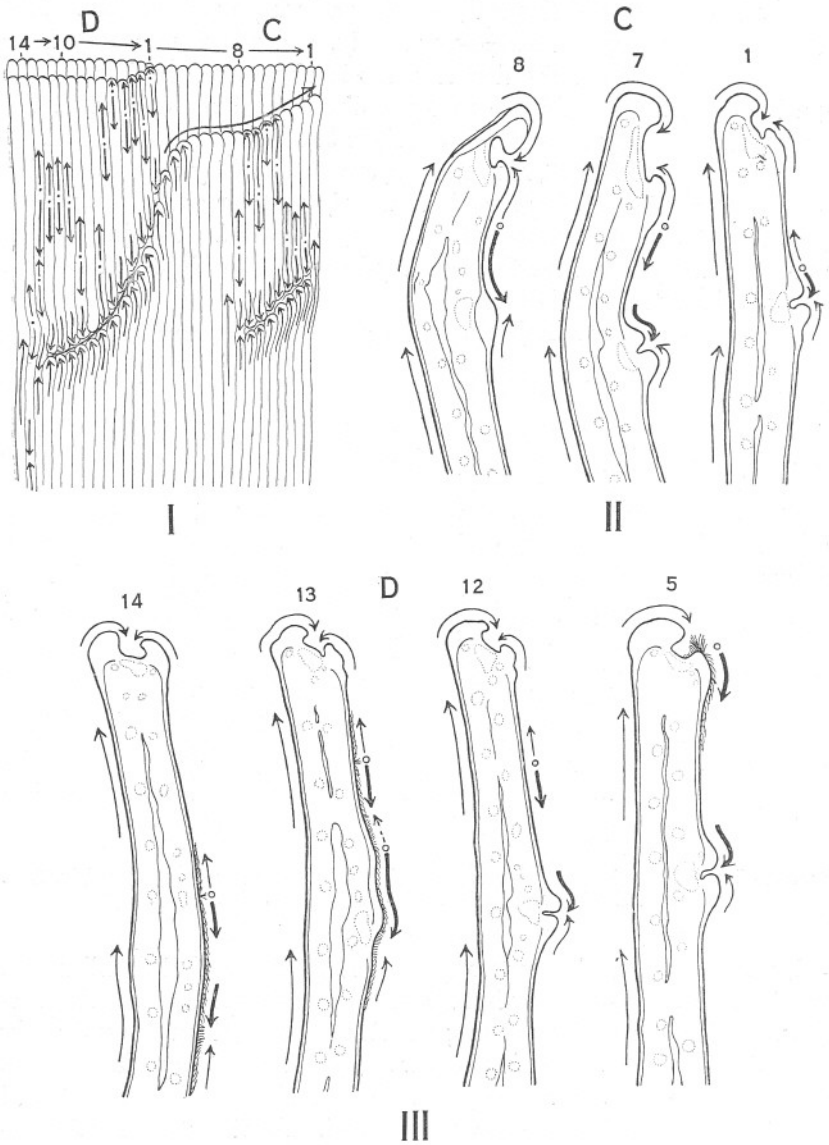


FIG. 9.—Secondary grooves C and D of the gill sketched in Fig. 7, I × 18½.

I. Surface view of filaments composing the secondary grooves. Owing to the accidental crushing of filament 8 of D, the point of reversal of the frontal cilia could not be determined.

II. Lateral views of representative living filaments of secondary groove C.

III. Lateral views of representative living filaments of secondary groove D. The broken arrow denotes a stretch with cilia uneven in appearance, though the current was in the direction indicated. On filament 5 an arrow, which should have pointed into the main grove, has been omitted.

were of the normal length of frontal cilia, but the direction of their beat was towards the anterior end of the gill, that is at right angles to their normal direction. The following filaments were normal in structure and ciliation.

Secondary groove B (Fig. 8, I), next in the series, was composed of seven grooved filaments and sloped slightly towards the main groove anteriorly. The filament (Fig. 8, II, filament 1) preceding the first grooved one was slightly abnormal in structure, but the direction of beat of the frontals was normal. The first and last grooved filaments only are figured (Fig. 8, II, filaments 2 and 8). The frontal surface of the filament following the last grooved one was raised into a slight projection in continuation of the secondary groove, and there was a break in the rows of latero-frontal and lateral cilia ; the reversal of the frontal cilia was only 0·61 mm. from the *main* groove. The next filament was normal both in structure and ciliation.

Secondary grooves C and D (Fig. 9, I) were separated by only seven filaments. In both grooves the slope anteriorly towards the main groove was noticeable, D actually joining the main groove, the sides of which were here very unequal. The filament preceding the first grooved filament of C was normal in structure and ciliation. The point of reversal of the frontals was close to the secondary groove on the first grooved filament (Fig. 9, II) ; it was nearest to the main groove on the fifth filament. Filament 8 following the last grooved filament, although possessing no groove, only a raised area, showed a change in beat of the frontal cilia. The frontal cilia on the projection, where the ciliary currents met, were of normal length but were beating anteriorly. The following filament was normal in structure and ciliation. Filaments from secondary groove D are shown in Figure 9, III. The fact that a reversal of beat occurred on filament 1 (Fig. 9, I), which is unusual, may perhaps be due to the main groove anterior to this filament being very unequally sided, and therefore possibly continuing the influence of the secondary groove. Filament 13 (Fig. 9, III), although grooveless, had two changes in ciliary beat ; the part marked with a broken arrow was rather uneven in beat. Filament 14 was structurally normal, yet had a reversal of the frontal cilia 1·8 mm. from the main groove. On both these filaments the frontal cilia at the meeting of the currents were of normal length, but the direction of their beat was towards the anterior end of the gill. The following filament was normal in structure and ciliation. Filament 8 in groove D could not be measured as it was inadvertently crushed.

Figure 10, I, is a surface view of a secondary groove (E) on the descending lamella of a left outer gill, where it was exposed owing to the shortness of the inner gill. It was between 3·6 mm. and 4·5 mm. from the main groove and sloped slightly ventralwards anteriorly. Figure 6, E (p. 928), is

the graph of this groove and separate filaments are shown in Figure 10, II. The first grooved filament showed no change in beat of the frontals; there was just the break caused by the groove with its long terminal cilia. The filament (Fig. 10, II, filament 14) following the last grooved filament had a distinct projection of its frontal surface, carrying long cilia beating

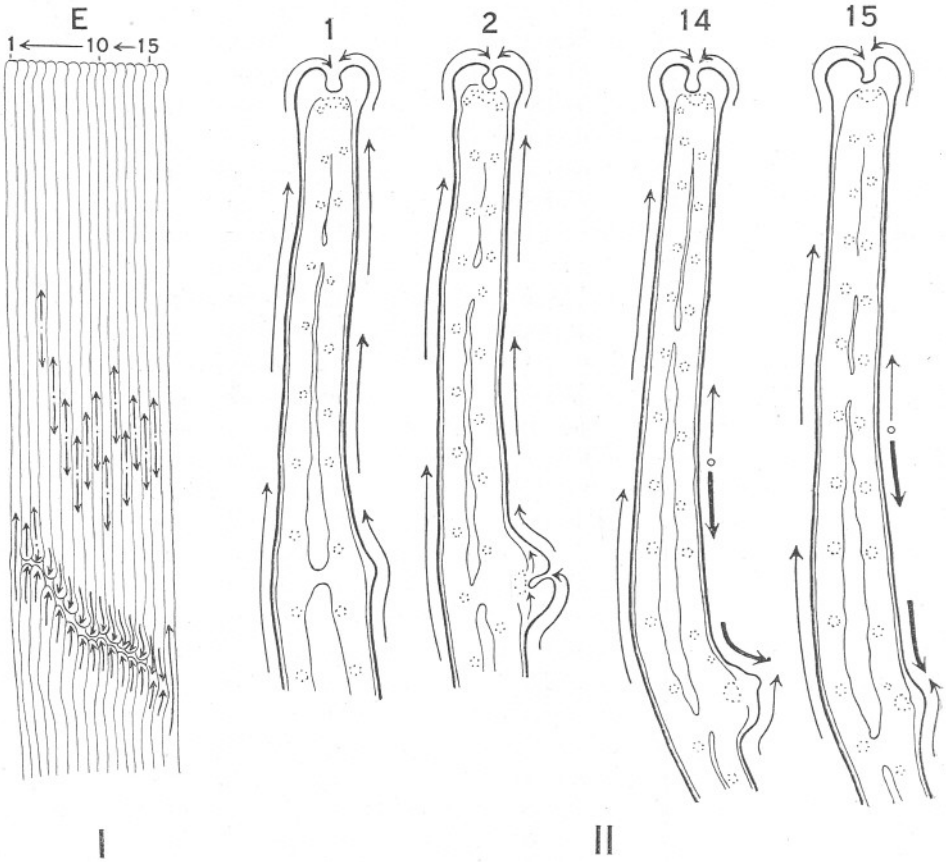


FIG. 10.—I. Surface view of filaments composing a secondary groove (E) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of certain of the living filaments.
I–II × ca. 18¼.

anteriorly, in continuation of the secondary groove, and reversal of ciliary current occurred. Filament 15 had a very slight projection and yet ciliary reversal again occurred: the following one was altogether normal. This secondary groove shows in a definite way the tendency, which is evident from most of the graphs, for the reversal of beat of the frontal cilia to occur nearer the secondary groove at the anterior than at the posterior

end, and that while a grooved filament at the anterior end of a secondary groove may have no reversal of ciliary current, at the opposite end filaments almost normal or normal in structure may yet have ciliary reversal.

Figure 11, I, is the surface view of a short secondary groove (F) on the descending lamella of a left outer gill, exposed by the shortness of the inner gill, and which at the anterior end joined the main groove. No change of beat of the frontal cilia occurred until the third grooved filament and none occurred on that following the last grooved filament (Figs. 6, F, p. 928 ; 11, I–II) ; this filament was slightly bent permanently, as were also the next few in the series.

Figure 12, I, is a rough sketch of the two left gills of a mussel with several short secondary grooves on the descending lamella of the outer

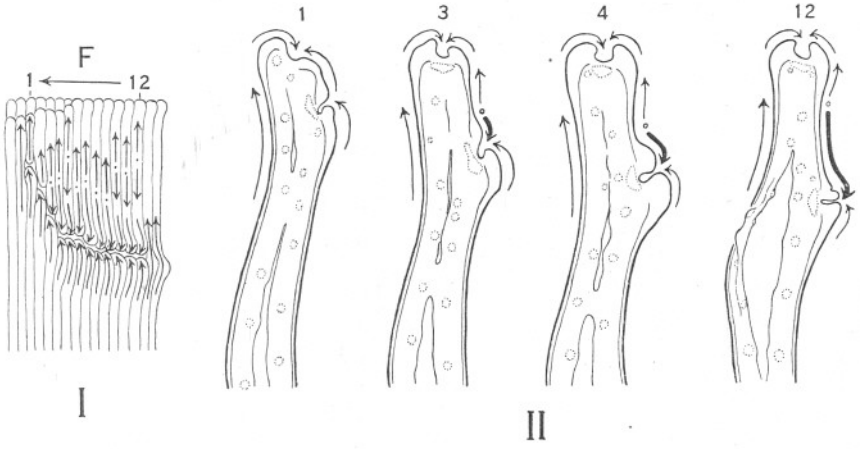


FIG. 11.—I. Surface view of filaments composing a secondary groove (F) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of representative living filaments.
I–II × 18¼.

gill. That nearest the anterior end of the gill was composed of twelve grooved filaments (Figs. 6, G, p. 928 ; 12, II) ; it was difficult to strip, as many inter-filamentar connections occurred near the secondary groove, holding several filaments together. Apparently no change occurred—but this is a little doubtful as the first two filaments stuck together—until the third grooved filament (Fig. 12, III, filament 3). The last, though slightly grooved, had no ciliary change, and the cilia clothing the groove were short and were beating ventrally.

On the same gill three tiny incipient grooves occurred in series. That marked H in Figure 12, I, is shown in surface view in Figure 12, IV, and its graph in Figure 6, H (p. 928). The two grooved filaments (one shown in Fig. 12, V) showed no ciliary reversal, only the groove with its long

terminal cilia interrupting the food current. It is interesting to compare this secondary groove with that composed of the same number of grooved filaments of Figures 6, A (p. 928), and 7, I–III (p. 930). The filaments of the remaining two tiny secondary grooves, of about four and six

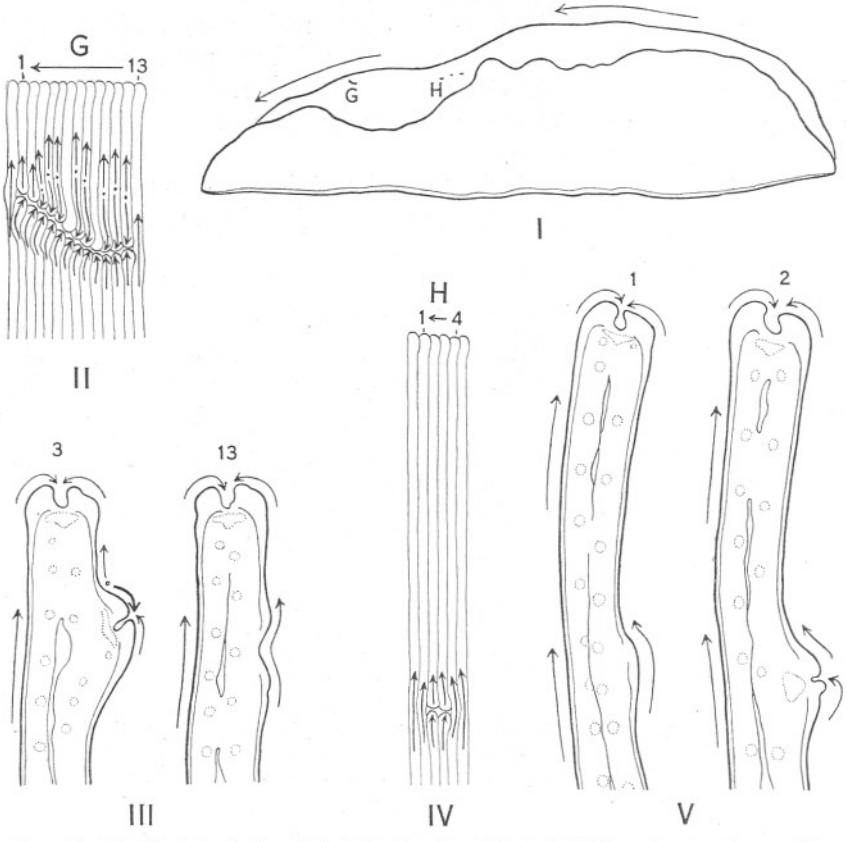


FIG. 12.—I. Sketch of gills of the left side of an infected Mytilus, showing the position of secondary grooves (those investigated are lettered) on the descending lamella of the outer gill where it was exposed owing to the shortness of the inner gill. From life.

II. Surface view of filaments composing secondary groove G. Owing to the fusion of filaments the point of reversal of beat of the frontal cilia on filaments 6 and 9 could not be determined.

III. Lateral views of two living filaments of secondary groove G.

IV. Surface view of filaments composing secondary groove H.

V. Lateral views of two living filaments of secondary groove H.

II–V × 18¼.

filaments respectively, were mostly like the first filament of group H (Fig. 12, V), though some were slightly grooved; there was no reversal of beat of the frontal cilia.

The gills of a *Modiolus modiolus* containing a pea-crab were found to be

affected ; those on the right (Fig. 13, I) more than those on the left. The inner right gill was very short in a small V-shaped area, with several short secondary grooves and some crumpling of the filaments near the

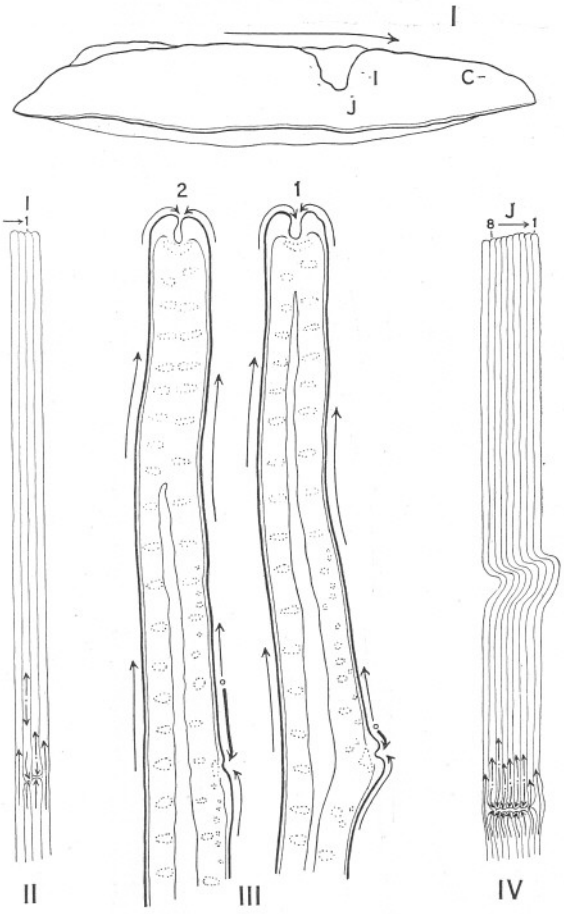


FIG. 13.—I. Sketch of gills of the right side of a specimen of *Modiolus modiolus*, which harboured a large female Pinnotheres, showing shortness of the inner gill in a small V-shaped area and several secondary grooves : those investigated are lettered ; I and J are on the ascending lamella of the inner gill, and C indicates the position of a secondary groove on the ascending lamella of the outer gill. Drawn from life. $\times \frac{2}{3}$

II. Surface view of filaments composing secondary groove I.

III. Lateral views of the two filaments composing secondary groove I.

IV. Surface view of filaments composing secondary groove J.

II–IV $\times$ ca. 12.

edge ; the crumpling made the filaments very difficult to strip, as where it occurs there is generally considerable fusion of the filaments side by side. (In the normal gill of *Modiolus modiolus*, as in that of *Mytilus*

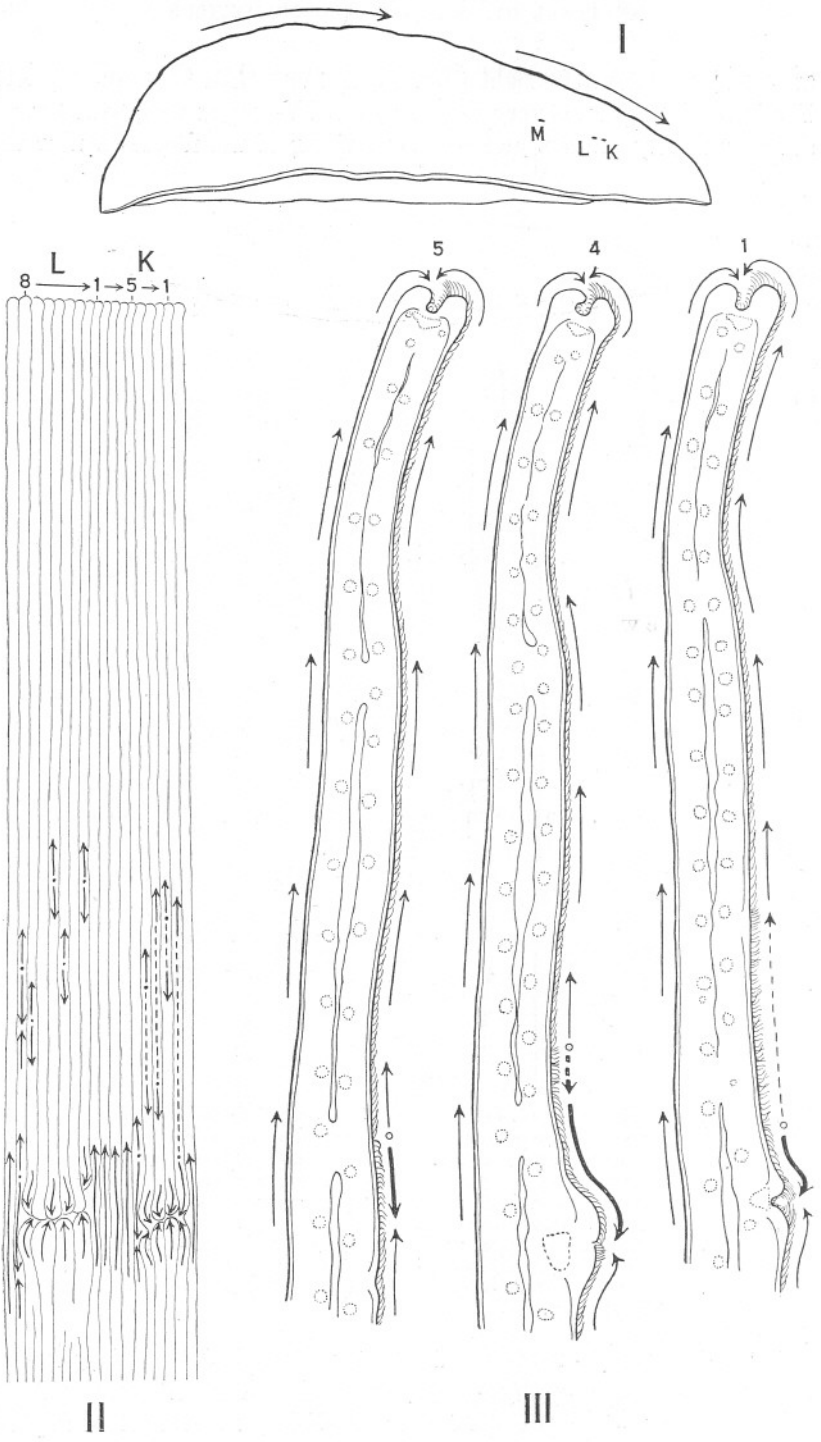


FIG. 14 (description opposite).

edulis,* there are no organic inter-filamentar connections, only ciliary junctions, and in the former most of the filaments have no inter-lamellar junctions, but an occasional filament has an inter-lamellar septum ; the septa vary in height.) In secondary groove I (Figs. 6, I, p. 928 ; 13, I and II) with only one grooved filament, that preceding the grooved one was normal in structure—except for a few extra ciliated discs—and ciliation. On the grooved filament (Fig. 13, III, filament 1) there was ciliary change very near the secondary groove : filament 2 with only a slight groove, which did not bear long terminal cilia, had reversal about 0·95 mm. from it. The following filament was normal except for a few extra ciliated discs. This secondary groove of one grooved filament would seem to show that the influence of the groove is by no means confined to the filament on which it occurs.

Measurements of the filaments forming the secondary groove J (Fig. 13, I) were difficult to obtain as ventral to the supernumerary groove they were permanently bent. The groove was of the same type as the previous one and the approximate changes in direction of the food current are shown in surface view (Fig. 13, IV) and in the graph (Fig. 6, J, p. 928). No ciliary reversal occurred until the second grooved filament and then was very near the secondary groove. This secondary groove shows the very unusual feature of the occurrence of the point of reversal on the last grooved filament very near (0·25 mm. from) the secondary groove. The frontal cilia on the following filament beat normally. Other secondary grooves—but of another type—on the gills of this specimen of Modiolus will be described later.

The division-line between the cilia beating in opposite directions is mostly definite and clear, with usually a few cilia beating in no definite direction. The three secondary grooves, therefore, on the right inner gill sketched in Figure 14, I, are of special interest in that certain filaments

LEGEND FOR FIGURE 14.

FIG. 14.—I. Sketch of right inner gill of an infected Mytilus, showing the position of three small secondary grooves K, L, and M on the ascending lamella. From life, natural size.

II. Surface view of filaments composing secondary grooves L and K. The broken arrows denote stretches over which the direction of beat of the frontal cilia was somewhat uncertain, but was mainly in the direction indicated. Note the fusion of certain filaments dorsal to the secondary groove L ; owing to the fusion the point of reversal of beat of the frontal cilia could not be determined on filaments 3 and 6.

III. Lateral views of three living filaments from secondary groove K. The small area with broken outline near the secondary groove of filament 4 denotes an area of fusion with the next filament.
II–III × 18¼.

* The difference between Modiolus and Mytilus in the shape of the ciliated discs might be noted (cf. Figs. 13 III and 12 III and V) and the possibility of the use of this character in taxonomy.

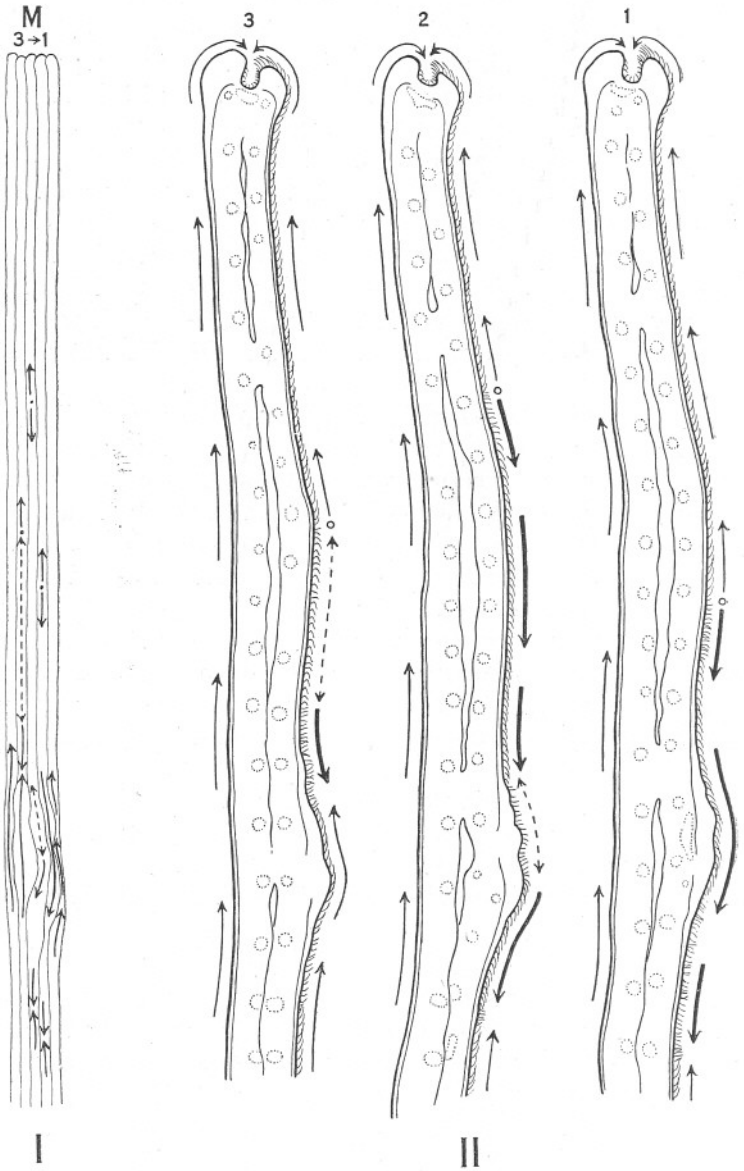


FIG. 15.—I. Surface view of filaments composing the region of enlarged filaments M (see Fig. 14 I). The double-headed arrows indicate stretches over which the current caused by the frontal cilia passed at different times in opposite directions.
II. Lateral views of three living filaments of this region.
I–II × 18¼.

from them showed a considerable area over which the frontals appeared to be somewhat uncertain in the direction of their beat. The cilia of these areas had a rough appearance and, when the separate filaments were supplied with powdered carmine, particles were first drawn on to the frontal surface, then flew off, though there was a general tendency for particles to travel in one direction or the other. The supernumerary grooves K and L (Fig. 14, II) which were between 6·0 mm. and 7·0 mm. from the main groove were separated by only four filaments of normal ciliation. The first grooved filament of K, preceded by a normal one, had a stretch of rough-looking cilia between 4·45 mm. and 6·15 mm. from the main groove over which the general direction of the ciliary current was towards the main groove (Fig. 14, III). The second grooved one had a similar stretch, between 4·4 mm. and 4·75 mm. from the main groove, but the direction of particles was chiefly towards the secondary groove. In filament 3 the corresponding area of irregularity was between 4·45 mm. and 5·6 mm. and the direction of the current was chiefly towards the main groove. Filament 4 was slightly grooved; the stretch of irregular cilia was between 4·9 mm. and 5·6 mm. (Fig. 14, III). The following filament (Fig. 14, III, filament 5) was practically normal in structure, though ciliary reversal occurred between 6·15 mm. and 6·75 mm. from the main groove; the cilia over this stretch were somewhat rough in appearance, but the direction of the ciliary current demonstrated by the movement of carmine particles was definitely in the reverse direction to the normal. The filaments in this supernumerary groove stripped singly with ease, those forming groove L, however, stuck badly owing to some fusion just dorsal to the groove (Fig. 14, II) and it was impossible to tell whether there were stretches of uncertain beating. Filament 1 came off singly; there was no reversal of current, the frontal cilia, however, appeared to be absent, or almost so, for a short distance (between 5·55 mm. and 6·75 mm. from the main groove) and particles collected dorsal to this stretch. The next six filaments tore off in two groups of three; the line of division between cilia beating in the normal and in the reversed direction was at 4·2 mm. and 4·8 mm., and 4·2 mm. and 5·2 mm. respectively from the main groove on the outer filaments of the two groups. The last filament, which stripped off singly, is of much interest; although structurally normal two changes of ciliary current occurred (Figs. 6, L, p. 928; 14, II).

