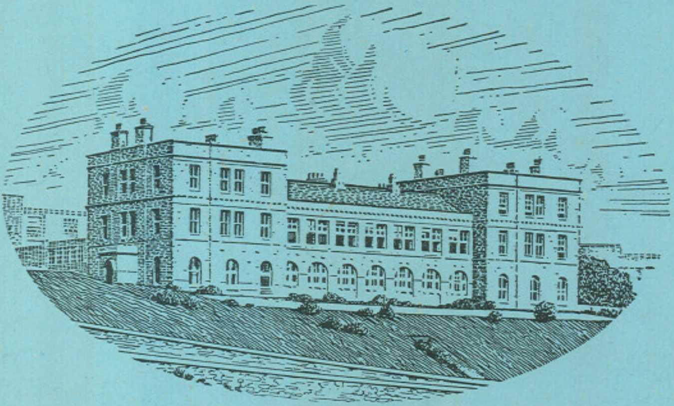
# JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXVIII, No. 3
*(issued December 1949 and completing Volume XXVIII)*

CAMBRIDGE
AT THE UNIVERSITY PRESS
1949

*Price Twenty-six Shillings net*

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# CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL *SCOMBER SCOMBRUS* L.

## II. A STUDY OF THE FISHERY IN THE SOUTH-WEST OF ENGLAND, WITH SPECIAL REFERENCE TO SPAWNING, FEEDING, AND 'FISHERMEN'S SIGNS'

By G. A. Steven, B.Sc., F.R.S.E.
Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1–6)

CONTENTS

### INTRODUCTORY SURVEY

In a previous paper (Steven, 1948), brief accounts are given of three distinct mackerel fisheries that at one time existed in the south-west of England—an inshore fishery in the English Channel carried on from Plymouth, a deep-sea fishery from Newlyn, Cornwall, and an inshore fishery from Newlyn and some other Cornish ports. One of these fisheries, the Plymouth one, no longer exists. After a few years of considerable activity following the termination of the 1914–18 war, this fishery collapsed in 1924 (Table I) and came entirely to an end a few years later. The small quantities of mackerel landed at Plymouth in subsequent years have been incidental catches by vessels fishing for herrings or pilchards.

The Cornish inshore fishery took place mainly at no great distance to seaward of the northern shore of the Devon-Cornwall peninsula and was carried on chiefly by small local craft, both wind- and motor-driven; but a number of visiting east-coast drifters used also to participate, especially during January and February, when stormy weather prevented their going very far to sea in search of other shoals in deeper waters beyond the Scilly Islands (Steven, 1948,

p. 520, fig. 3). Soon this fishery too fell upon hard times and the small local craft gradually abandoned mackerel fishing. In 1931 the local Fisheries Officer reported to the Cornwall Sea Fisheries Committee that, so far as local vessels were concerned, the fishery had arrived almost at the point of extinction.

The failure of both the Plymouth and Newlyn inshore fisheries was due to a decline in the quantity of fish in nearby waters, combined with low prices which made small catches unremunerative. The fall in fishing yield in those years is clearly reflected in the mean weight of fish per landing by the local vessels engaged in the Newlyn fishery. At no time[1] from 1906 (when reliable returns first became available) until 1927 did this average fall below 10 cwt. (Text-fig. 1), and was generally much higher. But with the single exception of 1928 the 10 cwt. figure was never again reached; in fact the individual landings were generally less than half that amount. These weights are a reasonably accurate index of the quantity of fish available on the fishing grounds because landings by local vessels represent only one night's fishing.

TABLE I. QUANTITY OF MACKEREL LANDED AT PLYMOUTH, 1919–38 INCLUSIVE (IN CWT.)

| Year | Quantity | Year | Quantity | Year | Quantity |
|---|---|---|---|---|---|
| 1919 | **15,521** | 1926 | 4080 | 1933 | 2200 |
| 1920 | **33,618** | 1927 | 3080 | 1934 | 1859 |
| 1921 | **18,117** | 1928 | 2582 | 1935 | 2401 |
| 1922 | **18,198** | 1929 | 3005 | 1936 | 2670 |
| 1923 | **15,551** | 1930 | 3109 | 1937 | 1669 |
| 1924 | 5,366 | 1931 | 3101 | 1938 | 1156 |
| 1925 | 5,229 | 1932 | 4709 | | |

Many of the steam drifters reacted to the decline in the inshore fish stocks by postponing their arrival in Newlyn until about the beginning of March in each year, when weather conditions permitted them to proceed at once to more distant fishing localities in the open sea well beyond the Scilly Islands, where better catches were to be had on different bodies of fish migrating in from the westward. But even as late as 1930 some steamers still endeavoured to obtain satisfactory catches in nearby localities in January and early February, but without success, and they worked at a loss until better weather in March enabled them to proceed to the distant grounds where better results were obtained. This was the very last year in which steam drifters fished from Newlyn as early as January. Since that time the steam-drifter fishery has opened invariably on the deep-sea grounds not earlier than the last days of February or the first days of March. But even the deep-sea grounds failed to provide satisfactory returns for all the participating craft and many of them gave up mackerel fishing altogether (Table II), their numbers falling from 90 in 1920 to 23 in 1940, the last year of normal fishing.

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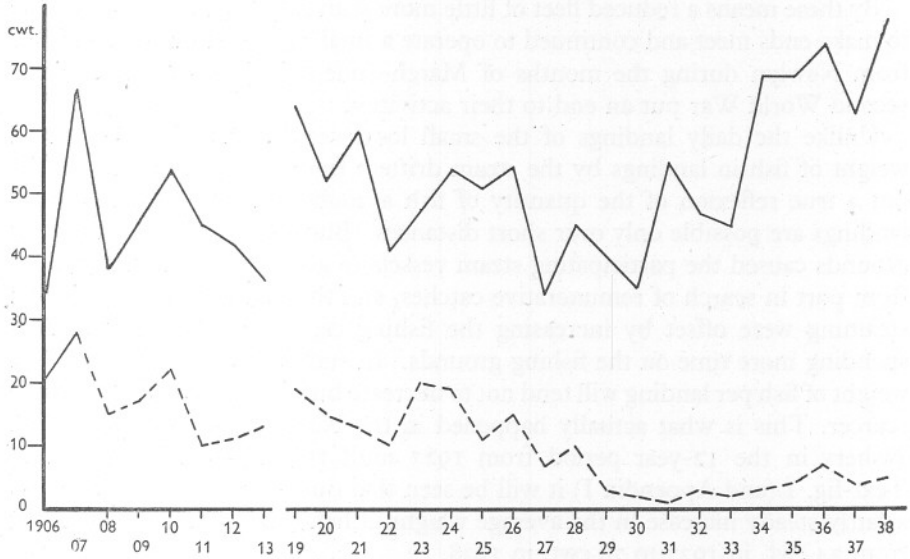
[1] War years excepted.

The steam drifters that did not give up fishing strove to maintain their catches at remunerative levels by working at ever increasing distances from land until eventually, from about 1927 onwards, it became the regular custom of most of the fleet to open the fishery every spring on grounds as much as 100 miles or more to seaward of the Bishop Rock (Scilly Islands) on bearings lying generally between W.N.W. and W.S.W.



Text-fig. 1. Mean weight in cwt. of mackerel per landing at Newlyn in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

### TABLE II. NUMBER OF STEAM DRIFTERS FISHING FROM NEWLYN IN THE YEARS 1920–40 INCLUSIVE

| Year | No. | Year | No. | Year | No. | Year | No. |
|---|---|---|---|---|---|---|---|
| 1920 | 90 | 1926 | 82 | 1931 | 47 | 1936 | 31 |
| 1921 | 60 | 1927 | 74 | 1932 | 43 | 1937 | 23 |
| 1922 | 80 | 1928 | 60 | 1933 | 43 | 1938 | 27 |
| 1923 | 80 | 1929 | 55 | 1934 | 35 | 1939 | 25 |
| 1924 | 68 | 1930 | 52 | 1935 | 34 | 1940 | 23 |
| 1925 | 87 | | | | | | |

Daily landings from these distant grounds obviously became impossible, so the practice of preserving the fish in ice was extended and improved to enable the ships to stay at sea for more than one night at a time on each fishing trip. Single landings at the beginning of the season, therefore, came to represent as many as 4 nights' fishing.