The group of filaments M (Fig. 15, I) could not be termed grooved and the elevations of the frontal surfaces did not bear long terminal cilia. In the first two filaments (Fig. 15, II) the area of reversal extended for some short distance dorsal to the abnormal region as though independent of it. On filament 2 for a short distance, between 5·1 and 5·6 mm. from the main groove, there was a tendency for particles to fly off the surface

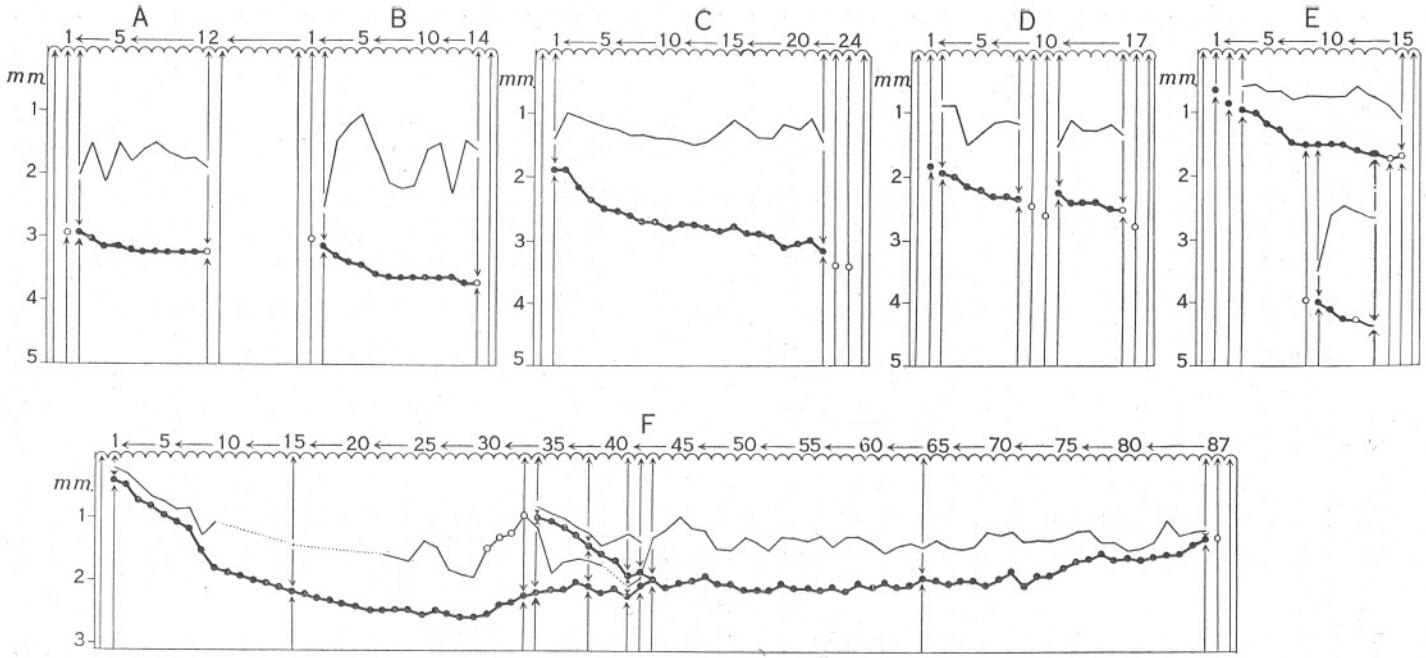


FIG. 16.—Graphs showing the relation of the distance of a secondary groove—raised on a slight projection above the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The signs used are as in Fig. 6, p. 928.

A and B were on L3 of one Mytilus.
C was on R4 } of one specimen of *Modiolus modiolus*.
D ,, L4 }
E ,, L1 } of different specimens of Mytilus.
F ,, L3 }

of the filament, but they occasionally passed first in one direction, then in the other. Between 3·4 mm. and 4·75 mm. from the main groove on filament 3 although particles mostly passed dorsally, at times they passed up and down. On all three filaments there were small stretches over which the cilia looked irregular in appearance, but particles passed more or less

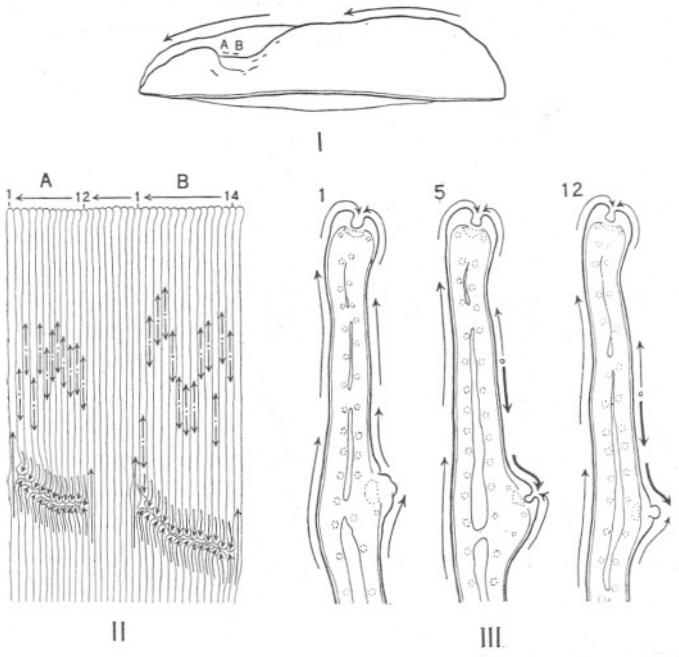


FIG. 17.—I. Sketch of gills of the left side of an infected Mytilus, showing shortness of the inner gill and several secondary food grooves. The two investigated, A and B, are on the descending lamella of the outer gill where it is exposed owing to the shortness of the inner gill. From life, $\times \frac{2}{3}$.
II. Surface view of filaments composing secondary grooves A and B.
III. Lateral views of three living filaments from secondary groove A.
II–III × ca. 12.

definitely in one direction. This apparent uncertainty in the direction of beat of the frontal cilia, over a short length of the filament between two areas in which cilia are definitely beating in opposite directions, is suggestive of the irregularity in beat during ciliary reversal of amphibian embryos described by Twitty (**40**, p. 331), and the impression obtained from the secondary grooves on this gill was that the reversal was unsettled.

Ciliation of Filaments Bearing Secondary Grooves Raised somewhat above the Surface of the Lamella.

In the group of graphs given in Figure 16 have been included those secondary grooves which show slightly more structural alteration of the filaments.

The secondary grooves A and B (Fig. 17, I) on the descending lamella of the left outer gill of a mussel, where it was exposed owing to the

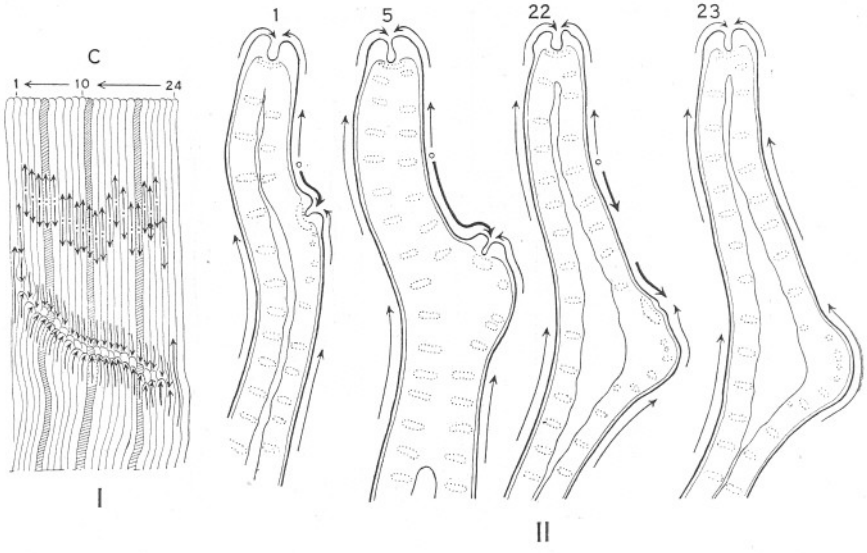


Fig. 18.—*Modiolus modiolus*.

I. Surface view of filaments composing the secondary groove C (see Fig. 13 I, p. 937).
The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.
I–II× ca. 12.

shortness of the inner gill, were separated by only seven normal filaments ; they both showed the characteristic ventral slope anteriorly (Fig. 17, II) and in both the filaments were slightly widened—from frontal to abfrontal surface—beneath the secondary grooves (Fig. 17, III, filament 5). Ciliary reversal occurred on the first grooved filament of A (Fig. 17, I and II, filament 2) ; the preceding one—although having long terminal cilia beating anteriorly—had no reversal (Fig. 17, III, filament 1), on the other hand, reversal occurred on a very similar filament (Fig. 17, III, filament 12) following the last grooved one. The appearance and ciliation of groove B may be gathered from Figures 16 and 17, II.

Two supernumerary grooves of a similar type were present on the gills

of the specimen of Modiolus previously mentioned. The position of groove C on the ascending lamella of the outer right gill is indicated in the sketch in Figure 13, I, p. 937. Groove D was in a similar position on the ascending lamella of the outer left gill. The form of the secondary groove C and the ciliation of the filaments may be gathered from the surface view of the entire groove (Fig. 18, I), the representative separate filaments (Fig. 18, II) and the graph (Fig. 16, C, p. 942). The filament preceding the first grooved one was normal in structure and ciliation.

In groove D ciliary reversal did not occur until the first well-grooved

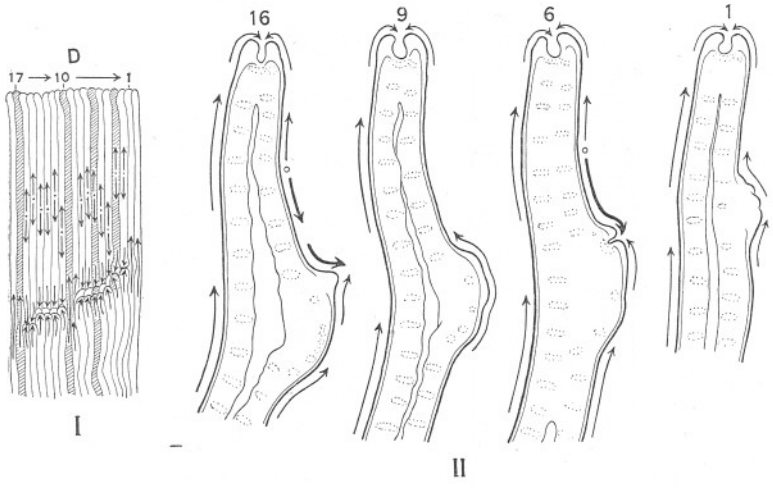


FIG. 19.—*Modiolus modiolus.*

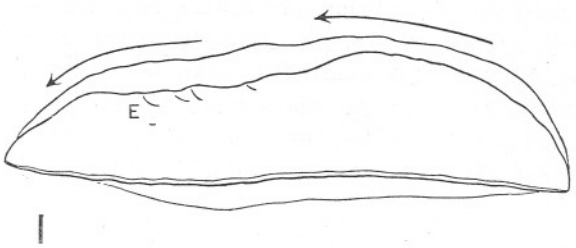
I. Surface view of filaments composing secondary groove D. This was on the ascending lamella of the outer left gill in a similar position to that of secondary groove C on the right gill (see Fig. 13 I, p. 937). The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.

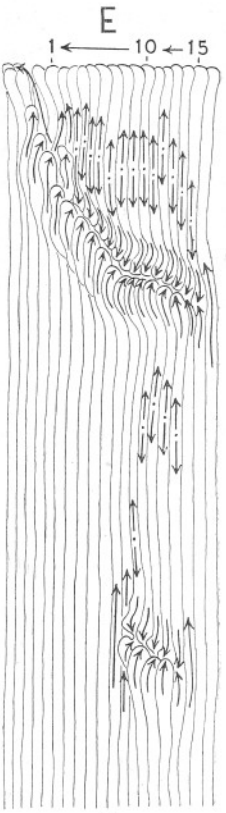
I–II × ca. 12.

filament, although the previous one had long terminal cilia, beating anteriorly, on a projection which was slightly grooved (Fig. 19, II, filament 1). Two grooveless filaments, but with a projection of the frontal surface, occurred between the eighth and eleventh filaments and most unexpectedly there was no reversal of stroke of the cilia on these ; they were very similar in structure and one is shown in Figure 19, II, filament 9. Figures 19, I–II, and 16, D (p. 942), sufficiently indicate the structure and ciliation of this groove.

Gills which have secondary grooves one above the other involving the same filaments would appear to have a possibility of as many changes of ciliary current as there are secondary grooves. In a gill with two secondary grooves one above the other (Figs. 20, I–II ; 16, E, p. 942) reversal occurred



I



II

FIG. 20.—I. Sketch of left gills of a Mytilus showing secondary grooves. The two, one above the other (E), were investigated. From life, natural size.

II. Surface view of filaments composing the secondary grooves. × ca. 18¼.

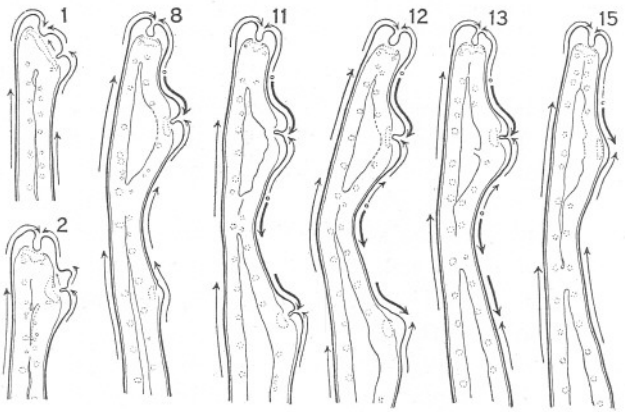


FIG. 21.—Lateral views of certain of the living filaments from the secondary grooves E (see Fig. 20). × ca. 9.

on certain filaments between them, as well as between the main groove and the more ventral secondary groove. The ventral and longer of the two grooves joined the main groove at the anterior end; the tiny—more dorsal one—also sloped in the same direction. In the longer secondary groove no ciliary change occurred until the third grooved filament, while beyond the opposite end of the groove it occurred on filaments 14 and 15, which had merely a projection of the frontal surface (Fig. 21, filament 15). In the tiny more dorsal groove reversal of stroke occurred on the first

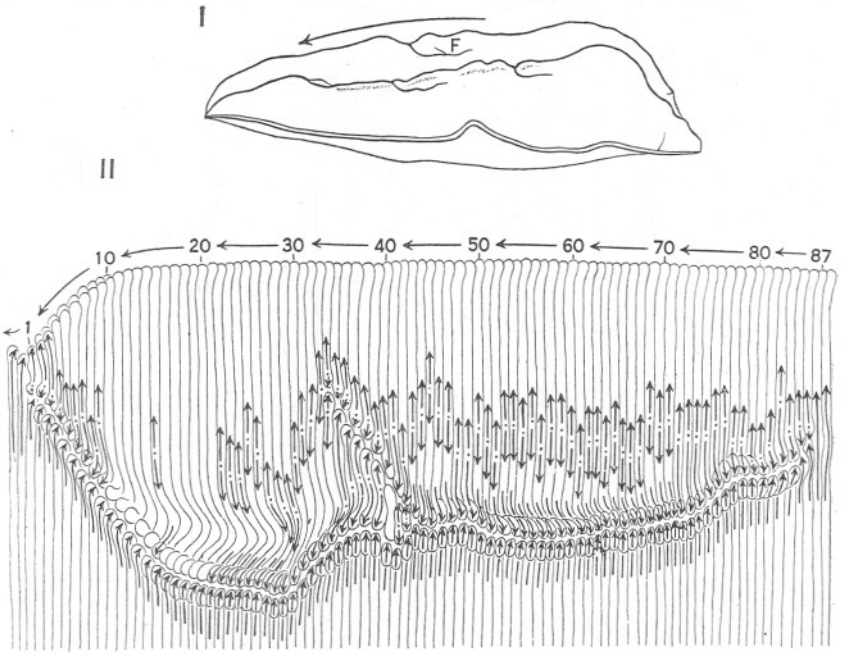


FIG. 22.—I. Sketch of left gills of an infected Mytilus, showing secondary grooves; that marked F was investigated. The stippling indicates abnormally heavy pigmentation. From life, natural size.

II. Surface view of filaments composing the secondary groove. Owing to fusion of certain of the filaments the point of reversal of beat of the frontal cilia could not be determined for filaments 10–14, 16–21, and 40. × ca. 18¼.

grooved filament and at the opposite end occurred not only on filament 12, which had a projection bearing long terminal cilia beating anteriorly, but also on the following one (Fig. 21, filament 13), which was normal so far as this secondary groove was concerned.

A long secondary groove involving 87 filaments and joining the main groove anteriorly had, roughly about the middle of its length, a short secondary groove leading from it (Fig. 22, I–II). The chief secondary groove was borne on a slight projection of the lamella, which over parts

of the groove faced dorsally, and is in this respect rather unusual. The filaments of this secondary groove stripped on the whole easily, but as will be seen from the graph (Fig. 16, F, p. 942) filaments 10 to 14 and 16 to 21 pulled off together ; a few others also gave trouble. It is interesting to compare filaments 33 and 34 (Fig. 23) ; on the former a division of the ciliary current occurs at the slight groove, while on the latter at about the same position two currents meet in the definite groove. The filaments composing this secondary groove showed a tendency for the non-groove-bearing ones (the ascending filaments) to be longer than those (the

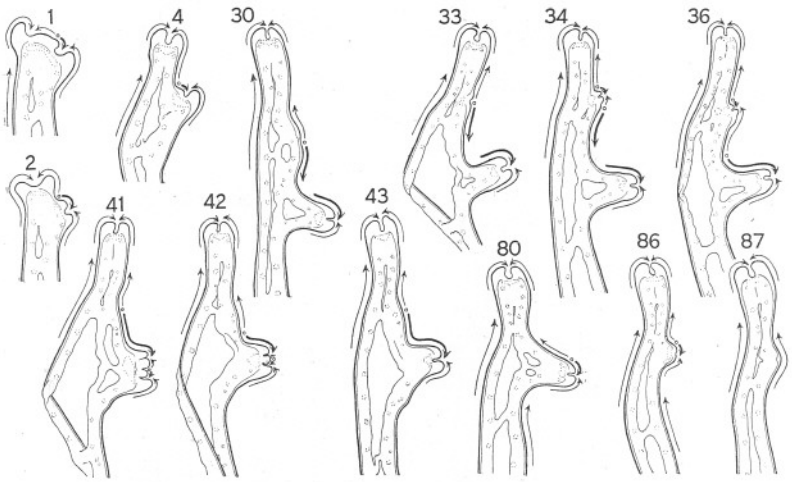


FIG. 23.—Lateral views of representative living filaments of secondary groove F (see Fig. 22). There was a tendency for the non-groove-bearing filament to be longer than that bearing the secondary groove, which made the spreading of the filaments on the slide for examination difficult. × ca. 9.

descending filaments) bearing a groove and to be bent outwards ; this made the spreading of some of the filaments on a slide for examination a little difficult. Figures 16, F (p. 942) ; 22, I–II ; and 23 sufficiently explain the structure and ciliation of this groove.

CILIATION OF FILAMENTS BEARING SECONDARY GROOVES ON THE EDGE OF SECONDARY FOLDS.

The group of secondary grooves from the gills of one mussel (Fig. 25, I), the ciliation of which is shown graphically in Figure 24, had most of them —with the exception of A, E, and F—in surface view the appearance of deep pockets, but single filaments showed that the appearance was deceptive, the groove being set directly on the surface of the lamella. The structure of some of them would appear to indicate that at one period of

their existence they had been deep pockets (see p. 925). In the secondary groove D from the ascending lamella of the right inner gill of this mussel (Figs. 25 and 24) the pocket must have reached almost to the lower food

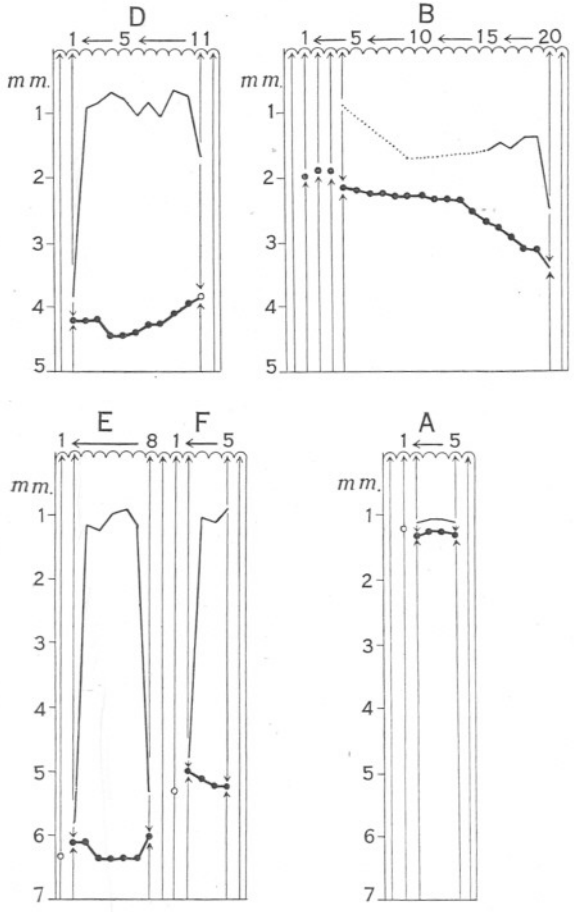


FIG. 24.—Graphs showing the relation of the distance of a secondary groove—on the edge of a secondary fold—from the main food groove on the gill of *Mytilus edulis*, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary grooves is shown in most instances. The signs are those used in Fig. 6, p. 928.

A, B, and D are on R1, and E and F on R3 of one Mytilus.

groove. The filament at either end of the groove was of about normal width—from frontal to abfrontal surface—but filament 1 had an extra number of ciliated discs. The filaments towards the middle of the groove, however, such as filament 5 (Fig. 26), showed fairly clearly the probable

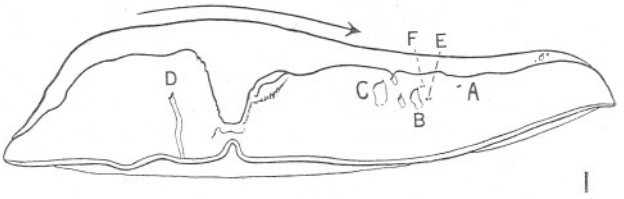
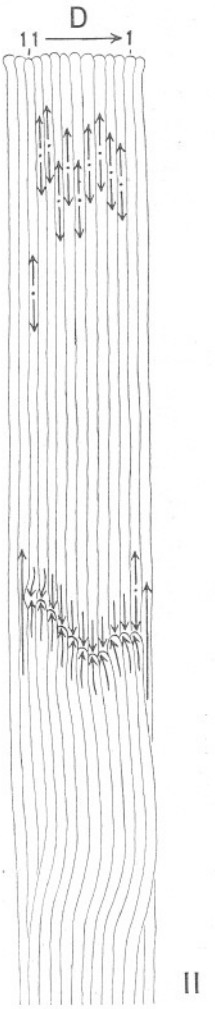


FIG. 25.



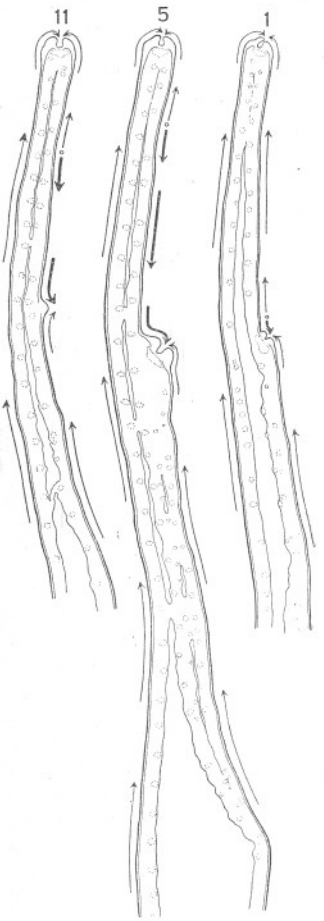


FIG. 25.—I. Sketch of gill of right side from an infected Mytilus, showing shortness of the inner gill and several secondary grooves and folds. Those investigated are lettered; E and F indicates the position of two secondary grooves on the descending lamella of the outer gill. The stippling indicates abnormally heavy pigmentation. Drawn from life, natural size.

II. Surface view of filaments composing secondary groove D. ×18¼.

FIG. 26.—Lateral views of representative living filaments of secondary groove D (see Fig. 25). × ca. 9.

previous history of the groove. With the exception of filament 1 the point of ciliary reversal on the filaments composing the secondary groove was much nearer the main than the secondary groove.