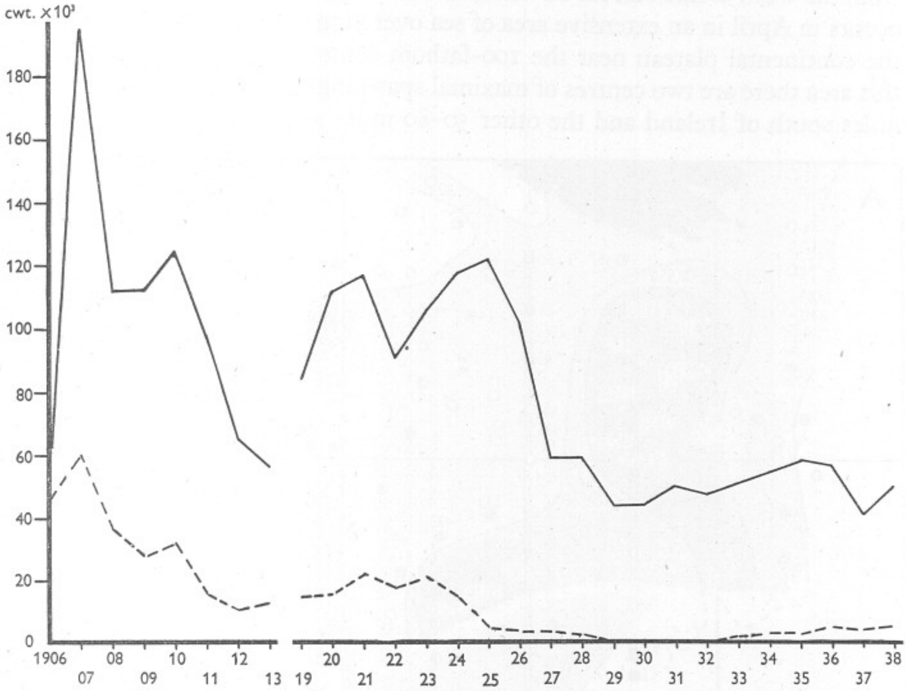
At the same time the fishing capacity of each drifter was also undergoing an important change. Before the war of 1914–18 the nets used by those craft were of a type known as 'fly nets' and had a standard size of about 20 yd. length and 5 yd. depth. On resumption of fishing after peace returned a larger 'footrope net' began to be introduced which is about 33 yd. long and just over 6 yd. deep. By about 1933 the old type had been almost entirely replaced by the new. The number of nets in each fleet remained unchanged at approximately 180. The fishing area of each drifter's fleet of nets was therefore almost exactly doubled, rising from approximately 18,000 sq.yd. to approximately 36,000 sq.yd.

By these means a reduced fleet of little more than a score of drifters was able to make ends meet and continued to operate a small deep-sea mackerel fishery from Newlyn during the months of March–June until the outbreak of the second World War put an end to their activities.

Unlike the daily landings of the small local vessels, therefore, the mean weight of fish in landings by the steam drifters from about 1927 onwards, is not a true reflexion of the quantity of fish available on the grounds. Daily landings are possible only over short distances. But scarcity of fish on nearby grounds caused the participating steam vessels to go farther and farther away from port in search of remunerative catches, and the additional costs of extra steaming were offset by increasing the fishing capacity of the nets and by spending more time on the fishing grounds. In such circumstances the mean weight of fish per landing will tend not to decrease but to increase as fish become scarcer. This is what actually happened in the Newlyn Deep-Sea Mackerel Fishery in the 12-year period from 1927 until 1938. From inspection of Text-fig. 1 (and Appendix I) it will be seen that during those years there was a fairly steady increase in the average weight of fish per steam-drifter landing from 34 cwt. in 1927 to 78 cwt. in 1938.

There was no corresponding increase in the total yield of the fishery. This, in fact, from 1927 onwards, remained remarkably constant (Text-fig. 2), because, although the mean weight per landing increased, the number of landings decreased. This decrease in the number of landings was due only in part to the increased length and duration of the fishing trips. Another and more important cause was a gradual decline in the public demand for mackerel. This is indicated by their market value on first sale (Table III), which fell steadily from 19*s*. 5*d*. per cwt. in 1929 to only 9*s*. 11*d*. in 1936. There was a slight recovery to 13*s*. 8*d*. in 1937, but another fall to 12*s*. 4*d*. in 1938.

More mackerel could have been landed by the existing fleet if the demand for them had existed; for from about 1930 onwards the skippers of steam drifters working from Newlyn voluntarily agreed from time to time to stay in port for from 1 to 3 days after each landing in order not to cause a glut of unwanted fish on a sluggish market. In some years approximately 20% of possible fishing time was lost in this way. The Statistical Tables of Sea Fisheries in England and Wales contain data covering the total landings of mackerel at Newlyn and the total number of landings by the different kinds of vessels, but no information is given either with the Tables or in the Official Reports (1906–38) concerning such changes in the fishery as have been briefly described above. Unfortunately, therefore, the official statistics concerning the Newlyn deep-sea fishery for mackerel have little or no biological significance. Important factors other than the availability of fish on the fishing grounds have greatly influenced both the number and size of individual landings and the total yields—factors that have not been taken into consideration during the compilation of the tables nor recorded with them.



Text-fig. 2. Total landings of mackerel at Newlyn (in thousands of cwt.) in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

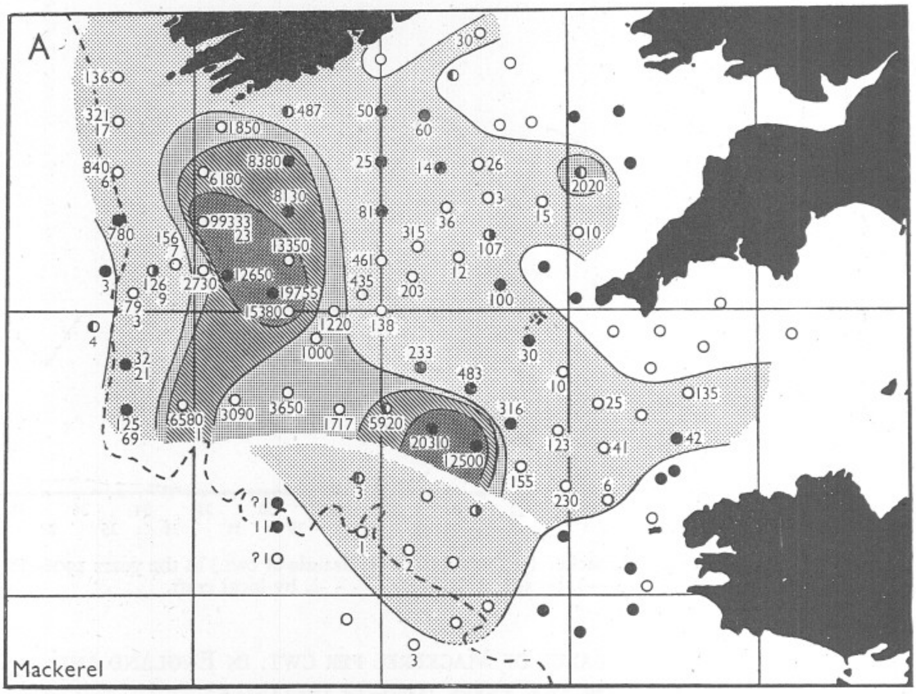
Table III. Average Value of Mackerel per cwt. in England and Wales for the Years 1919–38 inclusive[1]

| Year | Value | Year | Value | Year | Value | Year | Value |
|---|---|---|---|---|---|---|---|
| 1919 | 39*s*. 10*d*. | 1924 | 17*s*. 9*d*. | 1929 | 19*s*. 5*d*. | 1934 | 11*s*. 3*d*. |
| 1920 | 15*s*. 1*d*. | 1925 | 16*s*. 4*d*. | 1930 | 17*s*. 9*d*. | 1935 | 11*s*. 7*d*. |
| 1921 | 21*s*. 6*d*. | 1926 | 17*s*. 1*d*. | 1931 | 14*s*. 7*d*. | 1936 | 9*s*. 11*d*. |
| 1922 | 16*s*. 9*d*. | 1927 | 19*s*. 5*d*. | 1932 | 13*s*. 9*d*. | 1937 | 13*s*. 8*d*. |
| 1923 | 15*s*. 10*d*. | 1928 | 17*s*. 2*d*. | 1933 | 12*s*. 3*d*. | 1938 | 12*s*. 4*d*. |

[1] From Statistical Tables of Sea Fisheries.