Grooves E and F (Figs. 24, p. 949; 25, I, p. 950; 27, I) from the descending lamella of the outer right gill of the same mussel are perhaps of a similar

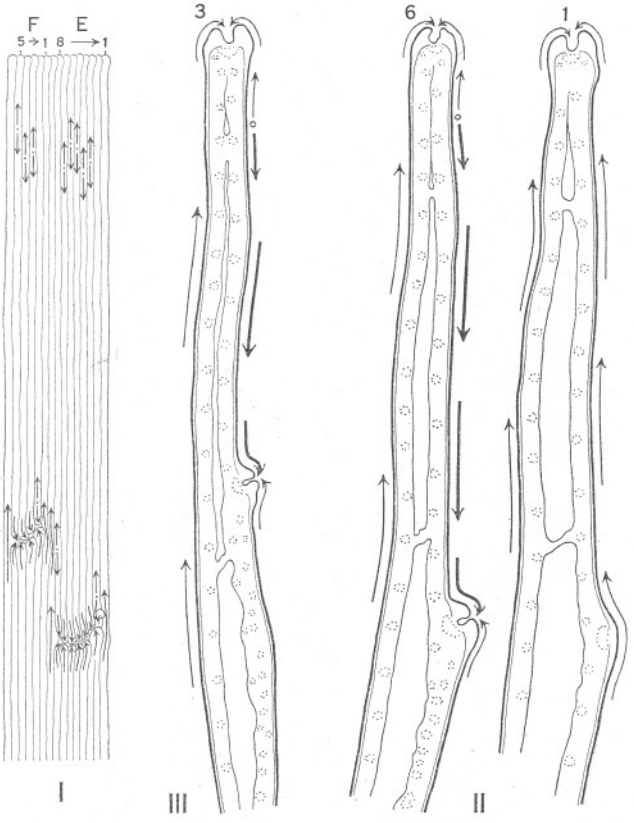


FIG. 27.—I. Surface view of filaments composing secondary grooves E and F (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments from secondary groove E.
III. Lateral view of living filament from secondary groove F.
I–III× ca. 12.

type to groove D, though fusion of the filaments has gone considerably further, and the irregularity in position and number of the ciliated discs is all that remains to indicate their possible origin. The two grooves were separated by only two filaments of normal ciliation but were not on the same level. Their structure and ciliation is evident from Figure 27, I–III.

It is characteristic of both of them, as of the groove previously described, that except for the first grooved filament in each and the last grooved one of E, the reversal of stroke of the frontals occurred close to the main groove. Filaments 2 and 3 of secondary groove E were fused for a short distance dorsal to the groove (Fig. 27, I).

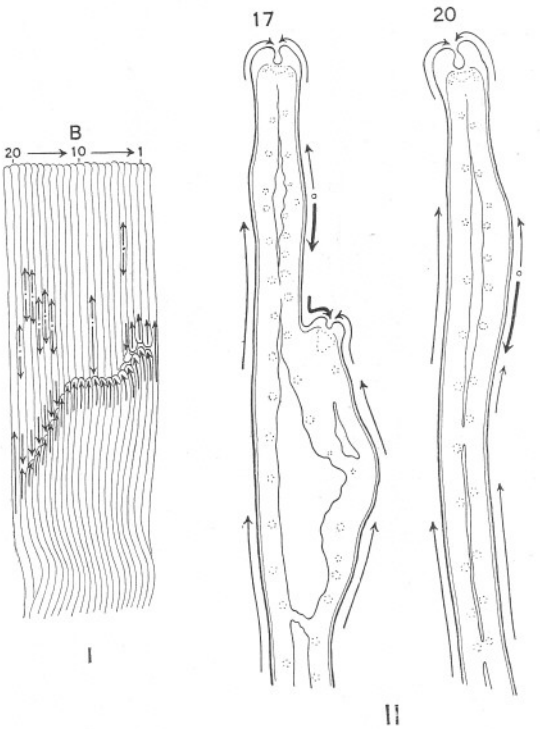


FIG. 28.—I. Surface view of filaments composing secondary groove B (see Fig. 25 I, p. 950).
Owing to the fusion of certain of the filaments the point of reversal of beat of the frontal cilia was not determined for filaments 5–8 and 10–14.
II. Lateral views of two living filaments from secondary groove B.
I–II× ca. 12.

Groove B (Figs. 24, p. 949 ; 25, I, p. 950 ; 28) is apparently structurally of a similar type to secondary grooves D, E, and F, but so far as could be judged from very scanty data—the filaments stripped very badly owing to a great deal of fusion occurring—it would not have given the same type of graph as the three previous grooves. Filament 20, following the last grooved one (Fig. 28, II), is interesting in that although structurally normal, ciliary reversal of the frontals occurred.

Groove A (Figs. 24, p. 949 ; 25, I, p. 950 ; 29, I–II) was possibly of

the same type structurally as the preceding grooves. Reversal of stroke of the frontal cilia occurred very near the secondary groove on the four filaments composing it, though the point of division on the fourth and fifth filaments is somewhat uncertain as they stuck together.

The 19 or 20 filaments of groove C (Fig. 25, I, p. 950) were of the type drawn in Figure 29, III, and probably the groove was originally a deep pocket. So much fusion occurred between the filaments that no attempt was made to strip the groove systematically. The point of reversal at least

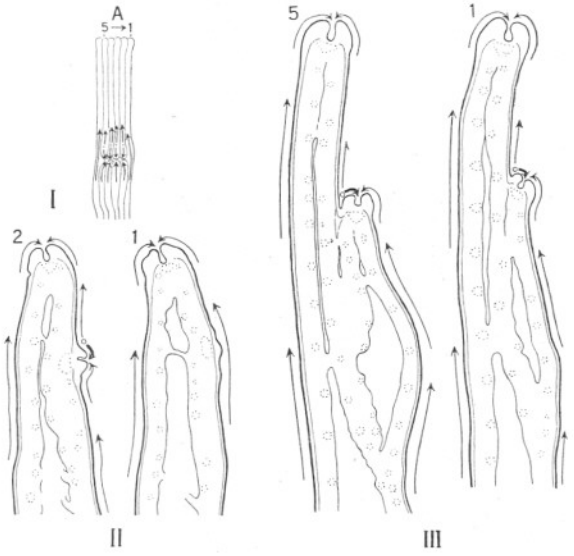


FIG. 29.—I. Surface view of filaments composing secondary groove A (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments of secondary groove A.
III. Lateral views of two living filaments of secondary groove C (see Fig. 25 I).
I–III × ca. 12.

on the first five grooved filaments was exceedingly close to the secondary groove (Fig. 29, III, filaments 1 and 5), so that it is unlikely that it would have given a graph anything approaching the type of D, E, and F.

It is evident from the foregoing observations that the ciliation of filaments bearing secondary grooves, which—from the structure of the filaments composing them—would appear to have been at one time at the edge of deep pockets, is not always of the striking type shown in the graphs of D, E, and F (Fig. 24, p. 949) in that reversal occurred close to the secondary groove. (Fusion of the 'pocket' will bring the point of reversal apparently nearer the secondary groove.)

A deep pocket near the posterior end of the right outer gill of another mussel, the groove of which joined the main groove and then diverged, is shown in the rough sketch in Figure 30, I. It is probable that pockets of this type and in this position, that is near the posterior adductor muscle, are not due to injury caused by a pea-crab, even when one is present. Figure 5, I, p. 926, shows a filament from a pocket of similar type and position. The filaments of the secondary fold shown in Figure 30, I, were not systematically stripped ; filament A was the first grooved filament,

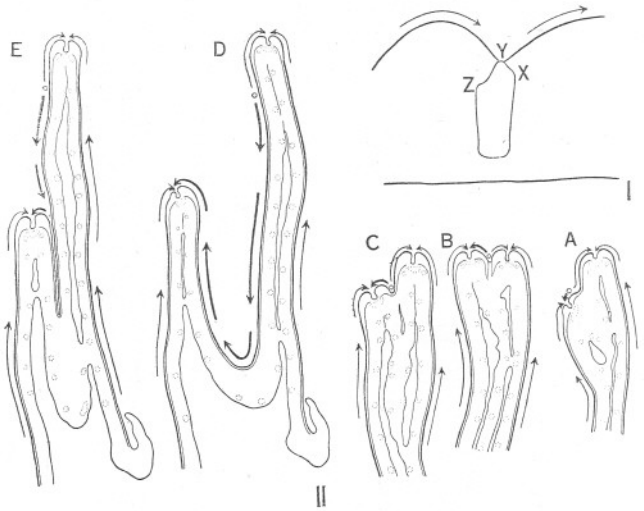


FIG. 30.—I. Rough sketch of a secondary fold or pocket on the descending lamella of the right outer gill of a Mytilus, near the posterior adductor muscle.
II. Lateral views of living filaments from the fold. Filament A was from position X, filament B from about the position Y, and filaments C, D, and E from between Y and Z. × ca. 9.

filament B was from about the position of Y where the secondary groove was on the same level as the main food groove, and filaments C, D, and E were from between Y and Z (Fig. 30, II). Considerable fusion had occurred except between Y and Z, so that the pocket was obliterated as indicated by filaments A, B, C, and E ; at some point between Y and Z an open pocket existed as shown by filament D ; filament E is from near the posterior edge of the pocket (i.e. near Z). The point of reversal of stroke of the frontals on filaments D and E perhaps lead one to expect that if the filaments had been stripped consecutively the graph would have been of the type of D, E, and F, Figure 24 (p. 949).

Ciliation of Filaments Bearing Secondary Grooves on the same or nearly the same Level as the Main Groove.

The position of a secondary groove of fourteen filaments on the descending lamella of a left inner gill is shown in Figure 31, I. It was so near the main groove that it might be described as a double main groove (Fig. 31, II), and yet ciliary reversal occurred on all the filaments except

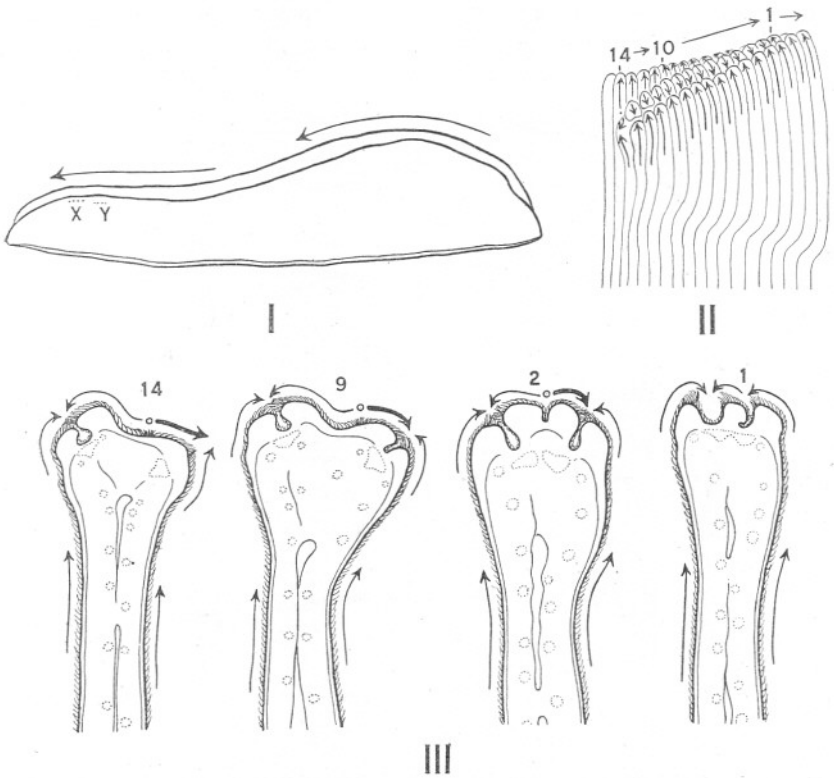


Fig. 31.—I. Sketch of left gills of a specimen of Mytilus: X indicates the position of a secondary groove on the descending lamella of the inner gill, and Y the position of one on the descending lamella of the outer gill. (Secondary groove Y was not investigated.) Drawn from life, natural size.

II. Surface view of living filaments composing secondary groove X. Camera lucida outline.

III. Lateral views of representative living filaments from secondary groove X. II–III × 18¼.

the first; it occurred on the filament (Fig. 31, III, filament 14) following the last grooved filament. On filaments 8 to 12 the point of division between cilia beating in the normal and the reversed direction tended to move slightly towards the secondary groove. Ciliary reversal does not always occur on grooves of this type (see Fig. 35, II, filaments 18–21, p. 963).

Ciliation of Filaments Bearing Secondary Grooves at the Free Edge of the Gill.

As previously mentioned, when a gill is short owing to injury by a large pea-crab the edge is occasionally slightly folded over with some fusion to the lamella (Figs. 4, p. 924 ; 32, I). In such cases very occasionally a secondary groove is present at what is now the free edge of the gill, and a change in the direction of the current caused by reversal of the frontal cilia may occur between the two grooves. Figure 32, II, is the surface view of

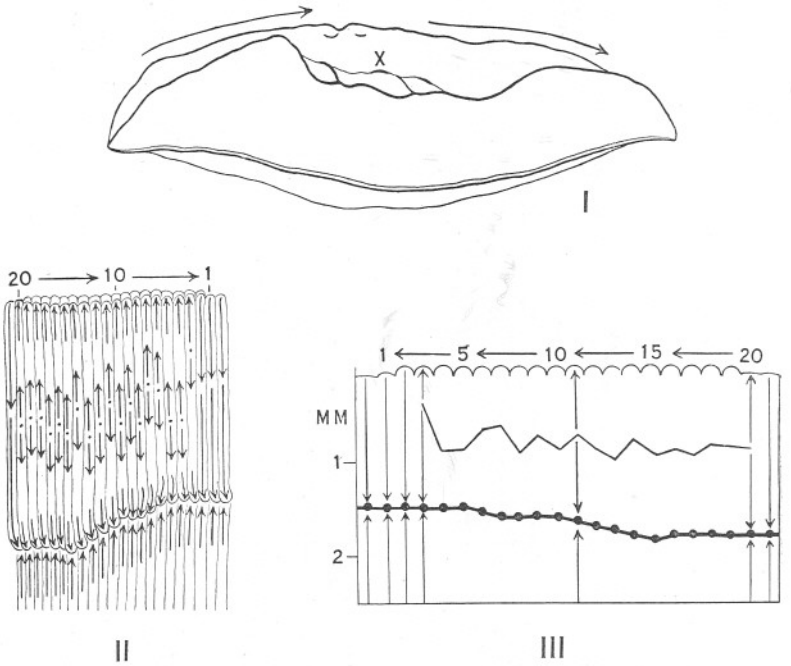


Fig. 32.—I. Sketch of gills of right side of an infected Mytilus, showing shortness of the inner gill and folding over of the free edge with, in certain places, the formation of secondary grooves at what is now the free edge of the gill. The part marked X was investigated. Two secondary grooves are present on the descending lamella of the outer gill. From life, natural size.

II. Surface view of filaments composing the secondary groove X. The secondary groove is at the free edge of the gill, the main groove being folded over. $\times 18\frac{1}{4}$.

III. Graph showing the relation of the distance of a secondary groove X, at the free edge of the gill, from the main groove, which, owing to folding, runs across the surface of the gill, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. The main groove in this figure is denoted by filled-in circles, and the secondary groove at the free edge of the gill by semicircles. The arrows at the free edge of the gill show the direction of the food current in the secondary groove and also in the main groove. Distance from the free edge of the gill is marked in mm.

that part of the gill marked X in Figure 32, I, with the change in ciliary beat on the filaments indicated by arrows. From the graph (Fig. 32, III) it will be seen that although the secondary groove is in this instance at the free edge of the gill, there is still a tendency for the change to occur nearer the secondary groove at the anterior than at the posterior end; that while at the posterior end there is change of ciliary current although

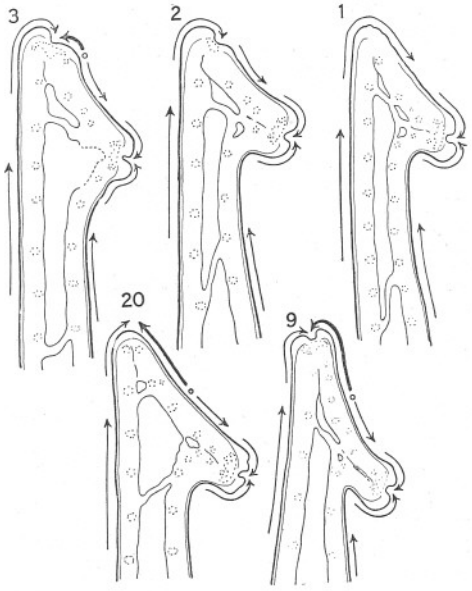


FIG. 33.—Lateral views of representative living filaments from secondary groove X (see Fig. 32). × ca. 12.

there is no groove at the free edge of the gill (filament 20), anteriorly on filament 1, which is enlarged at the edge, and filament 2, which has a shallow groove, there is no change (Fig. 33).

REVIEW OF LITERATURE ON CILIARY REVERSAL.

Known cases of the reversal of ciliary movement in the metazoa are rare, and considerable doubt exists with regard to some at least of those recorded. Purkinje and Valentin in 1835 (**35**) and Engelmann in 1868 (**13**, quoted by Parker, **31**) described reversal of ciliary current on the labial palps of mussels, while Grave (**15**) described it for the labial palps of the oyster; later writers (**1**, p. 129; **2**, p. 233; **22**; **28**, p. 167; **45**, p. 330), however, agree that on the palps of Lamellibranchs there are two permanent ciliated tracts in close proximity which beat in opposite directions and do not reverse their action, muscular movement

determining which set are effective (**1**; **2**; **28**; **41**). Parker (**31**) quotes some case of ciliary reversal in other animals.

Reversal of ciliary current on the lips of the sea anemone *Metridium marginatum* caused by the application of meat extract, potassium ions, etc., but not by mechanical means, has been described in detail by Parker (**30**; **31**). He states that the reversal is strictly local and lasts only as long as the stimulating substance is present, and that there is no evidence for assuming that it is under any form of nervous control.

Elmhirst (**12**) working on *Actinoloba dianthus* observed that "Longitudinal grooves run down the gullet, and when food is being swallowed the inflow is along the grooves; conversely a ciliary out-flow runs up the ridges, for example, when a bolus of waste is discharged it is passed out by the cilia on the ridges aided by a certain amount of contraction of the stomodæal wall. At times there is a vortex in the gullet when both sets of cilia are in action at once" (**12**, p. 151).*

In view of this Gray (**19**, p. 60) suggested that "since the oral disc of Metridium is ridged and its muscles are extremely sensitive to mechanical stimulation, one would like to be quite certain that the reversal of the currents observed by Parker is not due to two separate series of cilia which beat in opposite directions on the ridges and in the furrows."

Parker and Marks (**33**) have therefore repeated the experiments with Metridium. They hold that reversal most certainly occurs both of the ridge and groove cilia, though more easily effected in the case of the latter, and that while the cilia of the ridges ordinarily beat outwards and those of the groove beat commonly inwards, there is no evidence of a double system of cilia, one beating constantly outwards and the other constantly inwards on the lips of Metridium.

In a lecture delivered in the summer of 1928, at the Marine Biological Laboratory, Woods Hole, Gray (**19a**, p. 81) mentioned that he had seen "the convincing demonstration by Dr. Parker that a true reversal of the same ciliary current does actually occur" (in Metridium). He said "perhaps it is just possible to imagine that the reversal is due to a change in the 'tone' of the cilia. For such a suggestion there is some slight experimental evidence."

Torrey (**39**) described reversal of cilia on the lips and œsophagus of *Sargartia davisi*, effected in this instance by mechanical means. Here again the reversal was temporary.

Twitty (**40**) has described the reversal of ciliary action in amphibian embryos, induced by the application of the proper mechanical stimuli.

* Parker (**31**, p. 3) says: "So far as my experience extends, the application of various stimuli to the tentacles has never resulted in a reversal of the effective stroke of their cilia, and the same is true of the siphonoglyphs."

" Those found effective were : intimate contact of the epithelium with a foreign surface, e.g. the floor of a wax or glass dish ; immersion of the embryo in a dense, resistant medium ; contact with the egg membranes in which the embryo develops " (**40**, p. 327). He concluded that the cilia beat in the direction in which they encountered the least resistance. If the stimulus was removed the beat of the cilia returned to the normal after a certain time, which was longer than it had taken to reverse. He remarks that " one often gets the impression that the preference of normal over reversed action is remarkably slight if the conditions are arranged at all suitably " (**40**, p. 329).

The reversal of the beat of the frontal cilia of the gill filaments of *Mytilus edulis* is of a permanent nature. The filaments forming a secondary groove (Fig. 10, p. 934) were stripped one evening and the distance of the point of reversal from the main groove measured. The filaments were carefully kept in order in covered watch glasses and remeasured the next morning. The slight differences in the measurements were such as to be most probably due to error in measuring filaments which are, to a certain extent, contractile. If the ciliary action had been easily reversible, it might have been expected that the dissociation of a filament from its normal position in the gill might have induced a return to the normal direction of beat.

The only attempt to induce a return to the normal direction of beat by cutting off the secondary groove was made on two filaments of the type in Figure 5, I (p. 926), the secondary groove together with the folded part of the filament forming the outer wall of the pocket being cut off. When examined $3\frac{3}{4}$ hours later the points of division, which were 2·6 mm. and 4·1 mm. respectively from the main groove, were in exactly the same position ; when examined again after a further interval of 2 hours there was no change. More experiments of this kind are, however, required.

The possibility must not be overlooked that the ciliated epithelium of the gill filament over which reversal occurs, may have been formed by growth after the production of the secondary groove. If this should occur, the secondary groove would then probably have exerted some influence over the newly formed tissue, causing the cilia as they grew to beat towards it ; in this case it is realized that true ciliary reversal could not then be said to occur. In this connection the gills of the spat of *Mytilus edulis* up to about 3·4 mm. long have been examined and it was found that before the formation of a definite food groove—while there is merely a long tuft of cilia beating anteriorly at the ventral edge of the filaments—the frontal cilia on the very short ascending filaments beat ventrally. The following facts, however, would appear to be against the possibility of the ciliated epithelium over which reversal occurs, having

been formed entirely by new growth after the formation of the secondary groove :

1. The point of ciliary reversal on adjacent filaments is not at the same level ; graphs bring this out clearly.
2. The point of ciliary reversal is at some distance from secondary grooves set directly on the surface of the gill.
3. Ciliary reversal occurs on structurally normal filaments.
4. Little or no reversal of beat of the frontals may occur on all the filaments composing some secondary grooves, even when the filaments are produced into slight folds (Fig. 35, p. 963).

The type of ciliation of filaments forming secondary grooves such as D, E, and F in Figure 24 (p. 949), in which reversal occurs very much nearer the main than the secondary groove—with the exception of the first filament of each and also the last of E—would appear to be a strong indication that cilia, beating originally in the normal direction, had come to reverse the direction of their effective beat.

FIG. 34.

Lateral view of a living filament of a secondary fold on a Mytilus gill. The two food grooves are almost on the same level, and the change of current on the frontal surface of the filaments occurs at the depth of the fold. × ca. 9.

Figures 5, II (p. 926), and 34 show folds or pockets with the change of ciliary beat at the bottom of the pockets ; such might appear to have been formed subsequent to the secondary groove. Unfortunately these pockets were not stripped—a great deal of fusion occurring among the filaments—only one filament from about the middle being examined, so possibly the position of the point of division between cilia beating in the normal and in the reversed direction varied.

Detailed information on the growth (after the early stages studied by Rice, etc.) and the regeneration of the gill of Mytilus, however, will be needed before the origin of the folds or pockets can be decided. Bloomer (**5**), from observations on malformed specimens of *Anodonta cygnea*, concluded that though the animal is able to repair even extensive damage to the mantle-lobes, the gills are not regenerated, the animal being capable of living and thriving with very much aborted gills.

As a rough test as to whether regeneration of the gills of Mytilus occurred, a specimen was wedged open on June 5th, 1929, and several small pieces—more or less triangular in shape—were snipped from the ventral edges of the gills ; it was then allowed to close and put under

circulation in a tank. On September 26th (112 days later) the mussel was opened and the gills examined : they were found to have wedge-shaped pieces—roughly as large or larger than the pieces previously removed—missing from their ventral edges. In all cases, however, where the filaments had been cut across, new food grooves had formed. The mussel when opened was in very good condition, that is well fished, so that the non-occurrence of regeneration—with the exception of the food groove—could not be attributed to lack of food.

The result in this case may be regarded as an indication that a food groove only is regenerated after injury, at least at the free edge of the gills ; conditions governing growth and regeneration on the surface of the gills may, however, be different from those governing growth at the free edges.

Mussels are not infrequently found having gills with very jagged ventral edges.

One of the pieces cut from the gill had caused a state of affairs of some interest. It was in the shape of a long, narrow wedge, slanting very much antero-posteriorly, in such a way that the ventral ends of 13 filaments—forming a small triangular area—had been severed from organic connection with the gill, and apparently were only connected with each other by ciliary junctions, while the longest piece, forming the base of the triangle, was connected in the same manner with a normal filament. There is the possibility that organic inter-filamentar junctions may have been formed owing to compression by the cutting, but any such were not obvious and it is improbable that all filaments would have been so connected. The gill was preserved without pulling the filaments apart.

The dorsal cut ends of these apparently organically isolated pieces of filaments had in some cases rounded off and in others had formed a rough food groove, but all, except the shortest and the longest, had developed long terminal cilia, beating anteriorly, at the cut ends. Owing to the triangular shape of the piece the direction of the current produced by these was roughly anterior and dorsal, and met the current from the posterior part of the gill at the depth of the cut. There appeared to be no reversal of the ciliary current on these pieces of filaments, with the possible exception of some very tiny areas near the new groove on some of them, over which particles seemed to pass towards the groove ; the current, however, may have been caused by the newly formed terminal cilia.

The 13 pieces of filaments after 112 days were slightly swollen, as filaments of a gill cut from a mussel will generally become after several days in a finger-bowl of sea-water ; the cilia, however, were beating vigorously. These, most probably, organically isolated pieces of filaments had therefore in some cases at least regenerated a food groove by the transformation of material, and all with the exception of the shortest and

the longest had grown long terminal cilia beating in the same direction as those along the main food groove at the ventral edge of the gill. It is hoped to repeat this experiment.

Discussion on the Possible Causes of Ciliary Reversal.

From an analysis of the graphs of various secondary grooves it is evident that there is a distinct tendency for the change of ciliary current to occur nearer to the secondary groove at the anterior end of the groove than at the posterior end. In fact at the anterior end a filament with a definite groove may show little or no reversal, particles dorsal to the groove passing into and along it, but all particles ventral to it passing into the main groove. On the other hand, not only is the point of change generally further from the secondary groove at the posterior end, but there may be reversal of cilia on a filament with only a slight projection of the frontal surface, and in a very few instances on a filament perfectly normal except for the ciliary reversal. Cases such as shown in Figure 6, D and L (p. 928), where there are two changes of ciliary current on structurally almost normal filaments are very difficult of explanation, the only possibility seeming to be that the direction of beat is unsettled.

It would appear that the ciliary change is due to the effect of the secondary groove as a whole, and that the change does not occur on a filament entirely independent of its neighbours.

Lillie (**24**, p. 428) has explained the waves of co-ordinated beating such as occur in the rows of swimming plates of ctenophores in the following way : " . . . increased ciliary activity in one area excites adjoining areas to increased activity, so that a certain synchrony tends to be preserved between neighbouring cells. If ciliary activity, like other forms of contractility, is due to variations of electrical polarization at the surfaces of the contractile elements, an action-current must accompany each ciliary stroke, and its stimulating influence will be transmitted through the medium for some distance."

Wyman (**44**, p. 558) working on the gills of Unio observed that : " The transmission through the gill of the effects of warmth applied locally is apparent through increased rate of ciliary beat on adjacent gill tissue in all directions from the region of application." He offers an explanation similar to that of Lillie that : " The phenomenon might be explained by the stimulating effect of the action-current of the directly excited cilia on the neighbouring relatively quiet cilia," but remarks that " such an explanation, though in accord with the work on Unio, is inconsistent with certain of the observations of Kraft (**23**) on the tissue from the frog's pharynx."

Whether there is any possibility of an action-current being sufficiently

strong to reverse the beat of the frontal cilia of Mytilus, experiments will be necessary to determine.

The suggestion is also very tentatively made that the reversal of beat may be due to the mechanical resistance of a water current, set up by the

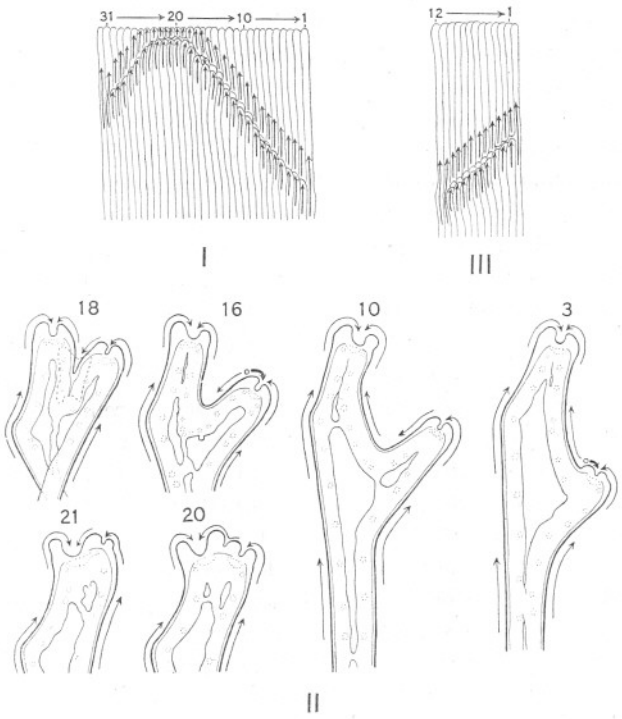


FIG. 35.—I. Surface view of filaments (Mytilus gill) composing a secondary groove which joined the main groove and then diverged. Little or no change of current occurred on the filaments.

II. Lateral views of representative living filaments from the groove. In filaments 3 and 10 especially, the outward bend—due to its greater length—of the non-groove-bearing filament is noticeable. In filament 18 the broken outline indicates an area of fusion with the next filament.

III. Surface view of filaments composing another secondary groove from the gill of the same mussel. They were of the type of filaments 3 and 10 of II, and little or no reversal of beat of the frontals occurred.

I–III× ca. 12.

long terminal cilia beating along the secondary groove. This suggestion would seem to account for the fact mentioned above that the change is generally closer to the secondary groove at the anterior than at the posterior end of the groove. Examination for a current set up by the

terminal cilia of the secondary groove, by means of powdered carmine, however, only revealed what appeared to be a weak one over the surface of the gill at the level of the secondary groove. This current was drawn into the groove at an acute angle.

That in some instances the change is very near the main groove indicating that the secondary groove appears to have more influence than the former, may perhaps be due to the fact that the secondary groove is on the surface of the gill and therefore any current set up by its long cilia would have more effect over the surface of the gill than would the main groove at its free edge.

One would expect the change in direction of beat to be a gradual and increasing one, and secondary grooves which have caused little or no change in direction of beat of the frontal cilia of the filaments of which they are composed, could be explained by assuming their recent formation. Examples of such grooves are those in Figure 35. After filament 18 of that in Figure 35, I, the secondary groove was almost on the same level as that of the main one for several filaments, then gradually diverged from it until at the 31st and last filament it was 0·8 mm. from the main groove. The filaments composing the secondary groove shown in Figure 35, III, were very similar in structure to filaments 3 and 10 in Figure 35, II. Particles on the gill dorsal to these secondary grooves passed into and along them, while those drawn on to the surface of the gill ventral to them passed almost entirely into the main groove.

The fact that experiments in transplanting pieces of ciliated epithelium from the roof of the mouth of the adult frog (**6** ; **25**) and from the trachea of the dog and the cat (**21**), reversing them in direction, have shown that the cilia on the transplanted pieces do not come to beat in the direction of the surrounding cilia of the host, the water current set up by them apparently having no effect, would seem to vitiate the possibility of the reversal of the frontal cilia of the gill filaments of Mytilus being due to the resistance set up by a water current. In Mytilus, however, the long terminal cilia of the grooves are considerably longer than the frontals, and might be expected to produce a stronger current, more likely to overcome the resistance of the frontal cilia.

Nervous control of ciliary action, chiefly of locomotor cilia, is known in certain forms (**8** ; **9** ; **10** ; **11** ; **26**) and Merton (**27**) contends " that reversal is always a manifestation of such regulation. He would thus class reversal as one of the spontaneous or voluntary responses of the organism " (quoted from Twitty, **40**, p. 326). Nervous control of the branchial cilia is said to occur in *Doliolum mülleri* (**14**). Grave and Schmitt (**16**) have described the presence of nerve-like structures lying immediately beneath, and parallel to the ciliated cells of the latero-frontal epithelium of Lampsilis, and in the epithelium itself a series of inter- and intra-

cellular fibrils with a suggested co-ordinating function. Bhatia (**4**) from an investigation of the latero-frontal cells of Mytilus has pointed out that in all probability the inter-cellular fibrils are cell walls, which, owing to the plane of the sections, are not seen in their entirety. Up to the present it has been found impossible to detect the operation of nervous elements in the epithelium or in the cells themselves of the gills of Mytilus (see Gray, **18**, p. 108); it would therefore appear to be unlikely that reversal of beat of the frontal cilia is due to nervous control.*

The work was done at Plymouth while holding a Miss Busk Research Studentship, 1927–28, and an Amy, Lady Tate Scholarship, 1928–29, of Bedford College. I wish to thank the College authorities for allowing me to continue to work at the Marine Station; the London University for granting me the use of their table; and the Director and Council of the Marine Biological Association for facilities. My thanks are also due to Miss Sexton for bringing to my notice an important reference to the literature, and to Mr. A. J. Smith for the photograph in Figure 3. And, finally I should like to express my deep indebtedness to Prof. J. H. Orton for the interest he has taken in the work, and for his advice and criticisms.

SUMMARY.

Permanent reversal of the frontal cilia on the gill filaments of *Mytilus edulis* has been found to occur naturally in the majority of cases where secondary or supernumerary food grooves are present on the gill. Such secondary grooves possibly arise as the result of injury; in some localities they are strongly correlated with the presence of a large female *Pinnotheres pisum* in the mussel. In these cases there is strong presumptive evidence that the secondary grooves are caused by mechanical injury from the claws of the crab. Considerable growth of inter-filamentar junctions, together with fusion of the filaments side by side, is common in secondary grooves and folds, and is especially marked in folds the filaments of which are somewhat askew.

The cavity of a fold or pocket practically always faces ventrally, and there is a definite tendency for the secondary grooves to slope ventrally and anteriorly.

The cavity of pockets would appear to be sometimes obliterated by

* While this account was in the press an interesting paper by S. B. Setna on "The Neuro-muscular mechanism of the gill of Pecten" was published in the *Q.J.M.S.*, Vol. 73, pp. 365–391, February, 1930. In describing the innervation of the gill and in connection with an unsuccessful attempt to determine the function of the subsidiary branchial nerve, he remarks: "While its sensory function cannot be denied, another possibility is that the cilia on the palps and the gills may be under nervous control. . . . On cutting the subsidiary branchial nerve, however, there is no evidence of reversal either on the gills or on the palps, nor does mechanical stimulation alter the direction of the ciliary stroke." (p. 382).

the concrescence of the filaments forming them; illustrations of the stages in the possible process are given.

Generally one or two filaments at either end of a secondary groove are raised into a projection in continuation of the groove; such projections may occasionally bear long terminal cilia beating anteriorly (i.e. at right angles to the normal direction of the frontal cilia), or may be covered with frontals of normal length, in some instances beating anteriorly and in others beating ventrally, according as to whether reversal does or does not occur on the filaments.

About 27 secondary grooves have been investigated, and it has been found that the reversal of beat of the frontal cilia of the gill filaments occurs over a variable distance between the secondary and main grooves. Particles drawn on to that part of the gill over which cilia beat in a reversed direction are carried dorsally into the secondary groove and along it until they reach a filament with normal ciliation, along which they are passed into the main groove. The direction of the current is the same in the secondary as in the main food groove, that is towards the mouth.

The metachronal wave is reversed with the reversal of stroke of the frontal cilia.

The point of division between cilia beating in the normal and in the reversed direction is not at the same level on adjacent filaments forming a secondary groove. Reversal is usually nearer the secondary groove at the anterior than at the posterior end of the secondary groove, and ciliary reversal may even occur on the following one or two ungrooved—and very rarely even on perfectly normal—filaments at the posterior end of the secondary groove; the graphs show this clearly. From a consideration of the graphs it seems apparent that the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella and each filament is not influenced by its own groove independent of its neighbour.

The ciliation of filaments composing certain secondary grooves, which from their structure would appear to have been originally at the edge of deep pockets, is of interest in that the point of division between cilia beating in the normal and in the reversed direction is much nearer the main than the secondary groove, with the exception of certain few filaments. This type of ciliation would appear to be a strong indication that cilia beating originally in the normal direction had come to reverse the direction of their effective beat.

The possibility is not overlooked that the epithelium bearing cilia beating in the reversed direction may be partly formed anew after the production of the secondary groove, whence the probability would be that the influence of the secondary groove may have caused cilia from the very beginning of their appearance to beat towards it (i.e. in the

reversed direction to the normal), in which case there would have been no true reversal.

Possible causes of the ciliary reversal in Mytilus are discussed. A little experimental work has been attempted, and it is suggested that a full explanation of the phenomena observed must await the result of an extended series of experiments.

LITERATURE.

1. Allen, W. R. The Food and Feeding Habits of Freshwater Mussels. Biol. Bull., Woods Hole. Vol. XXVII, No. 3, pp. 127–146, 1914.
2. Allen, W. R. Studies of the Biology of Freshwater Mussels. Biol. Bull., Woods Hole. Vol. XL, No. 4, pp. 210–241, 1921.
3. Beer, G. R. de. Growth. London, Arnold and Co., 1924.
4. Bhatia, D. The Structure of the Latero-frontal cells of the gills of *Mytilus edulis*. Q.J.M.S., Vol. LXX, pp. 681–692, 1926.
5. Bloomer, H. H. On some malformed specimens of *Anodonta cygnea* L. Journ. Malacol., Vol. VII, pp. 136–138, 1900.
6. Brücke, E. Th. von. Versuche an ausgeschnittenen und nach einer Drehung um 180° reimplantierten Flimmerschleimhaut-Stücken. Pflüger's Archiv. f. d. ges. Physiol., Bd. 166, pp. 45–54, 1916.
7. Carlgren, O. Über die Bedeutung der Flimmerbewegung für den Nahrungstransport bei den Actiniarien und Madreporarien. Biol. Zentralbl., Bd. 25, pp. 308–322, 1905.
8. Carter, G. S. On the nervous control of the Velar Cilia of the Nudibranch Veliger. Brit. Journ. Exp. Biol., Vol. 4, pp. 1–26, 1926.
9. Carter, G. S. On the structure of the Cells bearing the Velar Cilia of the Nudibranch Veliger. Brit. Journ. Exp. Biol., Vol. VI, pp. 97–109, 1928.
10. Copeland, M. Locomotion in two species of the Gastropod genus *Alectrion* with observations on the behaviour of Pedal Cilia. Biol. Bull., Woods Hole. Vol. XXXVII, pp. 126–138, 1919.
11. Copeland, M. Ciliary and Muscular Locomotion in the Gastropod genus *Polinices*. Biol. Bull., Woods Hole. Vol. XLII, pp. 132–142, 1922.
12. Elmhirst, R. I. Associations between the amphipod genus *Metopa* and Cœlenterates. II. The Feeding Habits of the Sea-Anemone *Actinoloba*. The Scottish Naturalist, pp. 149–152, 1925.

13. ENGELMANN, T. W. Ueber die Flimmerbewegung. Jena. Zeit. f. Naturwiss., Bd. 4, pp. 321–479, 1868.

14. FEDELE, M. Le attività dinamiche ed i rapporti nervosi nella vita dei Dolioli. Public. della Staz. Zool. di Napoli, Vol. 4, pp. 129–239, 1923.

15. GRAVE, C. The Process of Feeding in the Oyster. Science, N.S., Vol. 44, p. 178, 1916.

16. GRAVE, C., and SCHMITT, F. O. A mechanism for the co-ordination and regulation of ciliary movement as revealed by microdissection and cytological studies of ciliated cells of Mollusks. Journ. Morph., Vol. 40, pp. 479–510, 1925.

17. GRAY, J. The Effects of Ions upon Ciliary Movement. Q.J.M.S., Vol. LXIV, pp. 345–371, 1920.

18. GRAY, J. The Mechanism of Ciliary Movement. Proc. Roy. Soc., London, B., Vol. 93, pp. 104–121, 1922.

19. GRAY, J. Ciliary Movement. Camb. Univ. Press, 1928.

19a. GRAY, J. The Mechanism of Ciliary Movement. The American Naturalist, Vol. LXIII, pp. 68–81, 1929.

20. HERDMAN, W. A. Note on some points in the structure of the gill of the Ceylon Pearl-oyster. Journ. Linn. Soc. Zool., Vol XXIX, pp. 226–229, 1905.

21. ISAYAMA, S. Über die Flimmerrichtung an verkehrt zur Verheilung gebrachten Abschnitten der Trachea. Zeitschr. f. Biol., Bd. 82, pp. 155–156, 1924.

22. KELLOG, J. L. Ciliary Mechanisms of Lamellibranchs. Journ. Morph., Vol. 26, pp. 625–701, 1915.

23. KRAFT, H. Zur Physiologie des Flimmerepithels bei Wirbelthieren. Pflüger's Archiv. ges. Physiol., Bd. XLVII, p. 196, 1890.

24. LILLIE, R. S. The conditions determining the rate of conduction in irritable tissues and especially in nerve. Amer. Journ. Physiol., Vol. 34, pp. 414–445, 1914.

25. MERTON, H. Studien über Flimmerbewegung. Pflüger's Archiv. ges. Physiol., Bd. 198, pp. 1–28, 1923.

26. MERTON, H. "Willkürliche" Flimmerbewegung bei Metazoen. Biol. Zentralbl.; Bd. 43, pp. 157–163, 1923.

27. MERTON, H. Die verschiedenen Arten der Flimmerbewegung bei Metazoen. Naturwiss., Jahrg. 12, pp. 452–457, 1924.

28. NELSON, T. C. The Mechanism of Feeding in the Oyster. Proc. Soc. Exp. Biol. and Med., Vol. XXI, pp. 116–168, 1923.

29. ORTON, J. H. The mode of feeding of *Crepidula*, with an account of the current-producing mechanism in the mantle cavity, and some remarks on the mode of feeding in Gastropods and Lamellibranchs. Journ. Mar. Biol. Assoc., N.S., Vol. IX, pp. 444–478, 1912.

30. PARKER, G. H. The reactions of *Metridium* to food and other substances. Bull. Mus. Comp. Zool., Harvard, Vol. XXIX, No. 2, pp. 107–119, 1896.

31. PARKER, G. H. The Reversal of ciliary movement in Metazoans. Amer. Journ. Physiol., Vol. XIII, No. 1, pp. 1–16, 1905.

32. PARKER, G. H. The Elementary Nervous System. Philadelphia, 1918.

33. PARKER, G. H., and MARKS, A. P. Ciliary Reversal in the sea-anemone *Metridium*. Journ. Exp. Zool., Vol. 52, No. 1, pp. 1–6, 1928.

34. PECK, R. H. The Minute Structure of the Gills of Lamellibranch Mollusca. Q.J.M.S., Vol. XVII, pp. 43–66, 1877.

35. PURKINJE, J. E., et VALENTIN, G. De Phænomeno generali et fundamentali Motus vibratorii continui . . . Wratislaviæ, 4°, 96 pp., 1835.

36. RICE, E. L. Fusion of Filaments in the Lamellibranch Gill. Biol. Bull., Woods Hole. Vol. II, pp. 71–80, 1900.

37. RICE, E. L. Gill development in *Mytilus*. Biol. Bull., Woods Hole. Vol. XIV, pp. 61–77, 1908.

38. RIDEWOOD, W. G. On the structure of the gills of the Lamellibranchia. Phil. Trans. Roy. Soc., Lond. (B), Vol. 195, pp. 147–284, 1903.

39. TORREY, H. B. On the Habits and Reactions of *Sagartia davisi*. Biol. Bull., Woods Hole. Vol. VI, pp. 203–215, 1904.

40. TWITTY, V. C. Experimental Studies on the ciliary action of amphibian embryos. Journ. Exp. Zool., Vol. 50, pp. 319–344, 1928.

41. WALLENGREN, H. Zur Biologie der Muscheln. I. Die Wasserströmungen. Lunds Universitets Årsskrift, N.F., Afd. 2, Bd. 1, No. 2, 1905.

42. WILLIAMS, L. W. The Structure of Cilia, especially in Gastropods. Amer. Naturalist, Vol. 41, p. 545, 1907.

43. WRIGHT, F. S. Mussel Beds ; their productivity and maintenance. Ann. App. Biol., Vol. IV, No. 3, pp. 123–152, 1917.

44. WYMAN, J. Neuroid Transmission in ciliated epithelium. Journ. Gen. Physiol., Vol. VII, pp. 545–559, 1925.

45. YONGE, C. M. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, pp. 295–386, 1926.

46. YONGE, C. M. Feeding Mechanisms in the Invertebrates. Biol. Reviews and Biol. Proc. Camb. Phil. Soc., Vol. III, No. I, pp. 21–76, 1928.

Abstracts of Memoirs.

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Structure of Pearls.

By C. Amirthalingam.

Nature, *No.* 3091, *Vol.* 123, 1929, *p.* 129.

PEARLS from the tissues of a Pinna showed that the conchyolin layers may be arranged radially as found in Pinna shells or concentrically round the nucleus as in *Ostrea edulis* pearls ; in two cases, however, an alveolar layer was found round the nucleus with concentric layers on the outside. The nuclei of twenty-nine pearls out of thirty-two, were found to be conchyolin ; this observation supports the view that the origin of pearls is due to abnormal secretion of the epidermis.

C. A.

The Integration of Light by Photo-electrolysis.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 159–164.

It is possible to use a vacuum photo-electric cell for the integration of light. A Burt sodium cell gave 1·15 microamperes per 1000 metre-candles. On a bright November afternoon the production of alkali by the photo-electric current was observed in a dilute bicarbonate solution within 10 seconds, using brom thymol blue as indicator. The current may also be used for the deposition of copper. An average winter day should give about 0·13 mg. with the photometer horizontal ; in summer nearly 1 mg. might be expected.

W. R. G. A.

The Photo-electric Measurement of the Illumination in Buildings.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 173–187.

By the use of vacuum sodium photo-electric cells of the Burt type, together with suitable portable galvanometers, simultaneous measurements were made of the illumination in the open and in buildings ; the ratio expressed as a percentage, the daylight factor, is a useful index

of the illumination inside. This applies to diffuse skylight. A correction must be applied when the sun is shining, the illumination in the shade being multiplied by a factor β, which denotes the ratio of the reading of the photometer in the open site, to that obtained when the direct sunlight has been screened off. In an old church the daylight factor varied from 0·02 to 0·86 per cent for vertical illumination with the blue sensitive sodium cell. In a dwelling-house the factor immediately inside large windows was 7 per cent. The value in a well-lighted room is under 1 per cent. From this it follows that it is uneconomical to fit glass transparent to ultra-violet light in windows other than those that receive direct sunlight.

W. R. G. A.

Photo-electric Measurements of Illumination in Relation to Plant Distribution. Part II. Measurements with Portable Galvanometers.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 295–309.

By the use of Burt cells, robust Onwood micro-ammeters and suitable shunts simultaneous measurements were made of the vertical illumination in the open and in shaded sites. The photometer windows, as before, were sheets of double surface-flashed opalised glass. Large obliquity factors are thus avoided. The results obtained for measurements of the daylight factor agreed well with those determined by the rate of decomposition of uranyl oxalate solutions in quartz tubes. The daylight factor is not a constant, but varies somewhat according to the distribution of the illumination in the absence of sunlight. The factor is sufficiently constant to be a useful index of the light received at any spot. Data are presented showing the behaviour of certain plants growing in varying degrees of shade. In the deepest shade measured, daylight factor 1·3 per cent, only straggling branches of *Hedera helix* were found.

W. R. G. A.

The Uranyl Oxalate Method of Daylight Photometry and its Photo-electric Standardization.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 321–339.

The rate of decomposition of uranyl oxalate was compared with the reading of a potassium vacuum photo-electric cell which had been standardised by means of an open carbon arc. After making due allowance for the difference in the absorbing surfaces it was found that the

rate of decomposition of the standard solution, in quartz tubes, was 0·225 c.c. per hour per thousand metre-candles. Tubes of Monax glass required 1·14 times as long an exposure to produce the same result. This should not prevent their use for ecological work.

Measurements of the mean horizontal illumination were made at sea over two complete days by means of tubes suspended in the rigging, the average for the period from sunrise to sunset being 25,800 metre-candles on August 17 and 23,600 m.c. on September 18th, 1928.

The usual practice of exposing photo-sensitive liquids in vertical tubes measures the mean horizontal illumination. Exposure in a spherical flask measures the total illumination. This is desirable for some purposes.

W. R. G. A.

The Photo-chemical and Photo-electric Measurement of the Radiation from a Mercury Vapour Lamp.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. R. Dub. Soc., 1929, *Vol.* 19, *pp.* 355–361.

The uranyl oxalate method was used to study the rate of deterioration of a quartz mercury lamp. The decrease in radiation appears to be non-selective, or nearly so, for the visible portion and near ultra-violet as compared with the middle and far ultra-violet stopped by 4·0 mm. of Pyrex glass. The Pyrex transmitted 40 per cent, clear Corex A (8·2 mm.) 70 per cent and red-purple Corex A (10·2 mm.) 19 per cent.

Radiation from a mercury arc produces erythema of the skin of the upper arm when it suffices to decompose roughly 0·056 mg. of crystalline oxalic acid per sq. cm. in 3 minutes, under standard conditions.

Changes in a mercury arc may be followed with a glass vacuum sodium photo-electric cell of the Burt type. The 4 mm. Pyrex sheet transmitted enough radiation to produce a current 75 per cent of that with unscreened cell; the red-purple Corex A transmitted 33 per cent with a new lamp and 30 per cent with a lamp which had been in use for 360 hours. Double surface-flashed opal glass, 1·8 mm. thick, cut down the current to 46–47 per cent. Owing to the fact that the cell is not equally sensitive to radiation of different wave-lengths these figures are not percentages of the energy transmitted.

When first switched on the radiation from a mercury arc on a 200-volt town supply (A.C.) falls to about one-half of its initial value within a little over a minute. It then increases rapidly, reaching a maximum approximately fifteen times the minimum value within 5 or 6 minutes from the start.

W. R. G. A.

Methods for the Photo-electric and Photo-chemical Measurement of Daylight.

By W. R. G. Atkins and H. H. Poole.

Report of the Conference of Empire Meteorologists, Agricultural Section, London, 1929, *pp.* 67–89. *Reprinted in Biological Reviews,* 1930, **5**, 91.

The photo-electric current may be measured by suitable (portable) galvanometers, or continuously by means of a recording galvanometer. The potentiometer null method (H. H. Poole) can be used at sea, as can also the neon lamp method (J. H. J. Poole) which integrates the current over a short period and thus gives a measure which is independent of the large variations from moment to moment, caused by waves. Integration over longer periods may be carried out at sea or on shore by photo-electric production of alkali or deposition of copper.

The colour sensitivity, standardisation and constancy of photo-electric cells are discussed, also the optical conditions to be considered in such measurements.

The authors' previous photo-electric work is summarised, especially with regard to seasonal changes in illumination.

W. R. G. A.

The Action of Adrenaline and of Certain Drugs upon the Isolated Crustacean Heart.

By W. A. Bain.

Quart. Journ. Exp. Phys., Vol. XIX, 1929, *pp.* 297–308.

The effect of Adrenaline, Ephedrine, Ergotoxine, Pilocarpine, and Atropine upon the isolated perfused heart of the crabs *Maia squinado*, *Cancer pagurus*, and *Carcinus mœnas*, is described and eleven tracings given. The perfusion method adopted is described, the perfusion medium being sea-water adjusted to a suitable pH by means of hydrochloric acid —all fluids used in any one experiment having the same pH.

Adrenaline, in all active concentrations, is accelerator and, in the case of Cancer, augmentor in addition. Ephedrine, on the other hand, has no action on the crab heart. Ergotoxine is depressant, but it neither antagonises nor reverses the adrenaline effect. Pilocarpine (1/10,000) produces an action similar both qualitatively and quantitatively to that obtained with adrenaline (1/40,000), but the effect is immediately abolished by atropine sulphate (1/250,000) whereas the adrenaline effect cannot be so abolished even with the concentration of atropine as high as 1/40,000.

The almost identical nature of the response obtained with adrenaline and pilocarpine respectively suggests that a similar mechanism is responsible for each. The failure of atropine to abolish the action of adrenaline shows that this can hardly be so ; further, the similar failure of ergotoxine demonstrates that the conditions obtaining in the crustacean heart with respect to adrenaline may not be strictly comparable with those obtaining in the vertebrates.

W. A. B.

Influence of Age on the Temperature Coefficient of the Respiration Rate in Leaves of *Scolopendrium scolopendrium* Karst.

By J. Bělehrádek and M. Bělehrádková.

New Phytologist, Vol. XXVIII, 1929, *pp.* 313–318.

Oxygen intake in leaves of *Scolopendrium scolopendrium* Karst. under varied temperature was measured and it was found that the temperature cœfficient first increases and then decreases with the age of the leaves. Variations of temperature cœfficient with age, found in these experiments, are analogous to those previously described in animals. They are explained by the hypothesis that colloidal changes occur in the protoplasm with age, and that these are accompanied by variations of the viscosity, and thus of the rate of diffusion, in the reacting protoplasmic phases.

J. B.

On the Feeding Mechanism of the Copepods, *Calanus finmarchicus* and *Diaptomus gracilis*.

By H. Graham Cannon.

Brit. Journ. Exper. Biol., Vol. VI, No. 2, 1928, *pp.* 131–144.

Calanus finmarchicus and *Diaptomus gracilis* both feed automatically when swimming slowly and steadily through the water. A feeding current is produced which is filtered by the stationary maxillæ. Food so obtained is passed on to the mandibles by the maxillulary endites and setæ on the bases of the maxillipeds. The feeding current is a vortex passing through the mouth parts which results automatically from the swimming activities of the antennæ, mandibular palps and maxillules. The feeding vortex is caused to pass through the maxillæ by the combined activities of the maxillipeds and the maxillulary exites. The former suck water into the filter chamber between the maxillæ while the latter suck it out through the maxillary setæ. The views of Storch and Pfisterer on the feeding mechanism of *Diaptomus gracilis* are criticised. There is no

powerful antero-posterior swimming current as described by these authors. The swimming current is in the form of a vortex encircling the body and most marked at the sides in the angle between the body and the antennules.

H. G. C.

The Histology of the Alimentary Tract of the Plaice (*Pleuronectes platessa*).