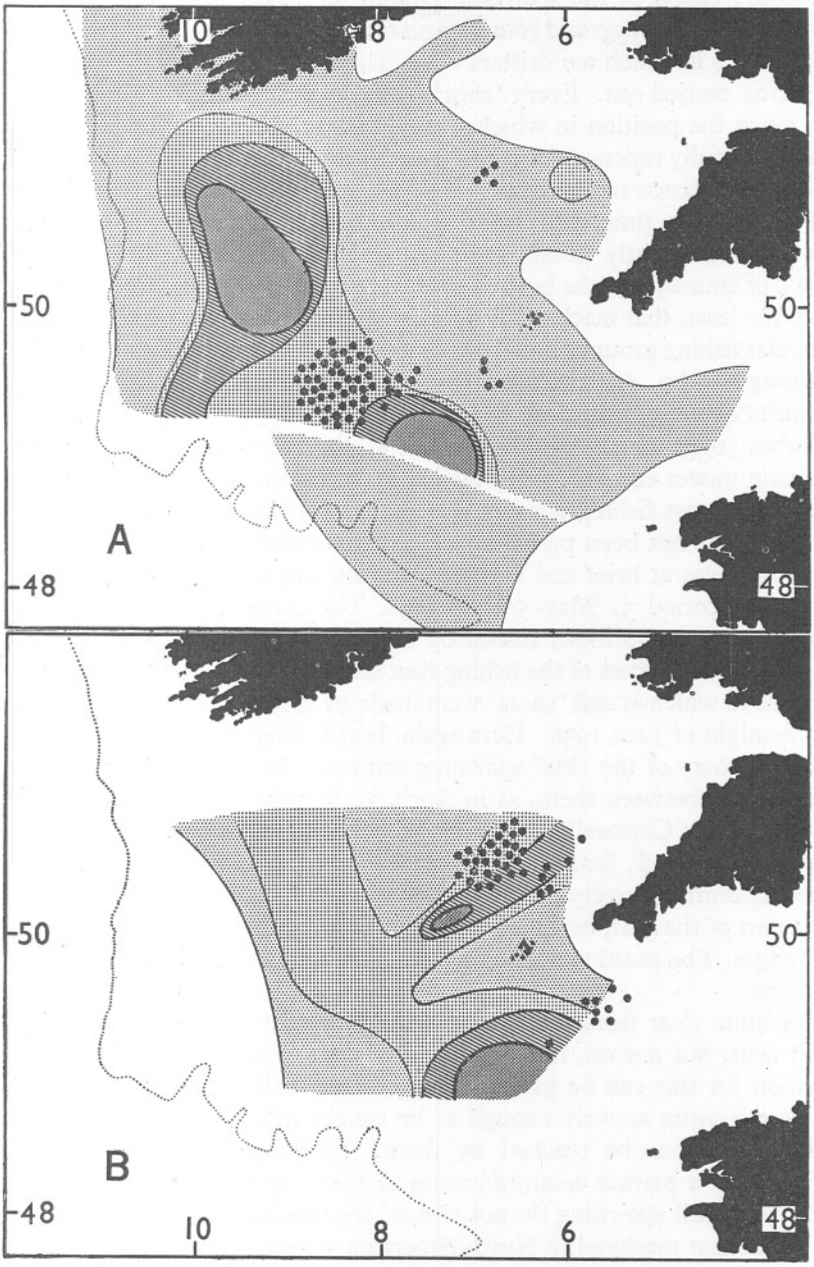
## POSITION OF THE FISHING GROUNDS IN RELATION TO SPAWNING AREAS

The Newlyn deep-sea fishery takes place on fish that are moving landwards from the west. While still far off-shore most of them spawn. Heaviest spawning occurs in April in an extensive area of sea overlying the outer (seaward) part of the continental plateau near the 100-fathom contour (Corbin, 1947). Within this area there are two centres of maximal spawning intensity, one lying 40–100 miles south of Ireland and the other 50–80 miles south-west of Bishop Rock.



Text-fig. 3. Distribution of mackerel eggs (1–1000; 1001–5000; 5001–10,000; > 10,000) and young stages in the Celtic Sea in April, 1938. Reproduced from Corbin, 1938, p. 74. For further explanation see text.

The general shape and extent of those spawning areas in April 1938—a typical year—are clearly shown in Corbin's fig. 5A (1947, p. 74) reproduced here as Text-fig. 3 (except for the omission of a coloured patch over the westernmost stations where young stages were recorded). The numerals in general refer to numbers of eggs, taken in half-hour oblique hauls with the 2 metre stramin trawl by the method described by Russell (1930, 1935). Some, however, attached to the westernmost stations, refer to the planktonic young stages—such as the lower of a pair, or single numbers outside the egg limit (*vide* the original for more exact details).



Text-fig. 4. Mackerel spawning grounds and the locus of mackerel fishing by Newlyn-based steam drifters: (A), in April, 1938; (B), in May-June, 1938. Stippling indicates density of mackerel eggs, as in Text-fig. 3.

Corbin's charts of the spawning ground for 1938 are copied in Text-fig. 4 with the number of eggs and young stages omitted, but having inserted upon them the positions in which ten drifters were fishing during the time that the survey was being carried out. Every 'shot' by each of those drifters is indicated by one dot in the position in which it was made. Fishing by those ten selected vessels was fully representative of the activities of the full fleet of twenty-seven vessels. Reference to the chart (Text-fig. 4A) clearly shows that the fishing fleet was at the time concentrating its attention upon a well-defined area between, and slightly to landward of, the two chief spawning centres. This means, of course, that the best catches were to be had there. It is remarkable, to say the least, that mackerel fishermen should so unerringly have found this particular fishing ground though quite unaware of the presence of any intensive spawning nearby, especially as these grounds lie right out in the open sea 130 miles or more from port.

Corbin (1947, p. 72) has shown that as the season advances the locus of spawning moves eastwards and decreases in intensity. At the same time the locus of greatest fishing activity also moves eastward (Steven, 1948, p. 523, fig. 4). It has not been possible in any year to make frequent surveys of the spawning areas at brief and regular intervals, but a second survey was made during the period 31 May–5 June 1938. The centres of maximal spawning were then in the positions shown by the dark stippling in Text-fig. 4B. On this chart the activities of the fishing fleet are also shown by dots indicating the positions in which actual 'shots' were made by representative ships during the first fortnight of June 1938. Here again, best fishing was found near the landward periphery of the chief spawning centres. The reason why fishing is not concentrated between them, as in April, is the presence of the Scilly Islands and the 'toe' of Cornwall in the very place where, in their absence, best fishing would be expected; for since good catches are obtained on the periphery of a spawning centre, the very best results of all should be found in a locality which forms part of the peripheries of two separate spawning grounds overlapping at their edges. The position of the highest fishing intensity in April fulfilled this condition.

It is quite clear from the fishing fleet's activities that best fishing is to be found near, but not on, the centres of maximal spawning intensity. No explanation for this can be given. The most probable reason is either that the fish do not swim actively enough to be caught in the drift nets or that they remain too deep to be reached by them. Ehrenbaum (1923, p. 5) records that Holt, in a private communication to him, expressed the conviction that mackerel in full spawning do not rise to the surface. Collins (1883, p. 277) also states that mackerel in North American waters sink during the season of reproduction and rarely appear in shoals at the surface. It should now be possible to obtain definite information on this point by investigating the spawning centres and fishing grounds with a suitable echo-sounder. Unfortunately, none was available on any of the ships with which these researches in the Celtic Sea were carried out. Arrangements are now being made for echo-sounder surveys to be carried out as soon as circumstances permit. Until this is done one can do no more than note the possibility that while spawning in deep water the fish may be either deep or relatively quiescent, or even both.

Since the fishing fleet does not catch spawning fish in the first part of the season, very few ripe mackerel arrive on the fish markets during the months of March and April. It is not until May and later that appreciable numbers of fish containing small quantities of ripe ova and sperm are landed. The explanation for this appears to be that those fish that have not yet completely spawned are now in much shallower water and cannot go down very deeply to do so. The result is that some spawning fish can now be taken in drift nets on fairly active spawning centres even though best fishing is still to be had on the periphery of such centres.

When the two inshore fisheries existed they depended on unripe fish that were in the first stages of migration to the spawning ground, i.e. they, too, worked on non-spawning populations.