By Ben Dawes.

Q.J.M.S., Vol. 73, *Part II, Oct.* 1929, *pp.* 243–274.

The alimentary tract of the plaice consists of the following regions: pharynx, œsophagus, stomach, duodenum intestine and rectum. In the pharyngeal and œsophageal regions the mucosa of the tract is intensely folded and the epithelium is liberally beset with goblet cells. Taste-buds occur in the pharynx, which is devoid of glands as is also the œsophagus. The œsophagus is sharply defined from the stomach. Gastric glands occur in all parts of the gastric mucosa, being shallower at the cardiac end of the organ. Each gland consists of 3 types of cells, columnar cells lining the crypt, cubical, mucus-producing cells forming the neck of the gland tubule, and granular cells forming the base of the tubule. Parietal or oxyntic cells do not occur, nor do goblet cells, in any part of the gastric epithelium. The intestinal mucosa is folded so as to simulate crypts and villi, but these structures do not occur. There is no differentiation of the epithelium except into goblet cells. Leucocytes probably do not play any important part in food absorption. The pyloric cæca exhibit the same histological structure as the intestine and probably perform similar functions. A well-developed valve occurs at the junction of the intestine and the rectum.

B. D.

The Early Prophases of the First Oocyte Division as seen in Life in *Obelia geniculata*.

By G. H. Faulkner, B.Sc.

Q.J.M.S., Vol. 73, 1929, *pp.* 225–242.

The nucleolus of the resting oocyte contains the whole of the chromatin of the nucleus. During the early growth phases the nucleolus elongates and then divides by a series of transverse fissions into fragments, each of which is a condensed pair of chromosomes. The two members of each pair subsequently separate and finally break down into a group of globules and are thus dispersed. The two members of the largest bivalent chromosomal element are unequal and probably represent an XY pair. The whole account is based on observations made on the living oocyte.

G. H. F.

Lipin Secretion in Elasmobranch Interrenal.

By A. H. H. Fraser, M.B., Ch.B., B.Sc.

Q.J.M.S., Vol. 83, 1929, *pp.* 121–134.

The paper describes the results of an intensive histological study of the interrenal of about thirty rays (*Raya clavata*). It was found that while the majority of glands correspond to the usual description of an ochre-yellow body, with the lipins confined to its constituent cells, a minority (about one in ten) show a brown coloration of varying intensity. When sectioned, these brown glands show evidence of active lipin secretion, in some cases the greatest concentration of lipin being in the interlobular capillaries.

Further, it is shown that in addition to the ordinary lobule commonly figured, the interrenal may show hypertrophied lobules, disintegrating lobules, and acini.

These various and histological pictures are interpreted as phases in a definite cycle of glandular activity, viz. :—

1. Resting lobule.
2. Distension of lobule.
3. Disintegration of lobule.
4. Formation of acinus.
5. Collapse of acinus.
6. Reformation of resting lobule.

From the acini a massive secretion of lipin takes place into the interlobular capillaries. The physiological importance of this phenomenon is emphasised.

The occurrence of melanin pigment in a minority of the glands is described, and evidence submitted of a relationship between the formation of melanin and the secretion of lipin. A. H. H. F.

Methods of Estimating Phosphates and Nitrates in Sea-Water.

By H. W. Harvey.

Cons. Perm. Internat. Rapp. et Proc. Verb. LIII, 1929, *pp.* 68–74.

Existing methods of estimating phosphates and nitrates in sea-water are reviewed and possible sources of error discussed. A colourimeter is described for more exact estimation of the very faint blue produced in the Atkins-Denigès method with sea-water containing less than 15 milligrams P_2O_5 per cubic metre, also a colourimeter for the rapid estimation of phosphate in sea-water samples on board ship. The former was demonstrated at the Conference held in October, 1928, at Oslo, where a more

robust instrument embodying the same principles was designed and later made by Messrs. Hellige to the order of Professor Johan Hjort. (See also "Report on the results of special investigations conducted at the University of Oslo in October, 1928," by Buch, Gaarder, Grau, Harvey, Schreiber, and Wattenberg, *ibid.*, pp. 95–115.)

H. W. H.

Hydrodynamics of the Waters South-East of Ireland.

By H. W. Harvey.

Journ. du Conseil, Vol. IV, 1929, *pp.* 80–92.

A simple method is described of calculating the velocity and direction of ocean currents from the distribution of density in the sea. The theoretical grounds on which this method, and a similar calculation by Werenskiold, rest are given. A comparison of the results obtained by this simple and rapid method, with results obtained by applying Bjerknes' Theorem, shows that the differences are not likely to exceed 5 per cent, which is of little consequence.

The currents, set up by differences in density, in the upper 60 metres of the sea lying to the south-east of Ireland, form a current system which is similar to the movement of the whole body of water as deduced by Matthews from the distribution of salinity.

The application of Bjerknes' Circulation Theory to this area, subject only to extremely slow currents, yields results which conform with conclusions based on entirely different evidence.

H. W. H.

The Maintenance of Life and Irritability in Isolated Animal Tissues.

By A. V. Hill, F.R.S.

Nature, Vol. 123, 1929, *pp.* 723–730.

This paper represents the Ludwig Mond Lecture delivered at the University of Manchester on March 6th, 1929. It refers to the conditions under which survival of isolated animal tissues can be secured, particularly in reference to their study in the laboratory. The influence of oxygen in maintaining the normal state is discussed. Reference is made to the experiments of Levin and of Furusawa on the "depolarisation" of crustacean nerve, and on the utilisation of oxygen by this nerve in maintaining its state or readiness to respond to a stimulus.

A. V. H.

The Heat Production and Recovery of Crustacean Nerve.

By A. V. Hill, F.R.S.

Proc. Roy. Soc. B., Vol. 105, 1929, *pp.* 153–176.

Levin, in 1927, published an account of certain new observations upon the electric change in stimulated crustacean nerve, and these observations were confirmed and extended by Furusawa in a paper published in 1929. It appears from these investigations that these non-medullated nerves are in a sense " depolarised " by activity and that in the presence of oxygen a recovery process occurs in which the state of polarisation is restored. The electric signs of activity in such nerve are much larger than in ordinary medullated nerve, and it seemed likely that an examination of the heat production during recovery might throw considerable light upon the process of restoration after activity.

The total heat per second of maximal stimulation is many times greater than in frog's nerve, and there is a clear division into two phases, initial and recovery. The initial process, completed during stimulation, yields only about two and a quarter per cent of the total heat. The recovery process, lasting for about 25 minutes at 16° C., supplies the remainder. The ratio of recovery to initial heat is about five times as great as in the case of frog's nerve. The result shows the importance of oxidative recovery, and confirms Furusawa's hypothesis that in the presence of oxygen a crab's nerve, " depolarised " by activity, is recharged by an active combustion process.

The limb nerves of Maia form an admirable preparation for such research.

A. V. H.

The Precipitation of Calcium and Magnesium from Sea-Water by Sodium Hydroxide.

By Eleanor M. Kapp.

Biological Bulletin, Vol. LV, No. 6, 1928, *pp.* 453–458.

Sea-water, after the addition of varying amounts of NaOH, was analysed for the amount of Ca and Mg left in solution. It was found that the amount of these ions precipitated depended on (1) the amount of NaOH added ; (2) the concentration of carbonate in the sea-water ; and (3) the extent to which equilibrium had been attained in the mixture.

E. M. K.

Lankester's "Gregarine" from the Eggs of *Thalassema neptuni*.

By D. L. Mackinnon and H. N. Roy.

Nature, *Dec.* 7, 1929.

Among twelve female specimens of *Thalassema neptuni* Gärtner examined at Plymouth, eight showed the developing eggs (in the nephridial sacs) heavily infected by a sporozoan. This is apparently the parasite described by Lankester (1881) as a "gregarine." Our preliminary investigation shows, however, that it is a coccidan. The adult trophozoite is a worm-like organism, which may reach the length of 400μ. We have noted all the main stages in development of the gametes and sporoblasts, and are continuing our investigation in the hope of demonstrating the schizogonic portion of the life-cycle and of determining the systematic position more exactly.

D. L. M. AND H. N. R.

Regeneration and Fragmentation in the Syllidian Polychætes (Studies on the Syllidæ. II).

By Yô K. Okada.

Arch. f. Entwick-mech. Bd. CXV, 1929, *pp.* 542–600.

Syllids regenerate easily the posterior segments, if the extremely anterior part is not cut, but anterior regeneration is variable according to the species employed. The regeneration capacity in *Syllis gracilis* and *Procerastea Halleziana* is limitless, and there is a complete recovery of the missing part, including a new formation of the entire system of the pharyngeal apparatus. In *Autolytus pictus* the anterior (before the 13th set. segment), the middle (from the 14th to 42nd set. segment) and the posterior part of the body behave quite differently in respect to their faculties of regeneration.

Fragmentation can be artificially caused by changing the salinity of the sea-water in which the experimental worms are kept (by adding fresh water according to E. J. Allen, 1921), or by subjecting the worms to a solution of KCl. In the first case a change of the osmotic pressure in the intestinal cavity would seem to be the main cause of the process of breaking, while in the latter case the fragmentation would seem to be provoked by an unusually strong constriction of the longitudinal muscles of the segments. The position of breaking is, however, predetermined by the special arrangement of megasepta, the presence of which can be seen by external observation through the transparent integument, as a particularly deep constriction in the alimentary tract.

Yô K. O.

On the Physiology of Amœboid Movement. V. Anærobic Movement.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 538.

The effect of lack of oxygen on a marine "Limax" amœba has been studied. Several methods have been used to remove oxygen.

In the absence of oxygen, gradually diminishing amœboid movement continues for 6 to 12 hours. The amœba then abruptly passes into an inactive condition. Anærobic activity is accompanied by morphological changes and an apparent rise in protoplasmic viscosity. There is a definite relation between the velocity of movement and the duration of anærobiosis.

Movement continues not only when oxygen is completely absent, but when the external medium has considerable reducing power.

Evidence is given that the energy of amœboid movement is supplied by an anærobic process, which allows movement to continue in the absence of oxygen.

It is suggested that the progressive diminution of anærobic movement is related either to the exhaustion of a precursor of the anærobic process or, more probably, to the accumulation of products of this process.

Oxygen is required for recovery after anærobiosis; this recovery occurs even after 48 hours, but anærobic inhibition of movement is ultimately irreversible. It is concluded that the anærobic processes of amœboid movement are normally accompanied by an oxidative recovery process.

Recovery is progressively delayed as the period of anærobiosis is increased beyond about 6 hours. Delayed recovery occurs in two stages; the amœba is at first inactive, and then suddenly resumes activity, as in immediate recovery. The delay is caused by increase in duration of the inactive phase. Delay in recovery increases long after all activity in the anærobic amœba has ceased, and is therefore not altogether dependent on activity. The delay may be related to the accumulation of an "oxygen debt."

The analogy with muscular and other forms of contractile activity is discussed.

C. F. A. P.

On the Physiology of Amœboid Movement. VI. The Action of Oxygen.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 555.

The effect of different partial pressures of oxygen on the movement of a marine amœba has been investigated.

With a limited oxygen supply, movement diminishes and ceases. But its duration is greatly prolonged when a trace of oxygen is present as compared with the duration under complete anærobiosis. The duration of movement increases with the oxygen pressure. After complete anærobiosis oxygen is required for recovery; prolonged activity in the presence of a trace of oxygen may therefore be due to this recovery process operating to a limited extent.

After a given duration of oxygen deficiency, the greater the deficiency has been the greater is the time required for the amœba to recover in aerated sea-water. The efficiency of the recovery process during oxygen deficiency therefore diminishes with the oxygen pressure.

As an oxygen pressure of 30–40 mm. Hg is approached the activity of the amœbæ increases. Above this critical pressure movement is maintained as long as in controls in aerated sea-water. Reduction of activity below this critical pressure does not seem to be related to difficulty of diffusion of oxygen into the amœba but to the diminished efficiency of the recovery process itself in the presence of insufficient oxygen.

The relation of the critical pressure to the oxygen pressure of the environment is discussed.

C. F. A. P.

On the Physiology of Amœboid Movement. VII. The Action of Anæsthetics.

By C. F. A. Pantin, M.A.

Proc. Roy. Soc. B., Vol. 105, 1930, *p.* 565.

The effect of certain anæsthetics on a marine amœba has been studied. The morphological changes and other effects of cyanide (below 10^{-1}M.) resemble those of oxygen deficiency. Activity progressively falls to zero; "Limax" movement is maintained till inhibition occurs. Inhibition is reversible even after 40 hours in 10^{-1}M. cyanide.

The effects of cyanide on the amœbæ are characteristic of its action on a respiratory mechanism. The minimal effective concentration lies between

10^{-5} and 10^{-6}M. Increasing the concentration to 10^{-1}M. only slowly increases the effect. The effect of a given cyanide concentration can be matched with that of a given oxygen deficiency in the medium.

The effects of cyanide recorded differ from the cytolytic effects recorded by Hyman in fresh-water amœbæ. It is suggested that such cytolysis is not due to cyanide, but to the great alkalinity and unbalanced potassium-ion concentration of KCN solutions.

The effects of sulphides on the marine amœba closely remembles that of cyanides.

Alcohols and chloretone cause inco-ordination of amœboid movement. At a certain liminal concentration movement becomes irregular, and it is inhibited by about 10 times this concentration. The effects do not resemble oxygen deficiency. The effectiveness follows the series methyl< ethyl < butyl and chloretone < amyl.

In the absence of oxygen, cyanides do not effect the behaviour of the amœbæ. This agrees with the supposition that cyanides act upon the respiratory mechanism in the amœba. Alcohols are even more effective in the absence of oxygen than in its presence.

Those anæsthetics (cyanides and sulphides) which induce effects resembling oxygen deficiency in the amœba are those which inhibit the cytochrome respiratory mechanism. It is suggested that the adverse effects produced by the anærobic processes causing amœboid movement are normally removed by an oxidative recovery process, which involves some respiratory mechanism similar to cytochrome.

C. F. A. P.

The Gregarines of Cucumaria; *Lithocystis minchinii* Woodc. and *Lithocystis cucumariæ* n.sp.

By H. Pixell-Goodrich, M.A., D.Sc.

Q.J.M.S., Vol. 73, 1929, *pp.* 275–287.

Cucumaria saxicola Brady and Robertson is shown to contain two neogamous gregarines whose life-histories have hitherto been confused with one another. One of these, *Lithocystis cucumariæ* n.sp., is exceptional in passing through all its stages in the respiratory trees of its host where the cysts form conspicuous opaque white spheres, up to ·5 mm. in diameter, easily seen on opening the body cavity. There is little doubt that spores enter and leave the host with currents of water through the cloacal aperture. This parasite has spores with long flattened tails similar to the type species, *L. schneideri* Giard, from Spatangoids.

About 18·5 per cent *C. saxicola* from Wembury Bay, Mewstone and Stoke Point were found to be infected.

The other gregarine, *L. minchinii* Woodc., is enclosed throughout most of its life in a cup-like outgrowth of the host's cœlomic epithelium and connective tissues. Its spores have peculiar episporal processes including a short tail.

From the same regions mentioned above, 40 per cent of the *C. saxicola* were infected with this species.

H. P. G.

The Comparative Morphology of the Elysioid and Æolidioid Types of the Molluscan Nervous System, and its Bearing on the Relationships of the Ascoglossan Nudibranchs.

By Lilian Russell, M.Sc.

Proc. Zool. Soc., London. Part 2, 1929, *pp.* 197–233.

Since Souleyet posed the problem of the phylogenesis of the Elysioid type in 1852, the taxonomists have solved it in one of two ways. Those impressed by the Æolidioid external morphology of Hermæa and Stiliger have included them in the Nudibranchs, while the close resemblance of the alimentary canal, and especially of the pharyngeal mechanism, in Elysioids and Lophocercoids, has led others to group these two types together as Ascoglossa. The above paper reopens the controversy, using as a criterion that system which has served most consistently as an index of relationship in the Gastropoda. The nervous systems of Elysia and certain Æolidioid types are compared in detail, the territorial distribution of all nerves being determined, and employed in ascertaining the homology of their ganglia of origin. A special attempt is made to render the representation and analysis of the visceral system as complete as possible. By this means the three ganglia of the visceral loop of Elysia are established as true homologues of the three primitive visceral ganglia of the Gastropod. This verification of homology makes it impossible to follow Pelseneer in deriving the Elysioids from Æolidioids with a naked visceral loop. It is further shown that the characteristic gastro-œsophageal ganglia have no homologues in Elysia. The Elysioid nervous system thus resembles the Lophocercoid in general plan, in the structure of the visceral system, and in the possession of retractile superficial eyes, auriculate tentacles with an organ of Hancock, genital nerves derived from the abdominal ganglion, and pedally innervated lateral appendages : the author accordingly proposes to sever the unnatural union of the Elysioids with the Nudibranchs, and to place them with their natural relatives, the Lophocercoids.

L. R.

The British Sea Anemones.

By T. A. Stephenson, D.Sc.

Vol. I, Ray Society publications, No. 113, *London*, 1928, *pp.* xiv+148.

This volume contains a general account of the morphology, colouration, development, bionomics and classification of the Actiniaria, with special reference to British forms. The account deals most fully with morphology, and is designed, apart from this, to give an introduction, in outline, to the study of Actinians, of such a nature as to render intelligible a more detailed account of them. It is followed by a classified list of the British species, of which 39 are recognised; and by a classified and a general list of literature. The second volume will contain full descriptions of the species, and further notes on their natural history. The illustrations in Vol. I represent in colour about half the species, the series to be completed in Vol. II; beyond this they illustrate morphology, histology, etc., and include a dedication page and some tailpieces after the manner of Forbes' *British Echinoderms*.

T. A. S.

A Contribution to Actinian Morphology: the Genera Phellia and Sagartia.

By T. A. Stephenson, D.Sc.

Trans. Roy. Soc. Edinburgh, Vol. LVI, p. 121.

The most serious gap in our knowledge of the anatomy of the British Actiniaria has been the almost complete absence of structural data referring to the genus Phellia. This paper describes the anatomy of the British forms which have been assigned to the genus; shows that the genus is heterogeneous; establishes *P. gausapata* Gosse as the type; creates a new genus *Cataphellia* for *P. brodricii* Gosse; and shows that *P. murocincta* Gosse is a form of *Sagartia troglodytes*, whilst *P. picta* Gosse is undoubtedly the young of *S. lacerata*. The status of the genus is discussed, after which the paper goes on to consider other matters. An account of the complex patterns developed on the peristome and tentacles of many anemones is given, and the value of the structure of such patterns as an index to relationships is pointed out. Lastly, the status of those variable species, *Sagartia elegans* and *S. troglodytes*, is discussed.

T. A. S.

Observations on the Function of Peroxidase Systems and the Chemistry of the Adrenal Cortex. Description of a New Carbohydrate Derivative.

By A. Szent-Györgyi.

Biochem. Journ., *Vol. XXII*, 1928, *pp.* 1387–1409.

Peroxidase plants contain a highly active reducing agent, which can be oxidised and reduced by biological systems, playing this way the rôle of a catalyst between different mechanisms of oxidation. The substance was crystallised, and identified as a hitherto unknown carbohydrate derivative, isomer to glucuronic acid. With regard to the chemical structure "hexuronic acid" is proposed for the name of the substance.

It is shown, that the adrenal cortex of mammals contains a strong reducing agent, specific for this organ. The substance has been isolated and found to be identical with "hexuronic acid" isolated from plants.

It is shown, that the interrenal bodies of elasmobranch fishes (*Scyllium canicula*) contain a strong reducing agent, which is specific for this organ, and shows the same reactions as the hexuronic acid of the mammalian adrenal cortex.

Chemical and physical properties of the hexuronic acid are described (M.P. 175–189, $[\alpha]_D^{21^\circ} = +24^\circ$).

The substance is studied in its relation to different biological oxidation systems. It is shown, that the substance gets oxidised in all systems, in which a phenol is oxidised to a quinone. The substance is not oxidised by the indophenoloxidase of animal tissues or by hæmatine compounds (cytochrom). The hexuronic acid is strongly reduced by the Hopkins glutathion system.

A. S.-G.

A Habit of the Common Periwinkle (*Littorina littorea* Linn.).

By D. P. Wilson.

Nature, *Vol. CXXIV*, 1929, *p.* 443.

On shores where there is little or no growth of the larger Fucoid algæ the periwinkles clinging to the boulders may be exposed to the sun for long periods. The risk of desiccation is lessened by the periwinkle's habit of sticking itself to the rock by secreting a film of mucus between the lip of its shell and the rock surface. This film soon dries, becoming brittle, and the mollusc then retracts and closes the opening of its shell with its operculum. On a steeply sloping surface it is nearly always orientated with the lip of the shell uppermost, the position in which there is least tendency for it to topple over.

D. P. W.

Marine Biological Association of the United Kingdom.

Report of the Council, 1929.

The Council and Officers.

The four usual meetings of Council have been held, at which the average attendance has been sixteen. The thanks of the Council are due to the President and Council of the Royal Society, in whose rooms the meetings have been held.

A Committee of seven members of the Council visited and inspected the Plymouth Laboratory and discussed with the members of the staff the scientific work upon which they were engaged. At the same time a sub-committee of the Fishery Advisory Committee of the Development Commission visited Plymouth and discussed the work of the Laboratory and organisation with the Committee of Council.

We have to record with regret the death of our President, Sir Edwin Ray Lankester, to whose energy, initiative and love for the science of Biology the foundation of the Association in 1884 was chiefly due. He was at first the Hon. Secretary, and as such was responsible for the collection of funds, the organisation of the Association and the building and equipment of the Laboratory at Plymouth. In 1890 he succeeded Professor Huxley as President, an office which he held until his death. To the last he followed with interest the details of the work that was done in the Laboratory, and had the welfare of the Association at heart.

Reference must also be made to the death of Mr. Walter Heape, the first Superintendent of the Laboratory, who was stationed at Plymouth while the erection of the building was in progress.

The Plymouth Laboratory.

The general good condition of the Laboratory buildings has been kept up, the outside painting of the Allen building and of the North building having been carried out. The walls of the ventilating shaft of the tunnel from the main Laboratory to the cliff under the road, which were showing

signs of decay, have been re-pointed, and the Plymouth Corporation have rebuilt the wall facing the road.

A new brick building 20 feet by 18 feet has been erected in the corner of the Citadel wall, behind the Allen block. This is used for the housing of the preserved dog-fish tanks and other specimens, and for the preparation of the dog-fish for preservation; it has given a considerable increase of storage accommodation in the old receiving-room in the main building. The latter room has been repaired and redecorated.

The engines and pumps for circulating sea-water through the aquarium and Laboratory tanks have worked efficiently throughout the year and no considerable repairs have been necessary.

The Ship and Motor-Boat.

The steam drifter *Salpa* has run satisfactorily, and has kept workers well supplied with the varying material required for a wide range of research. At the end of October the vessel proceeded to Dartmouth to undergo Lloyd's full-time survey and reconditioning. The work is being done by Messrs. Philip and Son.

The motor-boat *Gammarus* has been used continuously throughout the year for collecting in the Sound. One of the 3-h.p. motors has been replaced by a 6-h.p. Kelvin engine, the old motor being kept as a spare. The new engine has given a satisfactory increase in speed.

The Staff.

Dr. J. H. Orton, Chief Naturalist at the Laboratory, who first joined the staff in 1910, left at the end of September, on his appointment as Derby Professor of Zoology in the University of Liverpool.

Mr. C. F. A. Pantin, who held the post of Physiologist, left at the same time, on election to a Fellowship at Trinity College, Cambridge, and to a Lectureship in the same college.

Mr. V. C. Wynne-Edwards, one of the two student-probationers, left in August, having been appointed Lecturer in the Zoological Department of Bristol University.

Mr. F. S. Russell, who returned from the Great Barrier Reef Expedition in March, has been promoted from Assistant Naturalist to Naturalist, and has also undertaken the duties of Administrative Assistant, previously carried out by Mr. H. W. Harvey.

The post of Physiologist is being filled by the appointment of Dr. C. M. Yonge, the leader of the Great Barrier Reef Expedition, who was previously an Assistant Naturalist at Plymouth. Dr. Yonge will take up the appointment in January (1930) on his return to this country.

Mr. G. A. Steven, Student-Probationer, was promoted to Assistant Naturalist in October, in place of Mr. F. S. Russell.

Mr. G. M. Spooner of Christ's College, Cambridge, and Mr. J. S. Colman of New College, Oxford, who has been a member of the Great Barrier Reef Expedition, have been appointed Student-Probationers.

Another member of the Great Barrier Reef Expedition, Mr. A. G. Nicholls of Perth, Western Australia, has been sent to the Laboratory for a year by the Australian Commonwealth Council of Scientific and Industrial Research as a research worker.

Dr. Atkins gave a course of lectures on the methods for the photo-electric and photo-chemical measurement of light at the Imperial College of Science for the University of London, and also read a paper on the same subject, and demonstrated the apparatus used in his investigations to the Conference of Empire Meteorologists.

Mr. Pantin gave a course of lectures, with practical work, on General Physiology, at University College, London, and at Cambridge during the spring term.

Meetings at the Laboratory.

As already mentioned, a sub-committee of the Fisheries Advisory Committee of the Development Commission visited the Laboratory in March. The sub-committee consisted of Sir William Hardy, F.R.S. (Chairman), Sir John Marsden, Bart., Prof. G. Barger, F.R.S., Prof. G. I. Taylor, F.R.S., Dr. E. S. Russell, and Mr. E. H. E. Havelock (Secretary).

In April the International Council for the Exploration of the Sea, which was meeting in London under the Presidency of Mr. H. G. Maurice, C.B., came to Plymouth to see the Laboratory. The members of the staff and naturalists working at the Laboratory prepared exhibits illustrating their researches, which they demonstrated to the members of the Council on the afternoon of April 16th, and on the evening of that day the Council was entertained to dinner by the Mayor of Plymouth. On the following morning a joint meeting of the International Council and of the "Challenger" Society, which was attended by representatives from the other British Marine Laboratories, was held in the room used for our Easter classes. At this meeting scientific papers were read and useful and stimulating discussions took place.

In June the Physiological Society held a meeting at the Laboratory, when the work of the staff was again demonstrated, and the staff and visiting workers took part in the meeting of the Society.