Having spawned off-shore, the mackerel perform a return migration to the coast (Steven, 1948, p. 524). This return migration is not, therefore, a spawning migration as has been supposed for so long. It is simply a post-spawning anadromous migration during which the fish are actively feeding; nevertheless it cannot be said that they come inshore *in order* to feed.

## THE SPAWNING OF THE MACKEREL

Spawning takes place throughout the Celtic Sea during the period March till July. It increases very rapidly in intensity after the start, and by mid-April reaches a peak which lasts until May. Thereafter it decreases, until by the end of July it is only very slight. In the English Channel and also in the Irish Sea this slight residual spawning continues until August and even, in some years, until September (Corbin, 1947, p. 71).

This long-drawn-out spawning season is due, in part at least, to the fact that various populations of mackerel, converging on their off-shore spawning grounds from different winter quarters, both near and far away, do not all arrive there at the same time. When spawning activity is at its greatest—in the western part of the Celtic Sea in April—fish that wintered in the English Channel are still on their way westward (Steven, 1948, p. 520, fig. 3), and not yet fully ripe. It seems possible that this spread-over may be related not only to the different lengths of the migratory journeys but also to differences in the environmental conditions, particularly of temperature, in which the fish spend the winter. According to Cooper's analysis of such temperature data as exist for these areas (Appendix II, pp. 577–81), the waters over the greater part of the Celtic Sea are isothermal down to about 120 m. and in most years have appreciably higher temperatures than those of the Hurd Deep where many if not most of the Channel mackerel spend the winter. Most of the Atlantic Slope mackerel, however, spend the winter below the 120 m. level but they, too, unless they go very deep indeed—which is unlikely—are subject to warmer conditions than the English Channel population. Observations in 1927 and 1932 reveal that the mean winter temperature along the 150 and 200 m. contours in those years was about 0·9° C. higher than the mean temperature at the Hurd Deep; only at 500 m. in 1932 and at 800 m. in 1927 (position 50° 34′ N.; 11° 17′ W.) were Hurd Deep temperatures reached. Deep-water observations are also available for 1929, but Cooper regards that year as an exceptional one. Atlantic Slope water in that year was, at 200 m. depth, 2·5–2·8° C. warmer than the Hurd Deep; even at 986 m. the Atlantic Slope water was still 0·7° C. warmer. It seems clear, therefore, that mackerel wintering on the floor of the Celtic Sea, and in considerably deeper water at the outer edge of the continental plateau, are normally subjected to appreciably warmer conditions than others that spend the winter in the English Channel. Still others wintering near the bottom in the Smalls and Saltees areas will be also subjected to temperatures at least as low as those of the Hurd Deep.

Mackerel wintering around the various banks, knolls and gullies on the floor of the Celtic Sea, and in considerably deeper water at the edge of the continental plateau, are therefore not only nearer the spawning ground but are subjected to appreciably warmer conditions during their demersal period than others that spend the winter in the English Channel and in the Smalls and Saltees areas. It seems reasonable to suppose, therefore, that it is those fish that spend their demersal period in localities near the spawning ground, where also the warmer conditions prevail, that give rise to the early intensive spawning activity, followed by others from the more distant and also colder winter localities. There is also a possibility (supported by Cooper's theory of cascading waters from the shelf area down the side of the continental slope) that there may be a concentration of planktonic food organisms—chiefly copepods—at considerable depths along certain parts of the slope in February and March, especially in colder winters. Mackerel wintering in such localities, therefore, may also be better nourished (Cooper & Vaux, 1949).

Differences in winter temperatures may also be the factors underlying the later date of maximum spawning intensity on the chief North Sea spawning ground in the Skagerrak. Here (Ehrenbaum, 1914, p. 18; 1923, p. 11) the chief maximal spawning activity takes place a month later than in the Celtic Sea. It may be significant, therefore, that North Sea mackerel spend the winter in the vicinity of the Great Fisher Bank and northwards along the Norwegian Channel at least as far as the Viking Bank where winter temperatures are in general as much as 2–3° C. lower than those found in the Celtic Sea (Appendix II).

Another important factor contributing to the great spreadover of spawning activity in both space and time is that in every individual female the eggs mature in successive batches that are spawned one after the other during an extended period, the exact duration of which is not known. Ripe translucent eggs appear in the ovary distributed widely and irregularly amongst still unripe yellowish ova in earlier stages of development. This gives rise to a peculiar speckled appearance that, for want of a better term, has been called the 'plum-pudding' stage (Le Danois, 1938, p. 22,), of which an illustration is given in Pl. I, fig. 1. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Their presence can be ascertained only by opening up the ovary and examining the lumen in which a few ripe eggs will nearly always be found even after any particular batch has been shed. These must, however, be carefully looked for; a quick and superficial glance may easily miss them. An ovary that contained numerous ripe eggs in its lumen, but showed no external evidence of their presence, is illustrated in Pl. I, fig. 2. The existence of ovaries in this condition indicates that the final stages of the ripening process take place discontinuously in successive batches of eggs. Were the process a uniform and continuous one ripe eggs would always be visible externally in smaller or larger numbers throughout the whole period from the time that the first eggs ripen until the ovary is fully spent.

This mode of ripening of the eggs in mackerel ovaries is in marked contrast with the condition found in the herring, where all the eggs that are to be spawned in any one spawning season ripen more or less simultaneously, giving rise to the well-known 'mazy' condition in which large numbers of fully ripe eggs can be obtained from a single female at one time. This condition is never found in mackerel. Only a relatively small number of fully ripe eggs is ever present in a mature female at any time and a condition of easily recognized 'maziness' does not occur.

It was probably a more intimate and accurate knowledge of the ripening process in the ovary of the herring than of the mackerel that led Cunningham to make the misleading generalization (1889, p. 25): that in species of fish that swim in shoals and have pelagic and migratory habits the process of spawning is approximately simultaneous throughout the whole population in a given locality, proceeds very rapidly when once begun, and is limited definitely to one short period of the year. This generalization he wrongly applies to the mackerel in which he says: 'all the reproductive products in a given fish are matured and shed within a short space of time.'

The slightly later observations of Moore (1899, p. 5), however, are completely at variance with Cunningham's findings and in full agreement with the results of the present investigations. Moore draws attention to the fact that, in the same run of fish, individuals in very different conditions of maturity are found. The reason for this he very clearly points out to be due to the fact that 'the mackerel matures only a portion of the generation of eggs at one time', as a result of which the ovary 'becomes spotted all over, both externally and on the internal lamellae with translucent spots due to aggregations of the clear eggs'. This very early description of the 'plum-pudding' stage, and how it arises, appears not to have received from subsequent workers the attention it deserves.

Correlated with the extended spawning period in the female there is, in the male, a correspondingly long period during which ripe sperms are present in the testes. The male differs from the female in that from the time that ripe sperms first appear at the beginning of the season an appreciable amount of ripe sperm is always present until the fully spent condition is reached. As in the female, however, the quantity of ripe sexual products present in a male fish at any particular time is always relatively small. Ripe males are generally present in small numbers in commercial catches before ripe females appear in them (Table IV).

TABLE IV. PERCENTAGE OF FISH (IN COMMERCIAL CATCHES BY STEAM DRIFTERS) IN DIFFERENT MONTHS CONTAINING RIPE SPERM OR EGGS

Figures in brackets are the total numbers examined during three fishing seasons (1937–39).

| | Males | Females |
|---|---|---|
| March | 5·9 (584) | 0·0 (570) |
| April | 20·6 (569) | 7·9 (625) |
| May | 62·5 (578) | 52·2 (554) |
| June | 52·8 (625) | 47·6 (464) |
| July | 14·4 (223) | 17·3 (185) |

It will be seen from the table that the two sexes appear in the catches in approximately equal numbers.

## FOOD AND FEEDING

Adult mackerel spend part of each year in winter quarters on or near the sea-floor in the vicinity of banks and gulleys distributed over wide areas from shallow to deep water. In the English Channel, demersal concentrations of mackerel are found hard by the Vergoyer Bank off Boulogne, and by the numerous small sandbanks near Dieppe in only a few fathoms; and along the sides of the Hurd Deep in rather more than 40 fathoms. Elsewhere in the south-western area they occur at various depths in the neighbourhood of the Smalls and Saltees, around various banks and shoals on the floor of the Celtic Sea, and even along the Continental Slope itself, where they are regularly caught by British and other trawlers in depths of well over 100 fathoms 'west of Great Sole Bank' and elsewhere, especially in late February and March.