The Council recognise that meetings of this character have a most stimulating effect on the scientific activity of the Laboratory.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

Dr. C. Amirthalingam, London (Bionomics of oysters. Effect of temperature on fertilisation of Pecten).
Miss D. Atkins, London (Pinnotheres and Loxosoma).
C. Baschlin, Basle (Hydroids. Cytology).
R. Bassindale, Sheffield (Morphology of *Balanus balanoides*).
L. C. Beadle, Cambridge (Regeneration in Hydroids).
Dr. J. J. Bek, Utrecht (pH Estimations. Carnivorous Crustaceans and Prosobranchs).
A. L. Bennett, Cambridge (Sexual characters of Fishes).
N. J. Berrill, Montreal (Regeneration of Polychætes. Development of Ascidians).
Miss A. Bidder, Cambridge (Digestion in Loligo).
Dr. Cecil von Bonde, S. Africa (Fisheries).
Dr. H. Blaschko, London and Berlin (Excitation of Maia nerve).
Miss M. A. Borden, Canada and London (Respiration of marine invertebrates).
Miss E. M. Brown, London (Chemistry of sea-water).
Dr. G. P. Chandler, London (Action of nitrites on muscle).
Mademoiselle Choucroun, Paris (Mitogenetic rays).
G. L. Clarke, Harvard (Phototropisms of planktonic crustacea).
Miss M. H. Collet-Brown, Plymouth (Diatoms).
Miss C. I. Dickinson, Kew (Marine Algæ).
J. R. Dymond, Toronto (General Zoology).
Dr. N. B. Eales, Reading (General Zoology).
Miss G. H. Faulkner, London (Budding in Alcyonidium).
Dr. H. Fawzy, Egypt (Spermatogenesis and oogenesis in the Soles).
Prof. H. M. Fox, Birmingham (Spectrographic analysis of animal tissues).
Miss L. Garnjobst, Stanford, U.S.A. (Encystment in Protozoa).
Prof. E. S. Goodrich, F.R.S., Oxford (Annelids).
Dr. Pixell-Goodrich, Oxford (Parasitic Protozoa).
P. A. Gorer, London (Crustacean inhibitory nerves).
A. Graham, Edinburgh (Digestion in Anemones).
Dr. A. J. Grove, Sheffield (Biology of *Melinna adriatica*).
Dr. R. Gurney, Oxford (Larval Copepods).
T. J. Hart, Leeds (Life-history of Corophium).
E. Heron-Allen, F.R.S., London (Foraminifera).
Prof. A. V. Hill, F.R.S., London (Heat production of crustacean nerves).
A. D. Hobson, Edinburgh (General physiology of eggs. Echinus, etc.).
Dr. E. G. Holmes, Cambridge (Metabolism of crustacean nerve).
Prof. Sir F. G. Hopkins, Cambridge (Glutathione).
Dr. S. L. Hora, Calcutta (General Zoology).
A. Howard, Mawson Expedition (Hydrography).
Dr. J. J. Izquierdo, Mexico (Cardiac sympathetic phenomena).
Dr. I. Kahn, Moscow (Nerves of Maia).
P. Kirtisinghe, Ceylon and London (Enteric plexus in Fish).
D. J. Malan, Pretoria (Planarians and Cyanides).
Dr. K. Mansour, Egypt (General Zoology).
Miss I. Manton, Manchester (Algæ).
C. Matheson, Cardiff (Hydrography).
A. A. Nayal, Egypt (Marine Algæ).

Miss G. L. Naylor, Plymouth (Distribution of marine lichens and chemistry of cell wall of Fucoids).
A. G. Nicholls, Perth, Australia (General Zoology).
Miss E. A. T. Nicol, Edinburgh (Physiology of digestion in Sabella).
E. Ogden, London (Urea in Dogfish and Rays).
Dr. Yô Okada, Kyoto (Schizogamy of the Syllidæ).
R. J. Pumphrey, Cambridge (Action of ions on Mytilus muscle).
Dr. H. S. Rao, Calcutta (Sponges).
H. N. Roy, Calcutta and London (Protozoa of Polychæte worms).
Dr. W. A. H. Rushton, Cambridge (Neuro-muscular mechanism of Maia).
Miss G. F. Selwood, Portsmouth (Oysters).
Dr. K. Sembrat, Lwów, Poland (Cytology).
P. Sen, Calcutta (Plankton and Insects).
Miss F. A. Stanbury, Birmingham (Culture of Diatoms).
F. G. Stott, Manchester (Digestion in *Echinus esculentus*).
Dr. M. A. Thynne, Plymouth (Nematoda).
Dr. F. M. Turner, London (Freshwater Algæ).
Prof. D. M. S. Watson, F.R.S., London (Gas content and mechanism of swim bladder of fishes).
Miss E. J. Weil, Vienna and London (Influence of salt and fresh water on animals).
G. P. Wells, London (General Physiology).
Miss M. A. Westbrook, London (Algæ).
Prof. K. B. Williamson, Malay States (Water analysis).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by forty-two students from Oxford, Cambridge, London, Belfast, Manchester, Birmingham, and Reading.

Another Course was held during the Summer Vacation and attended by twenty-two students.

An Advanced Course in Comparative Physiology and Experimental Biology, conducted by Mr. C. F. A. Pantin, was also held during the Summer Vacation and attended by fourteen students.

During the Easter Vacation Dr. E. W. Shann brought a class of four boys from Rugby, Mr. J. M. Branfoot a class of nine from Oundle, two boys from Harrow and one from Malvern, and Mr. H. C. W. Wilson a class of six from Monkton Combe School, Bath.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of eight students from Chelsea Polytechnic.

General Work at the Plymouth Laboratory.

Mr. Ford has devoted another year to the study of the herring and its fishery at Plymouth, and has published a further three papers of the series commenced last year. With the conclusion of observations on the progress of the drift-net fishery in the winter of 1927–28, a survey of the results obtained since the beginning of work in 1924–25 was made, in an endeavour to apply them to the question of the prediction of future

fisheries. This analysis was published in the Journal of the Association, Vol. XVI, of May, 1929. The data collected during the season 1928–29, now under investigation, will be of especial interest with regard to this matter of forecasting.

Young herrings collected from the rivers Tamar and Lynher have been used to gain knowledge of the processes of transition from the transparent larval herring to the fully-scaled and silvery adolescent. A report is nearing completion in which it is shown that the alteration in position of fins and anus, and the changing body proportions during metamorphosis can largely be explained as the consequence of differential growth of the larva. Simple models constructed of tape and elastic have proved very helpful in this study.

During the winter of 1927–28, experiments in artificial fertilisation and hatching of herring eggs under known conditions of salinity were carried out. It was found that eggs could be fertilised and incubated successfully in water varying in salinity from 37·8 to 4·8‰, and that the specific gravity of the larvæ from these eggs was dependent upon the salinity of the water in which the eggs were hatched.

In October last, Mr. Ford and Mr. Steven took the opportunity to visit Grimsby and Billingsgate on their return from a meeting of the "Challenger" Society at Aberdeen. At Grimsby they were fortunate in witnessing the landing of a large catch from Greenland, and in addition were able to learn something of the chemical and bacteriological problems connected with the manufacture of fish-glue.

At Billingsgate they were conducted round the market by the Chief Inspector of the Fishmongers' Company, to whom they are greatly indebted, as well as to Mr. C. N. Hooper, the Clerk to the Company, who made the arrangements.

Dr. Orton has again given as much time as possible to the preparation for publication of his earlier and interrupted researches, while at the same time continuing his studies in Marine Bionomics. Observations on Echinus and Patella extending over a number of years have been summarised and published in the Journal. Some preliminary experiments on the habits of the whelk-tingle *Ocinebra erinacea*, obtained from different habitats, have shown that even young individuals originating from oyster-beds will readily prey upon oysters, whereas larger and (with little doubt) older Ocinebra derived from a situation where oysters seldom occur only rarely attack oysters. This tingle is generally acknowledged by expert conchologists as a widely distributed form and is apparently a good species, according to the accepted criterion of a species. The observations recorded, therefore, show that within an apparently good species considerable bionomical variation occurs involving physiological characters. Similar facts have been elicited in studies on Echinus (migration

and breeding), Patella (shell-shape, shell-structure), and Ostrea (shell-shape, shell-structure, and reproductive rhythm). It is suggested by Dr. Orton that in this kind of variation lies some of the raw material for the process—and the detection of the trend—of Evolution.

An account of experiments in the sea on anti-fouling paints, extending over a period of $3\frac{1}{2}$ years, has been prepared by Dr. Orton for publication in the current number of the Journal. In these researches the growth-inhibitive and preservative values of poisonous paints and other substances (15 substances in all) have been studied side by side with general researches on the rate of growth of Invertebrates. Some chemical analyses of the more important anti-fouling paints investigated were made by the Government Chemist at critical stages of the experiments and are included in the published work. It was found that the fundamental factors determining the capacity of a paint to prevent growth include :

(*a*) great resistance to erosion,
(*b*) a toxicity depending upon slow but efficient ionisation of toxic substances,
(*c*) great capacity to adhere to the surface painted, involving a degree of roughness and dryness of the surface painted.

It was proved by critical chemical analyses that gradual loss of toxicity of the more efficient poisonous paints—after about $2\frac{1}{2}$ to $3\frac{1}{2}$ years' immersion in the sea—was accompanied by gradual diminution of the toxic elements, arsenic, copper and zinc, in the paints. The concentration of toxic elements present in a paint when toxicity is at vanishing point can be determined in the sea biologically, and in this way may be determined the minimum rate of—and data useful for the regulation of —ionisation necessary to ensure toxicity in a given paint. It is believed that many useful practical and interesting biological points arise out of these researches.

The investigation on the variation in shell-shape in Patella in relation to environmental conditions has been continued. In this work a high-shelled form has been found on mussels and stones on Gas Works Island in Teignmouth Estuary, in what is regarded as an abnormal situation, i.e. near low-water neaps. It has been discovered, however, that seed mussels are relaid on this bed from time to time from a high-water situation in the locality. Thus it is possible that shell-form on Gas Works Island is a product of two environments during unknown periods. It is hoped to obtain critical information on the phenomenon by investigating conditions in estuaries in other parts of England where Patella and mussels occur naturally.

It was hoped to publish an account of observations and experiments

on the rate of growth and breeding phenomena in some common Ascidians in the current number of the Journal. The final preparation of the work had to be postponed in September, but it is Dr. Orton's intention to complete this and some other outstanding papers for publication in the future.

The continuous records of hydrographic data between Plymouth and Ushant have been maintained, and continue to be published in the Rapport Atlantique of the International Council. The year 1929 has been of interest, since in June high-salinity water appeared off Ushant and lay to the westward of the mouth of the English Channel. In the Eddystone area the surface layers were unusually warm in late summer, while the deeper water was cooler than in most previous years; at the end of August *Limacina*, common in warmer waters of more southerly latitudes, was abundant, although the low salinity did not indicate any inflow of Atlantic water having penetrated to this area.

Mr. H. W. Harvey has continued work on the oxidation of reduction products of strychnine, from which a method of estimating nitrates and nitrites had been evolved, samples of pure hydrostrychnine and strychnidene having been presented by the late Professor W. H. Perkin, F.R.S. Meanwhile the firm of Riedel-de Haen of Hannover have placed on the market a solution of reduced strychnine in sulphuric acid, which is satisfactory for this estimation, and probably obviates the need for further investigation at the present juncture. Delegates to the conference concerning methods of estimating nutrient salts in sea-water, held at Oslo in October, 1928, which was attended by Mr. Harvey, have since investigated the distribution of ammonium-nitrogen in the sea, and in connection therewith Mr. Harvey is investigating the direct utilisation of this source of nitrogen by cultures of marine diatoms, and the effect of nutrient salts on their rate of growth.

During the early part of the year Mr. Harvey was engaged in making arrangements for the survey of the River Tees estuary, and has visited the staff at Middlesbrough from time to time.

Dr. Lebour has continued the revision of the account of the Plymouth Marine Fauna, which is nearly finished and includes much new matter, especially as regards the breeding of the various species. It is hoped that it will soon be ready for publication. She has also worked at the crustacean larvæ of the district, giving special attention to those attributed by Sars to *Pandalus borealis* and *Pandalus bonnieri*, which she has now found belong to Caridion. As there were two distinct larvæ and only one known species of Caridion, a second species was searched for and found in the shore-form hitherto understood to be *Caridion gordoni*. It is now established that there are two species of Caridion in the district, one of which is new to science and has been named *Caridion steveni*. To this species

belong the larvæ known as *Pandalus bonnieri*. The adults of the deeper water form, *Caridion gordoni*, have not yet been found near Plymouth (although known from Cornwall), but the larvæ (Sars' *Pandalus borealis*) are common in the plankton and the post-larvæ are occasionally found. The post-larvæ and young of both species have been reared from the respective larvæ in the Laboratory and the young of *Caridion steveni* have been hatched from the egg. A paper on this subject is ready for publication.

Further work on other larvæ is still going on, species of Spirontocaris, Hippolyte, and several other forms having been hatched from the egg. This work on Caridion has cleared up much that was difficult to understand in the relations of the Caridea, and it is hoped that investigations of closely related forms will help still more. Pandalus being of commercial importance in places, it is essential that the larvæ should be rightly identified and easily recognised, and the fact that the two Caridion larvæ have for years been regarded as typical of Pandalus has confused considerably all work on the subject.

The book on Planktonic Diatoms, to be published by the Ray Society, is now in proof form and, it is hoped, will be published early next year.

Mr. F. S. Russell, since his return from the Great Barrier Reef Expedition in March, has been occupied in working up the results of material collected previous to his departure, in continuation of his studies on the vertical distribution of plankton. He has completed a paper on the vertical distribution of young fishes, and this, together with previously published results, gives sufficient data to base general conclusions on what to expect in the behaviour of the commoner species. There is a definite indication of difference in behaviour between the pelagic young of the summer spawners and those of the spring spawners, the former being considerably higher in the water. Routine weekly collections of young fish by oblique hauls with the ring-trawl are being continued, and there is now available information as to abundance of the various species over a period of five years. This will form a useful basis from which to watch for any violent fluctuations that may occur in future years.

Mrs. Sexton's work on the Mendelian inheritance of eye-colour and other factors in *Gammarus*, in which Miss Clark has given valuable assistance, is making progress. Special experiments have been carried out on the effect of breeding and rearing this amphipod at high temperatures, with the consequent production of new mutations. Mrs. Sexton has also been able to do a considerable amount of work in rearing the amphipod *Jassa*, which exhibits marked dimorphism.

Mr. B. Dawes' experiments on the relation between food and growth-rate of Plaice, which are being done at Pier Cellars, Cawsand Bay, for the

Ministry of Agriculture and Fisheries, are showing interesting but somewhat unexpected results. Mr. Dawes has also been able to do a good deal of work on the physiology of digestion of the Plaice.

During the early part of the year Mr. D. P. Wilson completed his researches on the larvæ of the British species of Sabellaria and has published an account of the work in the Journal. He has also continued his efforts to obtain the, as yet, unknown larvæ of a number of common Polychætes, and after many unsuccessful attempts at last succeeded in getting an artificial fertilisation of *Branchiomma vesiculosum*. Only a small proportion of each lot of fertilised ova gave rise to larvæ, which were removed and reared in finger-bowls. These larvæ were of special interest, as little is known about the development of Sabellids. In Branchiomma the pelagic development is short, the larva metamorphosing on the bottom before it is a fortnight old. Specially interesting is the fact that the great branchial crown on the head of the adult arises in the larva as a pair of lobes anterior to the prototroch. Each lobe branches to form a number of filaments and these increase in number as the worm grows older. The young worms have been reared to an advanced stage. The study of the Mitraria larva of *Owenia fusiformis*, commenced last year, has been continued, and this summer further rearings have been made. While living material was available special attention was paid to various obscure points, and especially to the complex system of muscle and nerve strands with which the larva is provided. The relations of these have been worked out as far as possible. A pair of larval nephridia was discovered, but owing to the minute size of the flame cells, and the difficulty of seeing clearly their fine cilia, the structure of these nephridia has not yet been fully made out. The metamorphosis of the Mitraria has been observed on several occasions and previous observations confirmed. A fairly large amount of fixed material, consisting of well-expanded larvæ and young worms, was obtained, and this, after embedding in celloidin and paraffin, is being sectioned for detailed study.

In order to obtain some idea of the bionomic conditions prevailing on the "corner" fishing grounds in the waters off Plymouth, a detailed study of the bottom fauna of the area has been carried out by Mr. G. A. Steven. Quantitative seasonal observations extending over a period of one year (August, 1928–July, 1929, inclusive) have been made, using the 1/10 square metre Bottom Sampler and the "Agassiz" Trawl, a method having been devised for obtaining quantitative hauls with the latter instrument. Investigations into the food actually eaten by the fishes within the area have been carried on simultaneously, over 2000 fishes comprising 29 different species having been examined in the course of the year. The principal food animals present on the "corner" grounds are Annelids and Crustacea. Lamellibranchs, and indeed all

Molluscs, are found only in exceedingly small numbers. Plaice, therefore, which normally depend largely upon molluscan food are very scarce. The only marketable flatfish at all common is the Lemon Sole (*Pleuronectes microcephalus*), which feeds almost entirely on Polychæta and can therefore find sufficient food to support it. When the entire fish population of the area is considered as a whole, it is found that the animals most commonly eaten are those which are most numerous on the ground. Within limits determined by size and by suitability in other respects, the fishes eat the organisms which are at hand. The same species of fish (e.g. Gadoids) trawled off another area on which different bottom animals predominate, reflected this difference in their diet. The feeding habits of a number of fishes have been studied, and close correlation is found to exist between the foraging methods adopted by fishes and the type of food animals normally eaten by them.

River Tees Survey.

Early in the year the Council of the Marine Biological Association undertook to carry out for the Department of Scientific and Industrial Research, a biological and chemical survey of the Estuary of the River Tees, in co-operation with a hydrographical survey undertaken by the Admiralty and a biological and chemical survey of the upper river by the Ministry of Agriculture and Fisheries.

Through the kindness of Sir Charles Parsons, K.B.E., F.R.S., a suitable building in the Cleveland Shipyard, Middlesbrough, was obtained at a nominal rental for use as a laboratory, and a motor-boat was purchased. A scheme embodying the more obvious problems to be investigated was drawn up and approved by a sub-committee of the Water Pollution Research Board, under the chairmanship of Professor G. C. Bourne, F.R.S., and by Dr. H. J. Calvert, the Board's Director of Research.

The Council placed Mr. H. W. Harvey, the Association's Hydrographer, in general charge of the work they had undertaken. Mr. W. B. Alexander, who had had considerable experience of biological research in Australia, was appointed Superintendent of the Laboratory at Middlesbrough, and made responsible for the biological investigation of the estuary. Dr. B. A. Southgate, Mr. W. H. Jackson, and Mr. J. Moor were appointed Physiological Chemist, Chemist and Chemical Assistant respectively. Work at Middlesbrough commenced at the beginning of April. Periodical reports upon its progress are being furnished to the Department of Scientific and Industrial Research, who will be responsible for the publication of the results.

Department of General Physiology.

Dr. Atkins and Dr. H. H. Poole have continued their collaboration on photo-electric photometry and a method was devised for integrating light, by using the photo-electric current to produce alkali or to deposit copper. About one-tenth of a milligram was deposited on a winter day, corresponding to an average vertical illumination of 10,000 metre candles for ten hours. Measurements were also made of the daylight factor in buildings and of the changes in the character and intensity of the light from a mercury vapour arc lamp. The uranyl oxalate method of daylight photometry was also standardized photo-electrically and the photo-chemical and photo-electric methods were compared in submarine work.

Dr. Poole was unable to visit Plymouth, but Dr. Atkins worked in Dublin for some weeks and a new submarine photometer was made in Trinity College and standardised in the laboratory of the Royal Dublin Society. This photometer has several improvements and is specially suited for the measurement of horizontal illumination. It has been used in conjunction with Dr. J. H. J. Poole's neon lamp photometer. This gives a time-integration and so enables one to measure the light immediately below the surface, where it is very unsteady.

Attention is now being paid to the changes in the colour of daylight under various conditions, using a new type of cell developed by the General Electric Co.

Work on the preservation of fishing nets was limited to the routine testing of nets already in water. Though the copper soap and tar treatment is most effective, it has been found that repeated treatments according to Dr. Olie's (Dutch) method give very good results. The cost of the reagents, cutch, followed by ammoniacal copper sulphate, is low.

Owing to the accumulation of data and the lack of an assistant, work on the minor constituents of sea-water had to be abandoned in the spring. This proved particularly unfortunate as meteorologically the year was a most exceptional one, in which well-marked differences in the normal plankton production might have been expected. The results already obtained are being prepared for publication. Interest centres in the variation in the dates at which the main phosphate consumption takes place in different years, also in the unequal rates of regeneration of phosphate and nitrate. In this connection a study was made of nitrite in sea-water. In the deeper cold water at Station E1 larger quantities of nitrite were found than have ever been recorded for sea-water, but only at the period (August) when nitrate regeneration was actively in progress. The production of nitrite is thus an indication of nitrate production and

can be tested for very readily. The difference between 20 metres on August 16th, 1928, at E1, with 0·2 mg. nitrite nitrogen per cubic metre and 25 metres with 38·3 mg. was most striking, the one showing an almost imperceptible pink with the reagents, the other a deep red.

Mr. Pantin has commenced a series of experiments to determine the action of ions on crustacean muscle. Though much work has already been done on the action of ions on rhythmically contractile organs such as the heart, there is much uncertainty in the interpretation of results on account of the complexity of these organs. By perfusing crustacean skeletal muscle with solutions of known composition and testing the excitability of the muscle with electric stimuli of known intensity, the effects of ions on the contractile mechanism and on the excitation mechanism are readily analysed and separated. A preliminary report of the methods has appeared in the Proceedings of the Physiological Society.

The results cannot yet be fully discussed, but it appears that the mechanisms of excitation and contractility in the cell cannot be treated entirely as separate entities, as has usually been assumed.

Preliminary experiments have also been performed on the effects of ions on the adaptation of *Gunda ulvae* to fresh-water and marine conditions. This organism is commonly subjected to violent changes in the salt content of the external medium. Fräulein E. Weil, working this summer under the direction of Mr. Pantin, found that the organism was able to withstand these changes by allowing the free passage of water in and out of its tissues. Subsequent work by Mr. Pantin indicates that this passage of water is controlled by the cations present in the medium.

The Library.

The pressure on the available space for shelves in the Library, to which attention was drawn in the Report of the Council last year, has become much more pronounced, and it is now a very difficult matter to store the new books, as they are being added from day to day. The erection of a new Library building has become most important; for the proper storage of books, so that ready access to them is possible, is essential to the efficient working of a Marine Laboratory.

The thanks of the Association are again due to numerous Foreign Government 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 reprints of their papers, which are much appreciated.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association.

AMIRTHALINGAM, C. *Structure of Pearls.* "Nature," Vol. CXXIII, 1929, p. 129.

ATKINS, W. R. G. *The Alkalinity of Sea-water.* Science of the Sea, edited by G. H. Fowler and E. J. Allen, 2nd edn., 1928, ch. II, pp. 76–92.

ATKINS, W. R. G., AND POOLE, H. H. *The Integration of Light by Photo-electrolysis.* Sci. Proc. R. Dub. Soc., Vol. XIX, N.S., 1929, pp. 159–164.

ATKINS, W. R. G., AND POOLE, H. H. *The Photo-electric Measurement of the Illumination in Buildings.* Sci. Proc. R. Dub. Soc., Vol. XIX, N.S., 1929, pp. 173–187.

ATKINS, W. R. G., AND POOLE, H. H. *Photo-electric Measurements of Illumination in relation to Plant Distribution,* Part II. *Measurements with portable Galvanometers.* Sci. Proc. R. Dub. Soc., Vol. XIX, N.S., 1929, pp. 295–309.

ATKINS, W. R. G., AND POOLE, H. H. *The Uranyl oxalate Method of daylight Photometry and its Photo-electric Standardization.* Sci. Proc. R. Dub. Soc., Vol. XIX, N.S., 1929, pp. 321–339.

ATKINS, W. R. G., AND POOLE, H. H. *The Photo-chemical and Photo-electric measurement of the radiation from a Mercury Vapour Lamp.* Sci. Proc. R. Dub. Soc., Vol. XIX, N.S., 1929, pp. 355–361.

ATKINS, W. R. G., AND POOLE, H. H. *Methods for the photo-electric and photo-chemical measurement of daylight.* Conference of Empire Meteorologists, 1929. (Agricultural Section.)

BAIN, W. A. *The Action of Adrenaline and of Certain Drugs upon the isolated Crustacean Heart.* Quart. Journ, Exp. Phys., Vol. XIX, 1929, pp. 297–308.

BĚLEHRÁDEK, J., AND BĚLEHRÁDKOVÁ, M. *Influence of Age on the Temperature Coefficient of the Respiration Rate in Leaves of Scolopendrium scolopendrium Karst.* New Phytologist. Vol. XXVIII, 1929, pp. 313–318.

CANNON, H. G. *On the Feeding Mechanism of the Copepods Calanus finmarchicus and Diaptomus gracilis.* Brit. Journ. Exp. Biol., Vol. VI, 1928, pp. 131–144.

COOK, S. F. *The action of potassium cyanide and potassium ferricyanide on certain respiratory pigments.* Journ. Gen. Physiol., Vol. XI, 1928, pp. 339–348.

FOWLER, G. H., AND ALLEN E. J. *Science of the Sea. An Elementary Handbook of Practical Oceanography for Travellers, Sailors and Yachtsmen.* Second Edition. Oxford. 1928.

FRASER, A. H. H. *Lipin Secretion in the Elasmobranch Interrenal.* Quart. Journ. Micr. Sci., Vol. LXXIII, 1929, pp. 121–134.

FURUSAWA, K. *The Depolarization of Crustacean Nerve by Stimulation or Oxygen want.* Journ. Physiol., Vol. LXVII, 1929, pp. 325–342.

GRAY, J. *The Mechanism of Ciliary Movement.* Amer. Nat., Vol. LXIII, 1929, pp. 68–81.

HARVEY, H. W. *Methods of estimating Phosphates and Nitrates in Sea-water.* Cons. Perm. Internat. Rapp. et Proc. Verb. LIII, 1929, pp. 68–74.

HARVEY, H. W. *Hydrodynamics of the Waters South-East of Ireland.* Journ. du Conseil, Vol. IV, 1929, pp. 80–92.

HILL, A. V. *The Heat-Production and Recovery of Crustacean Nerve.* Proc. Roy. Soc. B., Vol. CV, 1929, pp. 153–176.

HILL, A. V. *The Maintenance of Life and Irritability in Isolated Animal Tissues.* "Nature," Vol. CXXIII, 1929, pp. 723–730.

KAPP, E. M. *The Precipitation of Calcium and Magnesium from Sea-water by Sodium hydroxide.* Biol. Bull., Vol. LV, 1928, pp. 453–458.

LEBOUR, M. V. *Floating Plants (Phytoplankton) and Borderland Forms.* Science of the Sea, edited by G. H. Fowler and E. J. Allen, 2nd edn., 1928, ch. IV, pp. 150–164.

OKADA, YÔ K. *Regeneration and Fragmentation in the Syllidian Polychaetes (Studies on the Syllidae II).* Arch. f. Entwick., Bd. CXV, 1929, pp. 542–600.

ORTON, J. H. *Reproduction and Death in Invertebrates and Fishes.* "Nature," Vol. CXXIII, 1929, pp. 14–15.

ORTON, J. H. *Oyster Cultivation and related researches in the British Isles.* "Nature," Vol. CXXIII, 1929, pp. 208–210.

ORTON, J. H. *British Oyster Fisheries.* "Nature," Vol. CXXIII, 1929, pp. 451–454.

ORTON, J. H. *Habitats and Feeding Habits of Ocinebra erinacea.* "Nature," Vol. CXXIV, 1929, pp. 370–371.

ORTON, J. H., AND AMIRTHALINGAM, C. *The Oyster-drills in English Oyster-beds.* "Nature," Vol. CXXIV, 1929, pp. 298–299.

RUSSELL, L. *The Comparative Morphology of the Elysioid and Æolidioid Types of the Molluscan Nervous System, and its bearing on the Relationships of the Ascoglossan Nudibranchs.* Proc. Zool. Soc., 1929, pp. 197–233.

STEPHENSON, T. A. *The British Sea Anemones.* I. Ray Society. London, 1928.

STEPHENSON, T. A. *A Contribution to Actinian Morphology : The Genera Phellia and Sagartia.* Trans. Roy. Soc. Edin., Vol. LVI, 1929, pp. 121–139.

SZENT-GYÖRGYI, A. *Observations on the Function of Peroxidase Systems and the Chemistry of the Adrenal Cortex. Description of a new Carbohydrate Derivative.* Biochem. Journ., Vol. XXII, 1928, pp. 1387–1409.

WILSON, D. P. *A Habit of the Common Periwinkle (Littorina littorea)* Linn. "Nature," Vol. CXXIV, 1929, p. 443.

YOFFEY, J. M. *A Contribution to the study of the Comparative Histology and Physiology of the Spleen, with reference chiefly to its Cellular Constituents. I. In Fishes.* Journ. Anat., Vol. LXXX, 1929, pp. 314–344.

Finance.

The Council wish to express their gratitude to the Development Commissioners for their continued support of the work of the Association. They have to thank also for generous grants the Fishmongers' Company (£600), the British Association (£50), the Royal Society (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol, Birmingham, Leeds, Manchester, Sheffield and the Imperial College of Science.

Officers, Vice-Presidents, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1930–31 :—

President.

Lieut.-Col. The Right Hon. WALTER E. GUINNESS, D.S.O., M.P.

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. Sir AUSTEN CHAMBERLAIN, K.G., M.P.
The Right Hon. NOEL BUXTON, M.P.
Sir W. B. HARDY, F.R.S.
GEORGE EVANS, Esq.
Sir NICHOLAS WATERHOUSE, K.B.E.
Prof. W. C. MCINTOSH, F.R.S.
G. A. BOULENGER, Esq., F.R.S.
J. O. BORLEY, Esq., O.B.E.

COUNCIL.

Elected Members.

Prof. J. BARCROFT, C.B.E., F.R.S.
ALEXANDER BOWMAN, Esq., D.Sc.
Prof. A. E. BOYCOTT, D.M., F.R.S.
Capt. G. C. C. DAMANT, R.N., C.B.E.
Prof. J. STANLEY GARDINER, F.R.S.
RONALD D'O. GOOD, Esq.
Prof. E. S. GOODRICH, D.Sc., F.R.S.
Prof. A. C. HARDY.
Prof. A. V. HILL, F.R.S.
C. F. A. PANTIN, Esq.
C. TATE REGAN, Esq., F.R.S.
A. D. RITCHIE, Esq.
G. C. ROBSON, Esq.
J. T. SAUNDERS, Esq.
Prof. D. M. S. WATSON, F.R.S.

Chairman of Council.

Prof. E. W. MACBRIDE, D.Sc., F.R.S.

Hon. Treasurer.

GEORGE EVANS, Esq., 1 Wood Street, London, E.C.2.

Hon. Secretary.

E. J. ALLEN, Esq., D.Sc,, F.R.S.,
The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council :—

G. P. BIDDER, Esq., Sc.D.
E. T. BROWNE, Esq.
GEORGE EVANS, Esq.
H. G. MAURICE, Esq., C.B. (Ministry of Agriculture and Fisheries).
R. HOLLAND MARTIN, Esq., C.B. (Prime Warden of the Fishmongers' Company).
NIGEL O. WALKER, Esq. (Fishmongers' Company).
LOTHIAN D. NICHOLSON, Esq. (Fishmongers' Company).
Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).
J. GRAY, Esq., 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).

List of Annual Subscriptions

Paid during the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
Dr. W. M. Aders	1	1	0
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
Aikawa, Hiroaki, Esq.	1	1	0
G. L. Alward, Esq.	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S. (1928 and 1929)	2	2	0
C. Amirthalingam, Esq. (1928 and 1929)	2	2	0
The Rt. Hon. Lord Askwith, K.C.B., D.C.L. (1928 and 1929)	2	2	0
Miss D. Atkins	1	1	0
G. R. de Beer, Esq.	1	1	0
Mrs. M. G. Bidder	1	1	0
Birkbeck College	1	1	0
H. Moss Blundell, Esq. (1927–1929)	3	3	0
Mrs. H. Moss Blundell (1928 and 1929)	2	2	0
L. A. Borradaile, Esq., D.SC. (1928 and 1929)	2	2	0
E. G. Boulenger, Esq. (1927–1929)	3	3	0
Col. Sir Henry Bowles, Bart. (1928 and 1929)	2	2	0
Dr. A. Bowman (1928 and 1929)	2	2	0
Dr. J. Borowik	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Sir J. Rose Bradford, K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
Brighton Public Library	1	1	0
H. H. Brindley, Esq. (1928 and 1929)	2	2	0
Miss E. M. Brown	1	1	0
Prof. F. Balfour Browne (1928 and 1929)	2	2	0
R. Brown, Esq.	1	1	0
Mrs. E. T. Browne (1928–1930)	3	3	0
R. H. Burne, Esq. (1928 and 1929)	2	2	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Dr. W. T. Calman, F.R.S. (1928 and 1929)	2	2	0
J. N. Carruthers, Esq.	1	1	0
Dr. A. H. Church, F.R.S. (1928 and 1929)	2	2	0
Dr. James Clark	1	1	0
R. S. Clark, Esq., D.SC. (1928–1930)	3	3	0
Carried forward	56	14	0

	£	s.	d.
Brought forward	56	14	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
J. S. Colman, Esq.	1	1	0
J. F. Coonan, Esq.	1	1	0
J. Omer Cooper, Esq. (1927–1929)	3	3	0
L. R. Crawshay, Esq.	1	1	0
Miss D. R. Crofts, D.SC.	1	1	0
N. Cuthbertson, Esq.	1	1	0
Prof. O. V. Darbishire	1	1	0
F. M. Davis, Esq. (1928 and 1929)	2	2	0
G. Despott, Esq. (1928–1930)	3	3	0
Director-General, Coastguard and Fisheries Service, Alexandria	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
Prof. J. C. Drummond (1928–1930)	3	3	0
F. Martin Duncan, Esq. (1928 and 1929)	2	2	0
Prof. J. S. Dunkerley, D.SC., PH.D.	1	1	0
Howard Dunn, Esq. (1928–1929)	2	2	0
V. C. Wynne Edwards, Esq.	1	1	0
P. Eggleton, Esq. (1928 and 1929)	2	2	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
George Evans, Esq.	1	1	0
G. P. Farran, Esq. (1928–1930)	3	3	0
Dr. R. A. Fisher, F.R.S.	1	1	0
The Fisheries Survey Committee, Capetown	1	1	0
Dr. Hussein Fawzy	1	1	0
Lt.-Col. T. Fetherstonhaugh, D.S.O. (1929 and 1930)	2	2	0
Dr. Ernest Foot	1	1	0
Dr. E. L. Fox (1928–1930)	3	3	0
Prof. H. Munro Fox (1928 and 1929)	2	2	0
Tadashi Fujita, Esq.	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
J. S. Gayner, Esq. (1929 and 1930)	2	2	0
S. G. Gibbons, Esq. (1927–1930)	4	4	0
Ronald D'Oyley Good, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
A. P. Graham, Esq. (1928 and 1929)	2	2	0
Dr. Robert W. Gray	1	1	0
J. R. Groome, Esq.	1	1	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Carried forward	120	15	0

	£	s.	d.
Brought forward	120	15	0
Prof. A. C. Hardy	1	1	0
C. R. Harington, Esq.	1	1	0
H. W. Harvey, Esq.	1	1	0
T. J. Hart, Esq. (1930 and 1931)	2	2	0
Dr. J. C. Hemmeter (1928 and 1929)	2	2	0
C. C. Hentschel, Esq. (1928–1930)	3	3	0
Prof. Sidney J. Hickson, D.SC., F.R.S. (1928–1930)	3	3	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S. (1928 and 1929)	2	2	0
Dr. W. T. Hillier	1	1	0
Prof. K. Hirasaka	1	1	0
Prof. Lancelot T. Hogben, D.SC. (1926 and 1927)	2	2	0
F. R. Horne, Esq.	1	1	0
Capt. G. C. L. Howell	1	1	0
O. D. Hunt, Esq.	1	1	0
Hull University College	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., D.SC.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
Dr. G. Lapage	1	1	0
The Hon. Lionel Lindsay	1	1	0
A. G. Lowndes, Esq. (1928 and 1929)	2	2	0
J. R. Lumby, Esq.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
G. I. Mann, Esq. (1928 and 1929)	2	2	0
Prof. E. W. MacBride, F.R.S. (1928 and 1929)	2	2	0
Capt. W. N. McClean	1	1	0
D. J. Matthews, Esq. (1928 and 1929)	2	2	0
B. J. Marples, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd. (1928 and 1929)	2	2	0
W. S. Millard, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerjii (1929 and 1930)	2	2	0
National Museum of Wales (1928 and 1929)	2	2	0
A. G. Nicholls, Esq.	1	1	0
Miss G. L. Naylor	1	1	0
Carried forward	176	8	0

	£	s.	d.
Brought forward	176	8	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC. (1928 and 1929)	2	2	0
R. Palmer, Esq.	1	1	0
G. W. Paget, Esq. (1928 and 1929)	2	2	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan, Ltd. (1929 and 1930)	2	2	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library (1928 and 1929)	2	2	0
Portsmouth Municipal College	1	1	0
W. P. Pycraft, Esq. (1928 and 1929)	2	2	0
C. Tate Regan, Esq., D.SC., F.R.S. (1927–1929)	3	3	0
H. G. Regnart, Esq.	1	1	0
E. A. Robins, Esq. (1928 and 1929)	2	2	0
G. C. Robson, Esq.	1	1	0
T. C. Roughley, Esq.	1	1	0
E. S. Russell, Esq., D.SC. (1928 and 1929)	2	2	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
R. E. Savage, Esq. (1928 and 1929)	2	2	0
J. T. Saunders, Esq.	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Miss Lilian Sheldon	1	1	0
B. Webster Smith, Esq.	1	1	0
The Rt. Hon. the Earl of Stradbroke, C.B., C.V.O. (1928 and 1929)	2	2	0
States Committee for Fisheries, Guernsey (1928 and 1929)	2	2	0
A. C. Stephen, Esq. (1928 and 1929)	2	2	0
Mrs. N. S. Steven	1	1	0
E. J. Stream, Esq.	1	1	0
H. H. Sturch, Esq.	1	1	0
E. J. Tabor, Esq. (1928 and 1929)	2	2	0
Carried forward	233	2	0

	£	s.	d.
Brought forward	233	2	0
H. E. Tabor, Esq. (1928 and 1929)	2	2	0
J. M. Tabor, Esq. (1928 and 1929)	2	2	0
S. Takeda, Esq.	1	1	0
Prof. W. M. Tattersall	1	1	0
Sir Herbert F. Thompson	1	1	0
Harold Thompson, Esq., D.SC., (1928 and 1929)	2	2	0
Mrs. M. A. Thynne	1	1	0
Torquay Natural History Society (1928 and 1929)	2	2	0
Arthur Walton, Esq.	1	1	0
Alan H. Ware, Esq.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
W. H. Webster, Esq.	1	1	0
Mrs. F. J. Weldon	1	1	0
W. B. Woodrow, Esq. (1928 and 1929)	2	2	0
D. P. Wilson, Esq.	1	1	0
Dr. K. B. Williamson	1	1	0
R. S. Wimpenny, Esq. (1928 and 1929)	2	2	0
Ronald Winckworth, Esq.	1	1	0
C. M. Yonge, Esq., D.SC., PH.D. (1929 and 1930)	2	2	0
Total	£260	8	0

List of Composition Fees

Paid during the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
The Rt. Hon. Walter Guinness, D.S.O., M.P.	15	15	0
Miss E. A. T. Nicol	15	15	0
Leonard K. Elmhirst, Esq.	15	15	0
Geo. T. Atkinson, Esq.	15	15	0
Prof. W. Garstang, D.SC.	15	15	0
Prof. F. A. E. Crew, D.SC., M.D.	15	15	0
Total	£94	10	0

List of Donations to the General Fund

For the Year, 1st April, 1929, to 31st March, 1930.

	£	s.	d.
R. Hansford Worth, Esq.	5	0	0
Col. Sir Henry Bowles, Bart.	2	18	0
Dr. K. B. Williamson	2	2	0
Mrs. H. Roberts	1	0	0
Total	£11	0	0

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£ s. d.	£ s. d.
To Balance from 31st March, 1929 :—		
Cash in hand	16 11 3	
Cash at Lloyds Bank £178 1 3		
Less Coutts & Co.—Overdratt 130 4 7	47 16 8	64 7 11
,, Grants :—		
Ministry of Agriculture and Fisheries Grant from Development Fund	11,152 10 5	
Fishmongers' Company	600 0 0	
British Association	50 0 0	
Royal Society (Gore Fund)	50 0 0	11,852 10 5
,, Subscriptions		260 8 0
,, Composition Fees		94 10 0
,, Donations		11 0 0
,, Sale of Specimens		1,384 16 1
,, ,, Fish (*less* Expenses)		55 11 6
,, ,, Nets, Gear, and Hydrographical Apparatus		720 5 3
,, Table Rent (including Cambridge University, £105 ; Oxford University, £52 10s. ; London University, £52 10s. ; Bristol University, £25 ; Leeds University, £10 10s. ; Imperial College of Science and Technology, £10 ; Trustees of the Ray Lankester Fund, £20)		410 7 0
,, Tank Room Receipts		487 0 3
,, Interest on Investments :—		
4% War Stock	3 2 8	
4% New Zealand Stock (Including Repayment of Income Tax)	26 5 6	29 8 2
,, Repayment £51 National Savings Certificates		69 8 6
,, Sale of Dr. M. V. Lebour's Book		6 4 10

The Association's Bankers held on its behalf :—
£410 14s. 8d. New Zealand 4%, 1943-63.
£237 17s. 11d. 4% War Stock, 1929-42 (Deed Stock).

£15,445 17 11

PLAICE EXPERIMENTS

	£ s. d.
To Grant from Ministry of Agriculture and Fisheries	225 0 0
,, General Fund	98 2 1
	£323 2 1

Year 1st April, 1929, to 31st March, 1930. **Cr.**

FUND.

	£ s. d.	£ s. d.
By Salaries :—		
Director	1,200 0 0	
Physiologist	910 0 0	
Naturalists	3,271 14 6	
Hydrographer	594 3 4	5,975 17 10
,, Laboratory Wages (including National Insurances) ...		1,899 18 4
,, Annual Upkeep of Library		636 7 1
,, Scientific Publications :—		
Journal, Vol. XVI, Nos. 1 and 2	756 11 4	
Less Sales	160 17 4	595 14 0
,, Annual Upkeep of Laboratories and Tank Rooms :—		
Buildings and Machinery	340 12 11	
Electricity, Gas, Coal, and Water	212 10 4	
Chemicals and Apparatus	505 8 5	
Rates, Taxes, and Insurance	96 17 5	
Travelling	121 8 2	
,, "Challenger" Society Meetings	29 5 2	
Stationery, Postages, Telephone, Carriage, and Sundries	446 18 7	
Purchase of Specimens	156 2 6	1,909 3 6
,, Annual Maintenance and Hire of Boats :—		
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,604 17 7	
Coal and Water	350 1 3	
Maintenance and Repairs, with Nets, Gear, and Apparatus	1,718 12 9	
Boat Hire and Collecting Expeditions	19 16 9	
Insurance	333 10 8	4,026 19 0
,, Interest on Bank Loan		9 0 5
,, Purchase of £91 15s. 11d. 4% War Stock 1929–42 (Investment of Composition Fees)	91 10 0	
,, Purchase of £67 12s 8d. 4% War Stock, 1929–42	69 8 6	163 18 6
,, Plaice Experiments Account :—		
Expenditure in Excess of Grant from Ministry of Agriculture and Fisheries		98 2 1
,, Balance, 31st March, 1930 :—		
Cash in hand	22 19 7	
Cash at Lloyds Bank £176 6 10		
Less Coutts & Co.—Overdraft 68 9 3	107 17 7	130 17 2
		£15,445 17 11

AT CAWSAND.

	£ s. d.
By Salary of Mr. B. Dawes	225 0 0
,, Incidental Expenses	98 2 1
	£323 2 1

Examined and found correct,

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
25th *April*, 1930.

(Signed) N. E. WATERHOUSE, *Auditor.*
L. D. NICHOLSON } *Members of*
D. M. S. WATSON } *Council.*

Marine Biological Association of the United Kingdom.

LIST

OF

Governors, Founders, and Members.

1st June, 1930.

* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

I.—Governors.

The British Association for the Advancement of Science, *Burlington House, W.* 1 ..... £940
The University of Oxford ..... £762 10*s.*
The University of Cambridge ..... £867 10*s.*
The Worshipful Company of Clothworkers, 41 *Mincing Lane, E.C.* 3 ..... £600
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4 ..... £20,955
The Zoological Society of London, *Regent's Park, N.W.* 8 ..... £500
The Royal Society, *Burlington House, Piccadilly, W.* 1..... £915
Bayly, Robert (the late) £600
Bayly, John (the late)..... £600
Thomasson, J. P. (the late) £970
*G. P. Bidder, Esq., Sc.D., *Cavendish Corner, Cambridge* £3008
*E. T. Browne, Esq., B.A., *Anglefield, Berkhamsted* £1235

II.—Founders.

1884 The Corporation of the City of London £210
1884 The Worshipful Company of Mercers, *Mercers' Hall, Cheapside, E.C.* 2 ..... £341 5*s.*
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, E.C.* £100
1884 The Royal Microscopical Society, 20 *Hanover Square, W.* 1 £152 10*s.*
1884 Bulteel, Thos. (the late) £100
1884 Burdett-Coutts, W. L. A. Bartlett (the late) £100
1884 Crisp, Sir Frank, Bart. (the late) £100
1884 Daubeny, Captain Giles A. (the late) £100
1884 Eddy, J. Ray (the late) £100
1884 Gassiott, John P. (the late) £100
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late) £101
1884 The Rt. Hon. Lord Masham (the late) £100
1884 Moseley, Prof. H. N., F.R.S. (the late)..... £100
1884 The Rt. Hon. Lord Avebury, F.R.S. (the late)..... £100
1884 Poulton, Prof. Edward B., M.A., F.R.S., *Wykeham House, Oxford* £105
1884 Romanes, G. J., LL.D., F.R.S. (the late)..... £100
1884 Worthington, James (the late) £100
1885 Derby, the late Earl of £100
1887 Weldon, Prof. W. F. R., F.R.S. (the late)..... £100
1888 Bury, Henry, M.A., *The Gate House*, 17 *Alumdale Road, Bournemouth West* £100
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.* £315
1889 The Worshipful Company of Grocers, *Poultry, E.C.* 2 ..... £120
1889 Thompson, Sir Henry, Bart. (the late)..... £110
1889 Revelstoke, The late Lord £100
1890 Riches, T. H., B.A., *Kitwells, Shenley, Herts* £430
1902 Gurney, Robert, *Bayworth Corner, Boars Hill, Oxford* ..... £107 1*s.*
1904 Shaw, J., K.C., *Adderbury House, Banbury, Oxfordshire* £113
1909 Harding, Colonel W. (the late) ..... £115 15*s.*
1910 Murray, Sir John, K.C.B., F.R.S. (the late)..... £100
1912 Swithinbank, H., F.R.S.E., F.R.G.S. (the late) £100
1913 Shearer, Dr. Cresswell, F.R.S., *Anatomy School, Cambridge* £100
1913 Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., *Large Acres, Selsey Bill, Sussex* ..... £125 15*s.*
1920 McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7..... £100
1920 Buckland of Bwlch, The Right Hon. Lord (the late) £105
1920 Llewellyn, Sir D. R. £105
1921 Harmer, F. W. (the late)..... £100
1923 Worth, R. H., 42 *George Street, Plymouth*..... £120 15*s.*
1924 The MacFisheries, Ltd., 125 *Lower Thames Street, E.C.* 3..... £100

1924 Murray, Lady, 7 *Egerton Gardens, London, S.W.* 3..... £100
1925 The Institution of Civil Engineers, *Great George Street, Westminster*, S.W. 1 ..... £100
1927 Bidder, Miss Anna, *Cavendish Corner, Cambridge* £100

III.—Members.

1900 Aders, Dr. W. M., *Zanzibar, East Africa*..... £5 and Ann.
1928 Aikawa, Hiroaki, *Imperial Fisheries Institute, Fukagawa, Tokio, Japan* ..... Ann.
1923 Alexander, W. B., *Marine Biological Association, Cleveland Shipyard, Middlesbrough* £10
*1895 Allen, E. J., D.Sc., F.R.S., *The Laboratory, Citadel Hill, Plymouth* ..... £20 10*s.* and Ann.
1889 Alward, G. L., *Enfield Villa, Humberstone Avenue, New Waltham, Grimsby, Lincs.* ..... Ann.
1925 Amemiya, Dr. Ikusaku, *University of Tokyo* (*Agriculture and Fisheries Department*), *Tokyo, Japan* ..... Ann.
1927 Amirthalingam, C., *Department of Zoology, University College, Gower Street, W.C.* 1 ..... Ann.
1910 Ashworth, Prof. J. H., D.Sc., F.R.S., *Zoology Department, The University, Edinburgh* ..... Ann.
1921 Askwith, The Rt. Hon. Lord, K.C.B., D.C.L., 5 *Cadogan Gardens, London, S.W.* 3 .....£5 and Ann.
†1911 Astor, The Right Hon. the Viscount, 4 *St. James's Square, London, S.W.* 1 ..... £10 and *C.*
1910 Atkinson, G. T., *Fisheries Office, Esplanade, Lowestoft, Suffolk*... *C.*
1929 Atkins, Miss D., *Woodlands, Eridge Road, Crowborough, Sussex*... Ann.

1920 Baker, J. R., *New College, Oxford*, and *The Dell, Malvern Wells* £1 and *C.*
*1928 Barcroft, Prof. J., F.R.S., *Glenveagh, Grange Road, Cambridge*... Ann.
1923 Barnard, K. H., *South African Museum, Cape Town, South Africa* £10
1923 Barnard, T. T., *King's College, Cambridge* £11
1929 Bayliss, L. E., *St. Cuthbert's, West Heath Road, London, N.W.* 3 £10 and *C.*
1921 Bazeley, W. J., *The Cliff, Penzance, Cornwall*..... Ann.
1885 Beck, Conrad, C.B.E., 34 *Upper Addison Gardens, London, W.* 14 *C.*
†1907 Bedford, His Grace the Duke of, K.G., *Endsleigh, Tavistock* £20 and *C.*
1928 Beer, G. R. de, 4 *Holywell, Oxford* ..... Ann.
1926 Bělehrádek, J., M.D., *Docent of General Biology, Masaryk University* (*Medical Faculty*), *Brno, Czechoslovakia*..... Ann.

1925 Berrill, N. J., *McGill University, Montreal, Canada* ..... Ann.
1903 Bidder, Colonel H. F., *Ravensbury Manor, Mitcham, Surrey*..... Ann.
1910 Bidder, Mrs. M. G., *Cavendish Corner, Cambridge* ..... Ann.
1925 Birkbeck College, *Bream's Buildings, Fetter Lane, London, E.C.* 4 Ann.
1910 Bloomer, H. H., "*Longdown*," *Sunnydale Road, Swanage, Dorset* ..... Ann.
1921 Blundell, H. Moss, *Ministry of Agriculture and Fisheries, 43 Parliament Street, London, S.W.* 1 ..... Ann.
1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts*..... Ann.
†1910 Borley, J. O., O.B.E., M.A., 5 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1..... £1 1*s.* and Ann.
1928 Borowick, Dr. J., *National Scientific Institute of Agriculture, Zacisze* 8, *Bydgoszcz, Poland* ..... Ann.
1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge* £1 1*s.* and Ann.
1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8..... Ann.
*1884 Bourne, Prof. Gilbert C., M.A., D.Sc., F.R.S., *Tubney House, Abingdon, Berks.* ..... £8 3*s.* and Ann.
1898 Bowles, Col. Sir Henry, Bart., *Forty Hall, Enfield, Middlesex* £2 18*s.* and Ann.
*1924 Bowman, Dr. A., *Marine Laboratory, Wood Street, Torry, Aberdeen* ..... Ann.
*1928 Boycott, Prof. A. E., F.R.S., 17 *Loom Lane, Radlett, Herts.* ..... Ann.
1910 Bradford, Sir J. Rose, K.C.M.G., M.D., D.Sc., F.R.S., 8 *Manchester Square, London, W.* 1..... Ann.
1926 Branfoot, J. M., *Oundle School, Oundle, Peterborough, Northants* Ann.
1902 Brighton Public Library (Henry D. Roberts, Chief Librarian)... Ann.
1924 Brightwell, L. R., *White Cottage, Chalk Lane, Horsham, Sussex* Ann.
1918 Brindley, H. H., *St. John's College, Cambridge* ..... £2 2*s.* and Ann.
1886 Brooksbank, Mrs. Mary, *Compton House, Lindfield, Sussex* ..... *C.*
1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*... £45 and *C.*
1929 Brown, R., *Seale Hayne College, Newton Abbot, Devon*..... Ann.
1924 Brown, W. Hargreaves, c/o *Messrs. Brown, Shipley and Co., Founder's Court, Lothbury, E.C.* 2 ..... £10 10*s.*
1928 Brown, Miss E. M., 53 *Pepys Road, W. Wimbledon, S.W.* 20..... Ann.
1892 Browne, Mrs. E. T., *Anglefield, Berkhamsted, Herts* ..... £50 and Ann.
1925 Bull, Herbert O., *Dove Marine Laboratory, Cullercoats, Northumberland*..... Ann.
1920 Burne, R. H., M.A., F.R.S., *Royal College of Surgeons, Lincoln's Inn Fields, London, W.C.* 2 ..... £10 5*s.* and Ann.
1925 Bush, S. Frank..... Ann.

1926 Butler, R. R., *Chemistry Department, Municipal Technical School, Plymouth*..... Ann.
1897 Byrne, L. W., 7 *New Square, Lincoln's Inn, London, W.C.* 2 £2 2*s.* and Ann.

1908 Calman, Dr. W. T., F.R.S., *British Museum (Natural History), Cromwell Road, S.W.* 7 ..... Ann.
1920 Cannon, Prof. H. Graham, Sc.D., *The University, Sheffield*..... Ann.
1927 Carruthers, J. N., *Fisheries Laboratory, Lowestoft, Suffolk* ..... Ann.
1923 Carter, G. S., *Department of Zoology, The University, Glasgow*... Ann.
1923 Chapman, His Honour Judge, *Lindum House, Lincoln*..... £21 and *C.*
1910 Clark, G. S. R. Kitson, *Meanwoodside, Leeds*..... Ann.
1911 Clark, Dr. J., *Rosehill, London Road, Kilmarnock, Ayrshire*..... Ann.
1924 Clark, R. S., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen* ..... Ann.
1887 Clarke, Rt. Hon. Sir E., K.C., 2 *Essex Court, Temple, E.C.* 4... £25
1928 Coastguard and Fisheries Service, *Alexandria, Egypt*..... Ann.
1886 Coates and Co., *Southside Street, Plymouth*..... £3 3*s.* and *C.*
1925 Cockshott, Lt.-Col. A. M., R.A.S.C., "*Colaba*," *Ryeworth Road, Charlton Kings, Cheltenham Spa, Glos.* ..... *C.*
1928 Cole, Prof. F. J., D.Sc., F.R.S., *Zoology Department, The University, Reading* ..... Ann.
1885 Collier Bros., *Plymouth* ..... *C.*
1930 Colman, J. S., *The Laboratory, Citadel Hill, Plymouth* ..... Ann.
1923 Coonan, J. F., *Balmoral House, Mumbles, Glamorgan* ..... Ann.
1920 Cooper, J. Omer, 23 *Leazes Terrace, Newcastle-on-Tyne* ..... Ann.
1925 Cox, P., *Stone House, Godalming, Surrey*..... £10 10*s.*
1909 Crawshay, L. R., M.A., c/o *The Colonial Secretary, Belize, British Honduras, B.W.I.* ..... Ann.
1928 Crew, Prof. F. A. E., D.Sc., M.D., *Animal Breeding Research Department, University of Edinburgh* ..... *C.*
1929 Crofts, Miss D. R., D.Sc., *King's College for Household and Social Science, Campden Hill, W.* 8 ..... Ann.
1930 Cuthbertson, N., 3 *Blenheim Road, Plymouth*..... Ann.