Amongst the mackerel that winter on the bottom in the English Channel fish with packed stomachs are seldom found. On the other hand, not all of them are empty. The fish, therefore, though not feeding voraciously, are not entirely fasting.

In the Plymouth region 753 mackerel were caught by trawl on or near the sea-floor in the months of January–April during the years 1936–39. Of these 67% contained food consisting chiefly of *Nyctiphanes couchi*, mysids, small teleosts, and crangonids, but various other organisms were also represented (Table V).

It is obvious that while on or near the bottom in the English Channel the mackerel were feeding on such organisms as were suitable and available to them. By contrast, the stomachs of mackerel caught in drift nets near the surface in January have been almost entirely devoid of food. A few (just under 5% of the 138 fish examined) have contained traces of phytoplankton embedded in mucus and very occasionally traces of planktonic crustacea (copepods) have been present. Rather more plant material appears in the stomachs in February (just over 26% of the 116 fish examined) and copepod remains were identifiable in nearly 10% of them. But, on the whole, pelagic fish caught in these months, and also in December, can be regarded as fasting. This fasting period appears to be imposed upon the fish solely by the absence of suitable food in the upper waters at this time. On or near the sea floor where food is present they do not fast, and they break their fast afterwards at any time when opportunity offers. In samples of drift-caught mackerel in early spring, most of whose stomachs are empty or contain only minute traces of food, chiefly phytoplankton, it is not unusual to find an occasional individual whose stomach is packed tightly with small pelagic fish—generally *Maurolicus pennanti*, which occur in small and localized shoals.

TABLE V. PERCENTAGE OF BOTTOM-CAUGHT FISH (PLYMOUTH AREA) CONTAINING IN THEIR STOMACHS ONE OR MORE OF THE ORGANISMS LISTED BELOW

| Name of organism | Percentage of stomachs in which found (to nearest whole number) |
|---|---|
| *Nyctiphanes couchi* | 31 |
| Mysids | 26 |
| Small teleosts | 15 |
| Crangonids | 11 |
| Polychaetes | 3 |
| Amphipods | 2 |
| Pagurids | 1 |
| Other organisms | 7 |
| Stomachs empty | 33 |

Bullen (1912, p. 394) is therefore correct in stating that although mackerel obtain the smaller organisms of their diet by 'filtration' the larger ones are captured by 'selective feeding'. Selective feeding has been confirmed by Damant (1921, p. 42) by direct observation in the sea. In aquarium tanks of this laboratory mackerel are fed upon fragments of squid or other suitable food which they swallow as it sinks through the water by very obvious 'visual selection'. Bullen was in error, however, in thinking (1912, p. 403) that 'when feeding upon the minor forms of the plankton mackerel are incapable of assimilating other larger prey'. The phytoplankton present in the stomachs of pelagic mackerel in early spring can have been obtained only by filtering. It is equally certain that active fishes such as *M. pennanti*, several inches in length, must have been captured by Bullen's 'selective feeding' method. There can be little doubt that mackerel obtain their food by the most profitable method depending upon the size and kind of food organisms available to them; and that, at any time of the year and wherever they may be, they fast only if there is nothing for them to feed on.

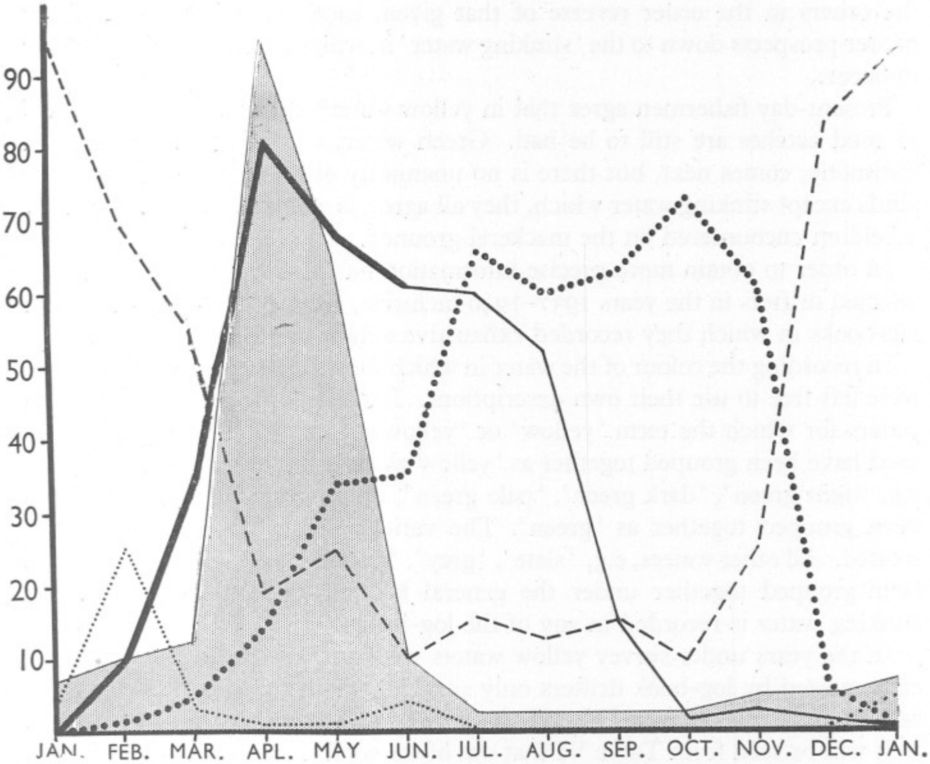
Most pelagic mackerel moving in an off-shore direction in the south-western area in the early months of the year are on migration to the spawning ground. In order to get there they leave the lower levels, where a certain amount of suitable food is available to them, for the upper layers where for a time there is practically none. The catadromous spring migration to the spawning areas is undertaken, therefore, irrespective of the presence or absence of food either at the beginning of the journey or on the way. Nevertheless, the migrating fish will at all times feed greedily if they can.

During March there is a rapid increase in the number of stomachs of pelagic mackerel containing food material—mainly copepods—and in the total quantity of food in each stomach. By the end of the month, and all through April and May, the fish feed predominantly on copepods, their stomachs being packed to bursting with these crustacea known to fisherman as 'red feed'. Although copepods predominate in the diet of the mackerel at this time a wide range of other planktonic organisms are also eaten. By about June yet another change takes place. Young pelagic stages of fish are now the mackerels' chief food, particularly *Clupea* spp., *Ammodytes* spp., and *Onos* spp. Considerable numbers of the larger crustacea also form part of the diet at this season and throughout the whole time that the fish are in shallow coastwise waters—euphausiids, mysids, the larger larvae of decapod crustacea such as *Corystes* and *Porcellana*, and even occasional pandalids, hippolytids, crangonids and similar organisms.

It will be seen (Fig. 5) that the fasting period is December—March which coincides with minimal plankton occurrence. When plankton becomes abundant the mackerel feed voraciously upon it, and continue to do so all the time that they are in off-shore waters. The change over to a predominantly fish diet, augmented with certain larger Crustacea, takes place when the mackerel have arrived back in inshore waters on their return from the spawning grounds.

## FISHERMEN'S SIGNS

When fishing for mackerel, especially in the Newlyn deep-sea fishery, the fishermen are influenced greatly in their choice of position for 'shooting' their nets by what are commonly known as 'fishermen's signs'. Large congregations of birds, especially diving gannets, are looked upon as good indications of the



Text-fig. 5. Diagram illustrating the changes in mackerel stomach contents in the course of one full year. The percentage of stomachs containing the chief types of food are shown thus: ......, phytoplankton; ━, planktonic crustacea, mainly copepods; ——, non-planktonic crustacea, i.e. crangonids, pandalids, etc.; ●●●, fish; - - -, empty stomachs. The contents over a whole month are recorded as for the mid-point of that month. Height of the stippled area indicates, in miles, on the same ordinate, the mean distance from land at which the mackerel examined were caught in each month.

presence of fish in worthwhile numbers. Even more reliance is placed upon the colour of the water. This has already been remarked upon by Bullen (1908, p. 287) who recognized five different kinds:

(i) Stinking water—water of a dull leaden colour having a recognizable and distinctly unpleasant smell.

(ii) Grey water—water similar in colour to the above but lacking the smell.

(iii) Blue water—very clear and transparent.

(iv) Green water—differing from blue water only in colour.

(v) Yellow water—turbid water of a distinctly yellow tint.