1922 Dale, H. H., C.B.E., M.D., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3 ..... Ann.
*1919 Damant, Captain G. C. C., R.N., C.B.E., *Thursford, Cambridge Road, East Cowes, Isle of Wight* ..... £5 and *C.*
1920 Darbishire, Prof. Otto V., *Botanical Department, The University, Bristol* ..... Ann.
1929 Darby, Dr. H. H., *Laboratorio Entomologico, Calzada Tacuba, 153, San Jacinto, Mexico, D.F.* ..... Ann.
1920 Davidson, Dr. W. Cameron, *Avonleigh, Acadia Road, Torquay*... Ann.

1925 Davis, F. M., *Fisheries Laboratory, Lowestoft, Suffolk*..... Ann.
1916 Delphy, J., *Faculté des Sciences de l'Université de Paris*, 12 *Rue Cuvier, Paris* ..... Ann.
1919 Despott, G., *Natural History Museum, Malta*..... Ann.
1915 Dick, G. W., J.P., c/o P.O. Box 28, *The Point, Durban, Natal, South Africa* ..... *C.*
1915 Director of Agriculture and Fisheries, *Travancore, Quilon, S. India* ..... Ann.
1925 "Discovery" Committee, 52 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1 ..... £73 10*s.*
1885 Dixey, F. A., M.A., Oxon, F.R.S., *Wadham College, Oxford* £26 5*s.* and Ann.
1910 Dobell, C. C., M.A., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3 ..... Ann.
1924 Dobson, H. V., J.P., *Bath and County Club, Bath*..... Ann.
1890 Driesch, Prof. Hans, Ph.D., *Department of Philosophy, The University, Leipzig* ..... *C.*
1924 Drummond, Prof. J. C., *University College, Gower Street, W.C.* 1 Ann.
1910 Duncan, F. Martin, 19 *Staverton Road, Brondesbury Park, London, N.W.* 2 ..... Ann.
1920 Dunkerly, Prof. J. S., D.Sc., Ph.D., *The University, Manchester* £2 2*s.* and Ann.
1921 Dunn, Howard, *Mevagissey, Cornwall*..... £2 and Ann.

1927 Eggleton, P., *Physiological Laboratory, University College, Gower Street, W.C.* 1 ..... Ann.
1929 Elmhirst, L. K., *Dartington Hall, Dartington, nr. Totnes, Devon* Ann.
*†1918 Evans, George, 1 *Wood Street, London, E.C.* 2 ..... £98 and Ann.
1923 Evans, W. Edgar, B.Sc., 38 *Morningside Park, Edinburgh* £9 5*s.* and *C.*
1928 Evans, Prof. C. Lovatt, F.R.S., *Institute of Physiology, University College, W.C.* 1..... Ann.
1885 Ewart, Prof. J. Cossar, M.D., F.R.S., *Craigybield, Penicuik, Midlothian* £26

1922 Farran, G. P., *Department of Fisheries*, 2 *Kildare Place, Dublin* £2 2*s.* and Ann.
1920 Farrer, The Hon. Noel, M.A., *The Red Cottage, Holmbury St. Mary, Dorking, Surrey* ..... £10 10*s.*
1929 Fawzy, Dr. Hussein, 11 *Rue Victor Cousin, Paris V*..... Ann.
1929 Fetherstonhaugh, Col. T., D.S.O., *Kirkoswald, Penrith, Cumberland*..... Ann.
1928 Fisher, Dr. R. A., F.R.S., *Rothamsted Experimental Station, Harpenden, Herts* ..... Ann.
1929 Fisheries Survey Committee, *Capetown* ..... Ann.

1929 Foot, Dr. Ernest, 50 *Norman Avenue, Stoke, Plymouth, Devon*... Ann.
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth, Devon*..... Ann.
1885 Fowler, G. Herbert, B.A., Ph.D., *The Old House, Aspley Guise, Bedfordshire*..... £15 10*s*. and Ann.
1920 Fox, Dr. E. L., 9 *Osborne Place, Plymouth*..... Ann.
1912 Fox, Prof. H. M., *Zoological Department, The University, Edgbaston, Birmingham* ..... Ann.
1924 Fraser, Miss E. A., D.Sc., *Dept. of Zoology, University College, Gower Street, W.C.* 1 ..... Ann.
1884 Fry, George, F.L.S., *Carlin Brae, Berwick-on-Tweed*..... £21
1928 Fujita, T., *Imperial Fisheries Institute, Fugakawa, Tokio, Japan* ..... Ann.
1929 Furusawa, K., *Osaka Medical College, Osaka, Japan*..... Ann.

*1906 Gardiner, Prof. J. Stanley, M.A., F.R.S., *Bredon House, Selwyn Gardens, Cambridge*..... £30 and Ann.
1907 Garstang, Prof. W., D.Sc., 35 *Weetwood Lane, Leeds*..... *C.*
1928 Gates, Prof. R. R., *Department of Botany, King's College, Strand, W.C.* 2 ..... *C.*
1924 Gayner, John S., *Hall Cottage, New Earswick, York*..... Ann.
1925 Gibbons, S. G., *Elora, Milltimber, Aberdeen* ..... Ann.
*1929 Good, R. D'O., *University College, Hull*..... Ann.
*1910 Goodrich, Prof. E. S., D.Sc., F.R.S., 6 *Park Town, Oxford* £7 and Ann.
1926 Graham, A. P., "*Inglenook*," 43 *Oakfield Road, Newport, Mon.* Ann.
*1912 Gray, J., F.R.S., *King's College, Cambridge* ..... £10 5*s*. and Ann.
1929 Gray, Dr. R. W., 8 *Hartley Road, Exmouth, Devon*..... Ann.
1920 Greenwood, J. F., *Gledhow, Oxenhope, Keighley, Yorks*..... £20
1924 Groome, J. R., *Ramridge Cottage, Weyhill, Andover, Hants* ..... Ann.
‡1928 Guinness, Lieut.-Col. The Rt. Hon. W., D.S.O., M.P., 10 *Grosvenor Place, London, S.W.* 1 ..... *C.*
1928 Gunther, E. R., "Discovery" Expedition, 52 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1 ..... *C.*

1926 Hacker, Dr. H. P., *Downe Cottage, Downe, Kent* ..... Ann.
1920 Hall, Wilfred, 9 *Prior's Terrace, Tynemouth, Newcastle-on-Tyne* Ann.
1924 Harding, Ambrose, *The Hall, Madingley, Cambridge*..... £35 10*s*.
*1923 Hardy, Prof. A. C., 32 *Park Avenue, Hull* ..... £1 1*s*. and Ann.
1929 Harington, C. R., *Greenfield, Bexmoor, Herts* ..... Ann.
*1885 Harmer, Sir Sidney F., K.B.E., D.Sc., F.R.S., *The Old Manor House, Melbourn, near Royston, Herts* ..... £34 11*s*.
1921 Harmer, T. B. £25
1925 Harmsworth, Cecil B., 13 *Hyde Park Gardens, W.* 2 ... £10 and Ann.
1929 Hart, T. J., "Discovery" Expedition, 52 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1 ..... Ann.

1924 Harvey, H. W., *The Laboratory, Citadel Hill, Plymouth* £5 5*s.* and Ann.
1910 Hefford, A. E., B.Sc., *Marine Department, Wellington, New Zealand* ..... Ann.
1926 Hemmeter, John C., Phil.D., M.D., LL.D., 739 *University Parkway, Baltimore, Md., U.S.A.* ..... Ann.
1925 Hentschel, C. C., *Biology Department, St. Bartholomew's Medical College, London, E.C.* 1 ..... Ann.
1926 Hickling, C. F., *Fisheries Laboratory, Lowestoft, Suffolk* £4 4*s.* and Ann.
1884 Hickson, Prof. Sydney J., M.A., D.Sc., F.R.S., 26 *Barton Road, Cambridge* ..... Ann.
*1926 Hill, Prof. A. V., F.R.S., *Physiological Laboratory, University College, Gower Street, London, W.C.* 1..... Ann.
1907 Hill, Prof. J. P., F.R.S., *Anatomical Institute, University College, London, W.C.* 1..... Ann.
1919 Hillier, W. T., M.R.C.S., 23 *Francis Road, Edgbaston, Birmingham* ..... Ann.
1921 Hindle, Prof. E., *London School of Hygiene and Tropical Medicine*, 1 *Keppel Street, W.C.* 1 ..... *C.*
1926 Hirasaka, Prof. K., *Zoology Department, Imperial University, Formosa* ..... £2 2*s.* and Ann.
1926 Hobson, A. D., *Zoological Department, The University, Edinburgh* Ann.
1925 Hogben, Prof. Lancelot T., D.Sc., *Zoological Department, University of Cape Town, Cape Town, South Africa*..... Ann.
1928 Holmes, Dr. E. G., *Pharmacological Laboratory, Cambridge*..... Ann.
1927 Horne, F. R., *Seale Hayne Agricultural College, Newton Abbot, Devon* ..... Ann.
1920 Howell, Capt. G. C. L., c/o *H. S. King & Co.*, 9 *Pall Mall, London, S.W.* 1 ..... Ann.
1918 Hoyte, P., "*Mutley*," *Elburton Cross S.O., Devon*..... Ann.
1929 Hull University College ..... Ann.
1928 Hunt, O. D., *Hillside, Court Wood, Newton Ferrers, Devon*..... Ann.
1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester* £5 and *C.*
1912 Huxley, Prof. J. S., *King's College, Strand, London, W.C.* 2 £4 and Ann.

†1899 Iveagh, The Rt. Hon. the Earl of, C.B., C.M.G., 11 *St. James's Square, S.W.* 1 ..... £45 15*s.*

1921 Jenkins, Mrs. W., *Westhide, Hereford* £50
1927 Jennings, D. A., *New College, Oxford*..... Ann.
1924 Jesus College, *Oxford* £50
1923 Judge, J. J., 2 *Apsley Road, Plymouth*..... 10*s.* 6*d.* and Ann.

1928 Kemp, Dr. Stanley, "*Beechwood*," *Beechwood Avenue, Weybridge* ..... Ann.

1928 King, Mrs. A. Redman, *Westwood Hall, Leeds, Yorks*..... Ann.
1927 Kirtisinghe, P., *Zoology Department, University College, Colombo* Ann.

1897 Lanchester, W. F., B.A..... *C.*
1928 Lapage, Dr. G., *Department of Biology, University College, Exeter* Ann.
1928 Laurie, Prof. R. D., *Department of Zoology, University College of S. Wales, Aberystwyth* ..... Ann.
1925 Lebour, Miss M. V., D.Sc., *The Laboratory, Citadel Hill, Plymouth* *C.*
1920 Lewin, Mrs., *Parkhurst, Abinger Common, Dorking, Surrey*..... £50
1924 Lindley, Miss J., 74 *Shooters Hill Road, Blackheath, S.E.* 3..... £25
1926 Lindsay, The Hon. Lionel, *Hambrook House, Chichester, Sussex* Ann.
1926 Lowndes, A. G., *Marlborough College, Marlborough, Wilts*..... Ann.
1924 Lumby J., R., *Fisheries Laboratory, Lowestoft, Suffolk*..... Ann.

*1910 MacBride, Prof. E. W., M.A., D.Sc., F.R.S., *Royal College of Science, South Kensington, S.W.* 7 ..... Ann.
1900 Macfie, J. W. Scott, 45 *Rodney Street, Liverpool*..... *C.*
1929 Mackinnon, Prof. D. L., D.Sc., *Department of Zoology, King's College, Strand, W.C.* 2 ..... Ann.
1925 Magdalen College, *Oxford* £25
1902 Major, Surgeon H. G. T., 24 *Beech House Road, Croydon, Surrey* *C.*
1925 Mann, G. I., "*Trencrom*," *Briar Road, Hartley, Plymouth*..... Ann.
1928 Manton, Miss S. M., M.A., Ph.D., *Zoological Laboratory, The Museums, Cambridge* ..... *C.*
1928 Marples, B. J., *Department of Physiology, Victoria University, Manchester* ..... Ann.
1885 Marr, Prof. J. E., M.A., F.R.S., *St. John's College, Cambridge*... *C.*
1910 Matthews, D. J., *Hydrographic Department, Admiralty, London, S.W.* 1 ..... Ann.
1926 Maude, J. C., *Redlap House, near Dartmouth, S. Devon*..... Ann.
*1912 Maurice, H. G., C.B., *Ministry of Agriculture and Fisheries,* 43 *Parliament Street, S.W.* 1 ..... Ann.
1920 McClean, Lt.-Col. Sir F. K., *Huntercombe Place, Henley-on-Thames* £10
1910 McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7..... Ann.
†1884 McIntosh, Prof. W. C., F.R.S., 2 *Abbotsford Crescent, St. Andrews* *C.*
1925 McPhail, Angus, *Cranford, Kidbrook Grove, Blackheath, S.E.* 3... £10
1923 Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd..... Ann.
1919 Millard, W. S., 70 *Mount Ephraim, Tunbridge Wells* £1 1*s.* and Ann.
*1905 Mitchell, Sir P. Chalmers, Kt., C.B.E., D.Sc., F.R.S., Secretary, Zoological Society, *Regent's Park, London, N.W.* 8 ... £5 and Ann.
1930 Moorhouse, F. W., *The University, Brisbane, Queensland*..... Ann.
1915 Morley, C. C., *Trelawne, Duloe, R.S.O., Cornwall*..... Ann.

1929 Mukerjii, Dr. J., 224 *Woodhouse Street, Leeds*..... Ann.
1928 Murakami, Jiro, *Kurodasho-mura, Takagaun, Hyogo-ken, Japan* Ann.

1884 Napier, Mrs., *Upton House, Sandwich, Kent* £20
1924 National Museum of Wales, *Cardiff*..... Ann.
1928 Naylor, Miss G. L., 261 *Trinity Road, London, S.W.* 8..... Ann.
1928 Neill, R. G., 434 *Liverpool Road, Birkdale, Southport*..... Ann.
1921 Newth, H. G., *The University, Edgbaston, Birmingham* ..... Ann.
1930 Nicholls, A. G., *The Laboratory, Citadel Hill, Plymouth* ..... Ann.
1929 Nicol, Miss E. A. T., 15 *Blacket Place, Edinburgh*..... *C.*
1928 Norman, J. R., *Natural History Museum, Cromwell Road, S.W.* 7 Ann.

1911 Oldham, Chas., *The Bollin, Berkhamsted, Herts*..... Ann.
1930 Olive, G. W., *Dauntsey School, West Lavington, near Devizes, Wilts*..... Ann.
1910 Orton, Prof. J. H., D.Sc., *Department of Zoology, The University, Liverpool* ..... £2 2*s.* and Ann.
1928 Otter, G. W., *Selehurst, Horsham, Sussex* ..... *C.*

1928 Palmer, R., *Department of Zoology, University College, Gower Street, W.C.* 1 ..... Ann.
*1923 Pantin, C. F. A., *Trinity College, Cambridge* ..... £20 15*s.*
1924 Pantin, Herbert, 72 *Shooters Hill Road, Blackheath, S.E.* 3... £52 10*s.*
1924 Pantin, W. A., *Christchurch, Oxford*..... £10 10*s.*
1927 Parker, The Hon. John H., *Saltram, Plympton, Devon* ..... Ann.
1928 Parsons, C. W., *Zoology Department, The University, Glasgow*... Ann.
1915 Pascual, Enrique, O.B.E., P.O. Box 8, *Galicia, Vigo, Spain*..... Ann.
1920 Pass, A. Douglas, *Wootton Fitzpaine, Charmouth, Dorset*..... £20
1925 Pawlyn Brothers, *Mevagissey, Cornwall*..... £5 and Ann.
1925 Pawlyn, T. A., *Mevagissey, Cornwall*..... £1 1*s.* and Ann.
1929 Peacock & Buchan, Messrs., Paint Manufacturers, *Southampton* Ann.
1925 Pentelow, F. T. K., *Fisheries Experimental Station, Barnard Castle, Northumberland* ..... 10*s.* 6*d.* and Ann.
1929 Percival, Prof. E., *Canterbury College, Christchurch, New Zealand* Ann.
1917 Phillips, Montagu. A., 57 *St. George's Square, London, S.W.* 1 *C.*
1924 Plender, Sir William, Bart., G.B.E., 51 *Kensington Court, W.* 8 £10 10*s.*
1906 Plymouth Corporation (Museum Committee) ..... Ann.
1910 Plymouth Education Authority..... Ann.
1929 Plymouth Public Library ..... Ann.
1924 Plymouth Proprietary Library, *Cornwall Street, Plymouth* ..... Ann.
1906 Port of Plymouth Incorporated Chamber of Commerce..... Ann.
1929 Portsmouth Municipal College ..... Ann.
1910 Porter, Mrs. H., 5 *Hanover House, Regent's Park, London, N.W.* 8 £10 5*s.* and Ann.

1913 Potts, F. A., M.A., *Trinity Hall, Cambridge* £26
1928 Proctor, W., *Bar Harbor, Maine, U.S.A.*..... Ann.
1919 Pycraft, W. P., *British Museum (Natural History), Cromwell Road, London, S.W.* 7 ..... Ann.

*1916 Regan, C. Tate, D.Sc., F.R.S., *British Museum (Natural History), Cromwell Road, S.W.* 7..... Ann.
1929 Regnart, H. C., 33 *Eskdale Terrace, Jesmond, Newcastle-on-Tyne* . Ann.
1928 Reid, D. M., *Science Schools, Harrow-on-the-Hill*..... Ann.
*1919 Ritchie, A. D., M.A., *The University, Manchester*..... £32 15*s.*
1924 Roberts, Sir James, Bart., *The Hall, Fairlight, near Hastings, Sussex* ..... £10 10*s.*
1926 Robins, E. A., "*Gorran*," 19 *Cassiobury Park Avenue, Watford, Herts* ..... £1 1*s.* and Ann.
*1922 Robson, G. C., *British Museum (Natural History), S. Kensington, S.W.* 7 ..... Ann.
1925 Rogers, T. Howard, 16 *Gt. Western Arcade, Birmingham*..... Ann.
1928 Roughley, T. C., *Technological Museum, Sydney, N.S.W.*..... Ann.
1928 Roy, H. N., *Zoological Department, King's College, Strand, W.C.*2 Ann.
1924 Rudge, Chas. H., *Trevean, St. Ives, Cornwall*..... Ann.
1922 Russell, E. S., D.Sc., *Ministry of Agriculture and Fisheries, 43 Parliament Street, London, S.W.* 1 ..... £1 1*s.* and Ann.
1927 Russell, F. S., D.S.C., D.F.C., *The Laboratory, Citadel Hill, Plymouth* ..... £2 2*s.* and Ann.

1927 St. Aubyn, Capt. the Hon. Lionel, M.V.O., *Saltram, Plympton, Devon* ..... Ann.
†1926 St. Levan, The Right Hon. Lord, C.B., C.V.O., *St. Michael's Mount, Marazion, Cornwall* ..... Ann.
*1911 Saunders, J. T., M.A., *Christ's College, Cambridge*..... £2 2*s.* and Ann.
1914 Savage, R. E., *Ministry of Agriculture and Fisheries, Fisheries Laboratory, Lowestoft, Suffolk* ..... Ann.
1901 Schiller, F. W., *Park House, Sandon, Stafford*..... Ann.
1909 Schuster, Edgar, D.Sc., 110 *Banbury Road, Oxford*..... Ann.
1884 Sclater, W. L., 10 *Sloane Court, London, S.W.* 1..... Ann.
1885 Scott, D. H., M.A., Ph.D., F.R.S., *East Oakley House, Oakley, Hants* ..... *C.*
1921 Scott, Peter, *Leinster Corner, Lancaster Gate, London, W.*2 ... *C.*
1928 Sen, B., *Vivekananda Laboratory, Baghbazar, Calcutta, India* ... Ann.
1922 Sewell, Major R. B. Seymour, I.M.S., *Zoological Survey of India, Indian Museum, Calcutta* ..... Ann.
1885 Sheldon, Miss Lilian ..... Ann.
1884 Skinners, the Worshipful Company of, *Skinners' Hall, E.C.*..... £42
1930 Smedley, N., Esq., *Raffles Museum, Singapore* ..... Ann.
1927 Smith, B. Webster, 9 *Tancred Road, London, N.* 4 ..... Ann.

1929 Smith, F. G. W., 79 *Edith Avenue, Mount Gold, Plymouth, Devon* Ann.
1925 Smith, Thos. and Wm., Ltd., *Guildhall, Newcastle-upon-Tyne*... Ann.
1930 Spooner, G. M., Esq., *The Laboratory, Citadel Hill, Plymouth*... Ann.
1924 States Committee for Fisheries, *States Office, Guernsey*..... Ann.
1925 Stephen, A. C., *Royal Scottish Museum, Edinburgh*..... Ann.
1930 Stephenson, T. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1 ..... Ann.
1930 Steven, Mrs. N. S., *Reservoir House, Skardon Place, Plymouth, Devon* ..... Ann.
†1921 Stradbroke, the Right Hon. the Earl of, K.C.M.G., C.V.O., C.B., *Henham Hall, Wangford, Suffolk*..... £5 5*s.* and Ann.
1924 Stream, Ernest J., M.A., *Wintringham Secondary School, Grimsby, Lincs.* ..... Ann.
1924 Sturch, H. H., 8 *Collingwood Villas, Stoke, Devonport* £1 1*s.* and Ann.

1926 Tabor, Eric J., *Imperial House, Pudding Lane, Billingsgate, E.C.* 3 ..... Ann
1926 Tabor, Harold E., *Imperial House, Pudding Lane, Billingsgate, E.C.* 3 ..... Ann.
1926 Tabor, J. M., *Imperial House, Pudding Lane, Billingsgate, E.C.* 3 Ann.
1919 Takeda, S., c/o 38 *Nichome, Utsubo-Kamidori, Nishiku, Osaka, Japan* ..... Ann.
1924 Tattersall, Prof. W. M., D.Sc., *Zoological Laboratory, University College, Cardiff* ..... Ann.
1922 Taylor, Joseph Allen, F.S.S., *The Haven, Montpelier Avenue, Bispham, Blackpool* ..... *C.*
1925 Telegraph Construction and Maintenance Co., Ltd., 38 *Old Broad Street, London, E.C.* 2 ..... £10 10*s.*
1930 Thomas, Sir Charles Howell, K.C.B., C.M.G., *Secretary, Ministry of Agriculture and Fisheries*, 43 *Parliament Street, S.W.* 1 ..... Ann.
1899 Thompson, Prof. D'Arcy W., C.B., F.R.S., *University, St. Andrews, Fife* ..... Ann.
1924 Thompson, Harold, D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen* ..... Ann.
1890 Thompson, Sir Herbert F., Bart., *The Old House, Aspley Guise, Beds* ..... £9 9*s.* and Ann.
1929 Thynne, Mrs. M. A., M.R.C.S., *Byron House, Stonehouse, Plymouth, Devon* ..... Ann.
1903 Torquay Natural History Society, *The Museum, Torquay*..... Ann.

1930 Vernon, R. C., Esq., 27 *Hamilton Gardens, Mutley, Plymouth*... Ann.

1919 Walker, Cecil F. A. ..... £5 and *C.*
*1920 Walker, Major Nigel O., O.B.E., *Medland Manor, Cheriton Bishop, Exeter, Devon* ..... £5 and Ann.

1928 Walton, A., *School of Agriculture, Cambridge*..... Ann.
1926 Walton, B. H., *Cawsand, Cornwall* ..... £2 2*s*. and Ann.
1927 Ware, Alan H., Ph.C., *Technical College, Tavistock Road, Plymouth*..... Ann.
†1906 Waterhouse, Sir Nicholas E., K.B.E., 3 *Frederick's Place, Old Jewry, London, E.C.* 2..... £5 and Ann.
1909 Waters, Arthur W., F.L.S., *Alderley, McKinley Road, Bournemouth* ..... Ann.
*1923 Watson, Prof. D. M. S., F.R.S., *Zoological Laboratory, University College, London, W.C.* 1..... Ann.
1920 Webb, Lieut.-Col. Sir Henry, Bart. *Llewynarthan, Castleton, Cardiff* £50
1928 Webster, W. H., "*Eocene*," *Fairfield Road, Barton-on-Sea, Hants* Ann.
1906 Weldon, Mrs. F. J., 3 *South Parks Road, Oxford*... £20 10*s*. and Ann.
1919 Wells, G. P., *Department of Zoology, University College, Gower Street, W.C.* 1 ..... *C*.
1930 Westbrook, Miss M. A., *Westfield College, London, N.W.* 3..... Ann.
1900 Willey, Prof. A., D.Sc., F.R.S., *McGill University, Montreal, Canada*..... £20
1929 Williamson, Dr. K. B., *The College of Medicine, Singapore* £2 2*s*. and Ann.
1927 Wilson, D. P., *The Laboratory, Citadel Hill, Plymouth*..... Ann.
1928 Wimpenny, R. S., *Coastguards and Fisheries Service, Alexandria, Egypt* ..... Ann.
1919 Winckworth, Ronald, M.A., F.R.G.S., *The Royal Society, Burlington House, London, W.* 1 ..... £1 and Ann.
1928 Wynne Edwards, V. C., *Department of Zoology, The University, Bristol* ..... Ann.

1927 Yonge, C. M., D.Sc., Ph.D., *The Laboratory, Citadel Hill, Plymouth* ..... Ann.

IV.—Associate Members.

1928 Cunningham, J. T., 35 *Wavendon Avenue, Chiswick, London*, W. 4.
1904 Freeth, A. J., *Fish Quay, North Shields.*
1904 Hurrell, H. E., 25 *Regent Street, Yarmouth.*
1904 Patterson, Arthur, *Ibis House, Great Yarmouth.*
1901 Sanders, W. J., *Rockvall, Brixham.*

THE

QUARTERLY JOURNAL

OF

MICROSCOPICAL SCIENCE

EDITOR:

EDWIN S. GOODRICH, F.R.S.

CONTENTS OF No. 290—NEW SERIES.
Part II, Volume 73, November, 1929.

MEMOIRS.

Subscription Price per Volume, £3 3s. net.
Single Parts £1 1s. net.

OXFORD UNIVERSITY PRESS
AMEN HOUSE, LONDON, E.C. 4

INDEX

OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of ARGYLL, Sir LYON PLAYFAIR, Lord AVEBURY, Sir JOSEPH HOOKER, Dr. CARPENTER, Dr. GÜNTHER, Lord DALHOUSIE, Professor MOSELEY, Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000, and from that time until 1926 a sum of over £6,500 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.

CONTENTS OF NEW SERIES, Vol. XVI., No. 3.

NOTICE.

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.

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, &c.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Plymouth.