According to Bullen best catches of mackerel at that time (1906 and 1907) were generally, though not invariably, to be had in yellow water,[1] followed by

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[1] This seems to have been first remarked upon by Pliny—quoted by D'Arcy Thompson (1947, p. 244)—who says: '*scombri quibus est in aqua sulphureus color*.'

the others in the order reverse of that given, each providing progressively poorer prospects down to the 'stinking water' in which mackerel are said never to occur.

Present-day fishermen agree that in yellow water[1] by far the best prospects of good catches are still to be had. Green water, according to their spoken testimony, comes next, but there is no unanimity of opinion about any other kinds except stinking water which, they all agree, is worst of all but fortunately is seldom encountered on the mackerel grounds.

In order to obtain more precise information on these and other points, ten selected drifters in the years 1937–1940 inclusive, were provided with special log-books in which they recorded exhaustive details of all their catches.

In recording the colour of the water in which they shot their nets the skippers were left free to use their own descriptions. For the purpose of tabulation all waters for which the term 'yellow' or 'yellowish' e.g. 'yellowish green', are used have been grouped together as 'yellow water'. All other shades of green e.g. 'light green', 'dark green', 'pale green', 'grass green' and the like have been grouped together as 'green'. The various 'blues' have been similarly treated. All other waters, e.g. 'slate', 'grey', 'paraffin oil', 'black', etc., have been grouped together under the general heading of 'other colours'. No stinking water is recorded in any of the log-books.

In the years under survey yellow waters were not very plentiful. They were encountered by log-book drifters only six times in 1937, eight times in 1938, and thirteen times in 1940. No yellow water was found by any of them in 1939.

It will be seen from Table VI that out of the total number of 27 shots made in yellow water during those four years no less than 21 (77·8%) yielded catches of over 10,000 fish, the average number per haul being 18,300.[2] Several catches of over 29,000 fish were made. In green water only 13·4% of the 918 catches consisted of more than 10,000 fish. In blue water, out of 183 catches only 1 had over 10,000 fish. The catches in other waters were poorer still.

It is quite clear from these log-book records that yellow water, when present, offers by far the best prospects of obtaining good catches. Yellow water is, unfortunately for the fishermen, not very plentiful, and in some years, as in 1939, may not occur at all.

Bullen (1908, p. 289) endeavoured by direct investigation to correlate the different kinds of water with the plankton present in it. Stinking water he found to be rich in phytoplankton and poor in zooplankton, but he was unable to offer any explanation of the reputed objectionable smell which he was himself unable to detect. He gave it as his opinion, though, that such an odour, if it did exist and could in fact be detected by fishermen, 'did not arise from the condition of plankton'. Long before Bullen's investigations, however, Pearcy (1885, p. 399), working near Shetland, had shown quite conclusively not

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[1] Described by some Cornish fishermen as 'cow-dung water'.

[2] To the nearest hundred.

only that herrings avoid stinking water but that the odours were correlated with the presence of *Rhizosolenia shrubsolei* and *Thallassiosira nordenskioldii* with which the herring nets sometimes became so heavily coated that little slimy heaps of those organisms were formed on the deck as the nets were hauled in.

Supporting evidence that shoaling fish such as mackerel and herring avoid water heavily populated with phytoplankton, such as the diatom *Rhizosolenia* or the flagellate *Phaeocystis*, is provided by Russell (1915, p. 30) for mackerel, and by Savage & Hardy (1935) for herring. Although, therefore, stinking water has not been reported in the course of these investigations there appears to be no doubt that when it does occur poor fishing must be expected in it.

TABLE VI. CATCHES IN DIFFERENT TYPES OF WATER

| Colour of water | Year | No. of shots | No. of shots having over 10,000 fish | Percentage of shots having over 10,000 fish | Average no. of fish per haul (to nearest hundred) |
|---|---|---|---|---|---|
| Yellow | 1937 | 6 | 3 | | |
| | 1938 | 8 | 5 | | |
| | 1939 | No yellow water | | | |
| | 1940 | 13 | 13 | | |
| | | 27 | 21 | 77·8 | 18,300 |
| Green | 1937 | 230 | 42 | | |
| | 1938 | 327 | 56 | | |
| | 1939 | 247 | 30 | | |
| | 1940 | 114 | 5 | | |
| | | 918 | 133 | 13·4 | 5,300 |
| Blue | 1937 | 88 | 0 | | |
| | 1938 | 25 | 1 | | |
| | 1939 | 31 | 0 | | |
| | 1940 | 39 | 0 | | |
| | | 183 | 1 | 0·6 | 2,600 |
| Other colours | 1937 | 18 | 0 | | |
| | 1938 | 38 | 0 | | |
| | 1939 | 34 | 0 | | |
| | 1940 | 32 | 0 | | |
| | | 122 | 0 | 0·0 | 2,000 |

In all other waters examined by him Bullen found zooplankton to be more plentiful than in stinking water, with phytoplankton also often present as well. In yellow water he found that phytoplankton was 'entirely absent' and that the zooplankton was confined almost entirely to three or four principal forms of which *Calanus finmarchicus* and *Pseudocalanus elongatus* were the most important.

Unfortunately, Bullen's data enable him to put forward only tentative explanations of the causes which give rise to the yellow colour and why, on the whole, yellow water is most likely to provide good catches. He quotes the 'somewhat conflicting opinions expressed by fishermen' to the effect that the coloration is due either to the presence of excrement arising from densely shoaling fish or to the abundant copepod 'feed' and adds that evidence provided by examination of certain plankton samples supports the latter view.

During the present investigations some of the skippers provided with log-books agreed also to work small townets and collect plankton samples from each position in which they shot their drift nets. They were all issued with exactly similar gear and given precise instructions for using it in such a way as to obtain reasonably comparable quantitative results. In spite of this the samples so obtained could not at first be relied upon from a quantitative point of view.

Nevertheless, their collection was continued and in due course many of the difficulties which vitiated their comparability were overcome so that some deductions could reasonably be drawn from them. These improvements arose in part because the skippers themselves found that, though by no means an infallible guide, their best catches of mackerel were generally obtained where the townet samples consisted of typical 'mackerel feed'—i.e. copepods in reasonable abundance—and they gradually learned to use the townets by standard methods for standard times in order to obtain comparable catches for their own information. It is therefore significant that, after the townets had been in use by selected skippers for one season, other skippers who at first would have nothing to do with them, asked, as a favour, to be issued with townets for their own use.

Examination of 300 samples retained as reliable, in association with the log-book records, support Bullen's finding that plankton catches in yellow water and light green water generally consisted almost entirely of copepods—chiefly *Pseudocalanus elongatus* and *Calanus finmarchicus*, with the former usually predominating both in numbers and in bulk. The largest samples of copepods also came from those two waters. These were preserved in formalin (5%) and having survived the war period have now been re-examined after an interval of more than ten years. In that time the preserving fluid in some of the jars containing copepods almost unmixed with other organisms such as *Limacina*, has acquired a yellow colour closely resembling that of the yellow waters on the fishing grounds. Certain yellow carotinoid substances from the copepods have gone into solution in the preservative fluid.

For some reason not understood, not all the copepod samples have liberated these yellow pigments into solution; but such samples, transferred into acetone, give the same tinge and depth of colour in a few months. There seems to be little doubt, therefore, that the underlying primary cause of the yellow coloration in the sea is the presence of copepods in concentrations so dense that their body pigments impart colour to the water. Such coloration will of course be augmented by their excreta in which the same pigments are present. Observation has also shown that the 'somewhat conflicting opinions expressed by fishermen' as quoted by Bullen (1908, p. 291) are probably not conflicting at all, and that the excrement produced by densely shoaling mackerel is also a contributory factor. Faecal matter expressed from mackerel is, in fact, generally of a yellowish or pinkish yellow colour. Mackerel, like most fish, tend to congregate in greatest numbers where their most acceptable food organisms are in greatest abundance (Herdman, 1913, p. 33). Both the fish themselves and their faecal matter will therefore be most plentiful in water already tinted by copepods and the effect of this will be to strengthen the yellow coloration.

In normal circumstances the distribution of copepods in high concentrations is characterized by its 'patchiness'; so also, in consequence, is the distribution of 'yellow water'. In years of unusual copepod abundance there will be an increase of yellow water in the form of more numerous patches, many of which will also cover greater areas. Since mackerel congregate in the yellow patches, the more numerous those patches are in any year and the greater their extent, the more favourable are the chances of their being found and fished in, with consequent benefit to the commercial fishery. In years of copepod scarcity the opposite will be true. This is in complete agreement with Allen's generalization (1909, pp. 396–97) that the catches of mackerel in May in the Newlyn deep-sea fishery are to some extent affected by the amount of sunshine in the same region during the previous February and March. This effect upon catches is an indirect and very interesting one. The phytoplankton crop depends, to some extent, upon the amount and intensity of sunlight in those early months. The abundance or scarcity of copepods is in turn partly dependent upon the magnitude of the phytoplankton crop upon which they chiefly feed. Copepod concentrations, being patchy in their distribution, cause mackerel to congregate in them, and those patches can be identified by the appearance of the water. *The effect of suitable amounts of sunshine in February and March is therefore to increase the number and size of the patches of sea in which good fishing is likely.* Obviously there must be a limit to this effect; for if, in any year, the conditions were so favourable that the greater part of the whole area consisted of yellow water rich in copepods there would be no localized concentrations of mackerel and therefore no improvement in the catches. Unfortunately, Bullen's statement with regard to zooplankton and the abundance of mackerel has for a very long time created a wrong impression. He states that 'the abundance or paucity of zooplankton during a certain number of years (1903–07) appears to be correlated with the greater or less abundance of mackerel'. It must clearly be understood that abundance of zooplankton cannot possibly increase the population of adult mackerel in the year in which it occurs. It is the 'catchability' of the mackerel already in existence that is affected and which may be reflected in the commercial catches.

## SUMMARY

Of the three mackerel fisheries that formerly existed in the south-west of England, only one, the Newlyn deep-sea fishery, now remains active. The fishing grounds worked by this fishery lie in the Celtic Sea as much as 100 miles to the westward of the Scilly Islands when the season opens in March,

but the distance off becomes progressively less as the season advances until, in June, when it finishes, the participating vessels are fishing close by the land. At all times best fishing is obtained on the periphery of the areas of chief spawning intensity.

The spawning season in the Celtic Sea is a very protracted one because (*a*) the fish do not all ripen and spawn simultaneously due to (i) the divergent conditions, especially of temperature, in which different groups spend the winter, and (ii) the different lengths of the migratory journeys they must make to reach the common spawning area; (*b*) in each individual female the eggs mature in successive batches that are shed one after the other over an extended period, the duration of which is not precisely known.

In the early months of the year pelagic mackerel are often found to be fasting. This is due simply to absence of suitable food in their environment at that time. The fish will always feed when food is available.

As a general rule most mackerel are caught in patches of 'yellow' water, the colour of which is caused chiefly by localized concentrations of copepods to which the fish are attracted for feeding. Copepod abundance at the height of the fishing season must be to some extent affected—indirectly through the phytoplankton—by the amount of sunshine earlier in the season. This explains Allen's correlation between early spring sunshine and commercial catches of mackerel in late spring and early summer.

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# APPENDIX I

## LANDINGS AT NEWLYN BY LOCAL CRAFT (SAIL AND MOTOR) AND BY STEAM DRIFTERS IN THE YEARS 1906–38 INCLUSIVE (WAR YEARS EXCEPTED)

| | Local craft | | | Steam drifters | | |
|---|---|---|---|---|---|---|
| Year | No. of landings | Total quantity in cwt. | Mean weight per landing (cwt.) | No. of landings | Total quantity in cwt. | Mean weight per landing (cwt.) |
| 1906 | 2159 | 46265 | 21 | 1850 | 62551 | 34 |
| 1907 | 2190 | 60121 | 28 | 2962 | 195565 | 66 |
| 1908 | 2709 | 36950 | 15 | 2944 | 112452 | 38 |
| 1909 | 1878 | 27549 | 17 | 2423 | 112189 | 46 |
| 1910 | 1476 | 31757 | 22 | 2281 | 124122 | 54 |
| 1911 | 1581 | 15871 | 10 | 2156 | 97185 | 45 |
| 1912 | 1255 | 13761 | 11 | 1572 | 65482 | 42 |
| 1913 | 806 | 10419 | 13 | 1537 | 56176 | 36 |
| 1919 | 786 | 15200 | 19 | 1311 | 84078 | 64 |
| 1920 | 1111 | 16470 | 15 | 2162 | 112683 | 52 |
| 1921 | 1721 | 21932 | 13 | 1963 | 116931 | 60 |
| 1922 | 1824 | 18280 | 10 | 2185 | 90555 | 41 |
| 1923 | 1036 | 20865 | 20 | 2249 | 106237 | 47 |
| 1924 | 750 | 14613 | 19 | 2182 | 117540 | 54 |
| 1925 | 430 | 4859 | 11 | 2412 | 122150 | 51 |
| 1926 | 290 | 4441 | 15 | 1888 | 102390 | 54 |
| 1927 | 559 | 3890 | 7 | 1707 | 58739 | 34 |
| 1928 | 273 | 2924 | 10 | 1301 | 58827 | 45 |
| 1929 | 387 | 983 | 3 | 1079 | 43670 | 40 |
| 1930 | 173 | 411 | 2 | 1223 | 43205 | 35 |
| 1931 | 77 | 112 | 1 | 925 | 50513 | 55 |
| 1032 | 202 | 525 | 3 | 1014 | 48119 | 47 |
| 1933 | 950 | 2321 | 2 | 1133 | 51223 | 45 |
| 1934 | 988 | 2912 | 3 | 905 | 55400 | 69 |
| 1935 | 694 | 3002 | 4 | 856 | 58885 | 69 |
| 1936 | 696 | 4547 | 7 | 777 | 57177 | 74 |
| 1937 | 1131 | 4274 | 4 | 643 | 40765 | 63 |
| 1938 | 935 | 5134 | 5 | 641 | 50207 | 78 |

# APPENDIX II

## DIFFERENCES IN TEMPERATURE IN FEBRUARY OF SEVERAL EUROPEAN WATERS IN WHICH MACKEREL LIVE

By L. H. N. Cooper, D.Sc., F.R.I.C.

In the course of these investigations into the life history of the mackerel, the question arose whether differences in temperature of the water occurred at the time of the winter minimum between, on the one hand, the Hurd Deep, and on the other, the waters south and south-west of Ireland and near the Viking Bank west of Norway.

### *Hurd Deep Observations*

Two lines of regular surface observations cross the Hurd Deep. These lines are worked at frequent intervals by merchant ships on shuttle service between Southampton and St Malo and between Plymouth and Guernsey. No doubt there is some uncertainty in these observations, as in all surface observations from merchant ships. Down to the level of the bottom of the English Channel vertical mixing is almost certainly thorough. We have no knowledge as to how thorough it is within the trench of the Hurd Deep.

Throughout the whole period of the Irish investigations a station was regularly worked on the Southampton—St Malo line over the eastern end of the Hurd Deep at 49° 54′ N., 2° 00′ W. Occasionally this point was omitted, but the adjacent position 50° 03′ N., 1° 55′ W. differs hardly at all in temperature and on a few occasions has been used instead.

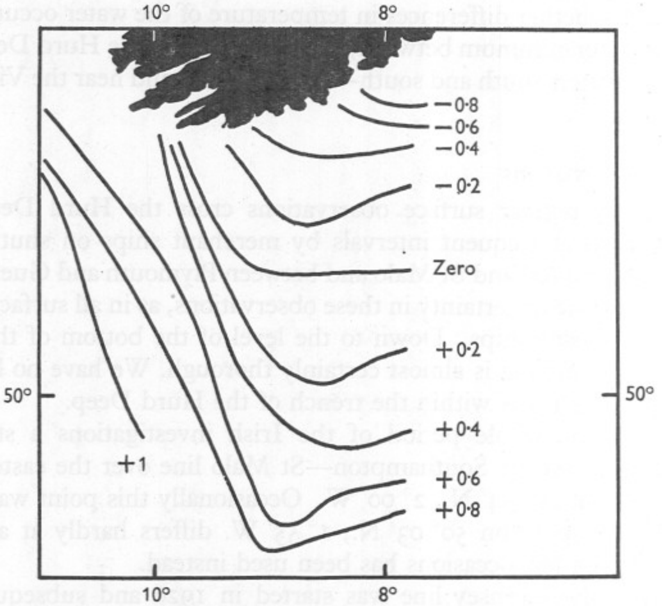
The Plymouth-Guernsey line was started in 1926 and subsequently was worked rather more frequently than the eastern line.

All data between the last January observation and 10 March have been abstracted from the *Bulletin Hydrographique* and, when necessary, graphed. The temperatures at each station about 1 and 19 February and 10 March were interpolated and the differences between the two stations evaluated. In general, the western station was the warmer, and for the eight years 1926–33, the position 49° 30′ N., 3° 02′ W. was on an average 0·4° C. warmer than the position 49° 54′ N., 2° 00′ W.

It is clear that a small temperature gradient along the length of the Hurd Deep is usual, and that the easternmost station for which most data is available lies in February over the coldest part of the trench.

### *Observations South of Ireland*

Serial temperature observations in the Irish area have been frequently taken in February and May, but in the other winter months there are few data. The cruises were worked between 20 and 22 January in 1921 and sometime between 2 February and 10 March in the other years. In each year the mid-point in time of the Irish cruise was taken and the temperature at that time at each of the Hurd Deep positions estimated by interpolation. In the years 1926–33 the temperature of the eastern half of the Hurd Deep has been taken as the mean of these. In 1921–25, the temperatures at the easternmost position, 49° 54′ N., 2° 00′ W., have been increased by the mean correction, 0·2° C., to make them comparable with the later years.



Text-fig. 6. Differences in February temperatures between the waters south and south-west of Ireland and those at the Hurd Deep in the English Channel. Lines of equal difference—positive warmer than the Hurd Deep; negative colder than the Hurd Deep. Years 1921–33.

These Hurd Deep temperatures provide the basis line for the subsequent calculations. This temperature was subtracted from each separate Irish observation between 1921 and 1933 to give a table of differences. The mean difference at each station was then evaluated and is plotted in Text-fig. 6. Lines of equal differences were then drawn which show that the inshore water south of County Cork was colder than the Hurd Deep, and that the water south of 50° 40′ N., and west of 09° 00′ W. was warmer. The surface water above the continental slope was about 1° C. warmer.

Quite clearly the year 1929 was peculiar and so has been omitted from these calculations. Air temperatures at Scilly and Valencia were normal, whereas at Guernsey in February they were 2·7° below average. Consequently, the water over the Hurd Deep was 1·5° C. colder than the 'normal differences' for the other ten years would lead one to expect. This story concerns surface temperatures.

Bottom temperatures were also needed. The Hurd Deep surface temperatures apply to the whole water column at least down to the depth of the bottom of the English Channel adjacent to the Deep.

In the Irish area the water was almost always isothermal down to at least 120 m. Only a few stations deeper than 120 m. had been worked, namely positions *R*, *S*, *T*, *PP*, *QQ*, *RR*, and *SS* all west of 9° 55′ W., and these only in 1927, 1929 and 1932. The year 1929 has already been stated to be exceptional and it is better to use only the years 1927 and 1932 for estimating mean conditions. In these years the mean temperatures along the 150 and 200 m. contours of the shelf was about 0·9° C. higher than the temperature at the Hurd Deep. The Hurd Deep temperatures were reached at station *SS* (50° 34′ N., 11° 17′ W.) at a depth of 500 m. in 1932 and at 800 m. in 1927. In the probably exceptional year 1929, the water at the 200 m. contour was 2·5–2·8° C. warmer than at the Hurd Deep. Even at 986 m. the water was still 0·7° C. warmer.

TABLE VII

| Date | Irish code letter | Position | Depth (m.) | Temp. (° C.) |
|---|---|---|---|---|
| 10. iii. 49 | *D* | 50° 36′ N., 8° 04′ W. | 5 | 9·97 |
| | | Labadie Bank | 25 | 10·00 |
| | | | 60 | 10·00 |
| | | *Sounding* | *70* | — |
| 9. iii. 49 | *F* | 49° 50′ N., 8° 00′ W. | 5 | 10·30 |
| | | | 50 | 10·30 |
| | | | 125[1] | 10·30 |
| | | *Sounding* | *123* | — |

[1] Wire angle >45°; true depth much less than metres of wire out.

If high temperature is a factor favouring early spawning of the mackerel, those in the Celtic Sea south of 50° 40′ N. and west of 09° 00′ W. should in most years spawn earlier than those near the Hurd Deep.

### *The Winter of* 1949 *in Waters South of Ireland*

Steven reported (3 March 1949) that the mackerel in the area south of Ireland had started spawning several weeks earlier than normal. Since at Plymouth the winter had been remarkably mild, it seemed likely that high temperatures of the water to the westward might have been associated with the early spawning. The opportunity occurred to obtain temperatures on 9–10 March along the meridian 8° 00′ W. (Table VII).

Suitable comparable temperatures had been obtained by the Irish Fisheries Service in the years 1921–22, 1924–34 and 1938, whilst surface observations are available for other years. In 1937 water as warm was present in the area of stations *D* and *F* between mid-February and mid-March, but was evidently a short-lived intrusion into a part only of the area south of Ireland. Over the whole area for the whole of the winter, the season 1936–37 was evidently markedly colder than 1948–49. Apart from this doubtful year, it is necessary to go back to 1921 to find a similar one; even that year certainly was not warmer.

It is therefore not unreasonable tentatively to correlate the abnormally early spawning of mackerel in February and March 1949 with the notably high water temperatures.

*Observations on the Western Declivity of the Norwegian Channel*

During winter mackerel congregate along the western declivity of the Norwegian Channel or northern extension of the Skagerrak in the latitudes of the Orkney and Shetland Islands (p. 564). In these waters a number of hydrographic stations have been worked by the Norwegian research vessels *Johann Hjort* and *Armauer Hansen* in January or February. The suitable stations worked there in 1938 and 1939 find no counterpart in simultaneous Hurd Deep observations.

TABLE VIII

| Depth (m.) | Deficiency in temperature (° C.) | |
|---|---|---|
| | 7. i. 37 | 27. i. 37 |
| 100 | 2·4 | 2·1 |
| 125 | 2·4 | 2·1 |
| 150 | 2·5 | 2·0 |
| 200 | 2·8 | 2·0 |
| 250 | 3·3 | 2·0 |
| 300 | 3·7 | 2·0 |

TABLE IX

| Depth (m.) | Deficiency in temperature (° C.) |
|---|---|
| | 3. ii. 37 |
| 100 | 2·7 |
| 125 | 2·4 |
| 150 | 2·7 |
| 200 | 2·8 |

In 1937 on 7 and 27 January, on the parallel of latitude 60° 46′ N., the temperatures of the bottom water bathing the western declivity of the Channel were lower than the Hurd Deep mean temperatures on the same date by more than 2° C. (Table VIII).

On the parallel 59° 17′ N., on 3 February 1937, the corresponding values were as shown in Table IX.

In 1937, mackerel in these waters were subjected to temperatures about 2·5° C. lower than at the Hurd Deep.

February 1930 seems to have provided an unusually small difference in temperatures, whereas January 1931 was more 'normal' (Table X). The parallel of latitude worked in both years was 60° 08′.8N.

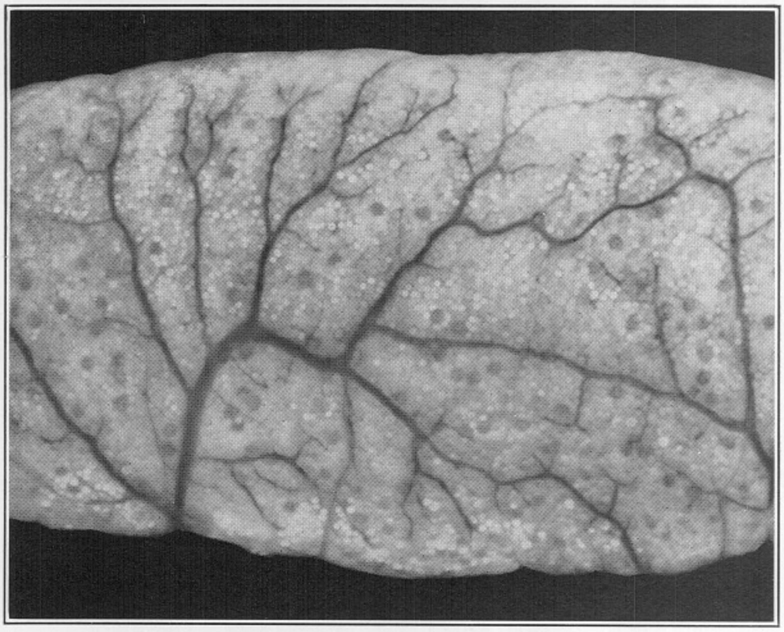


Fig. 1.

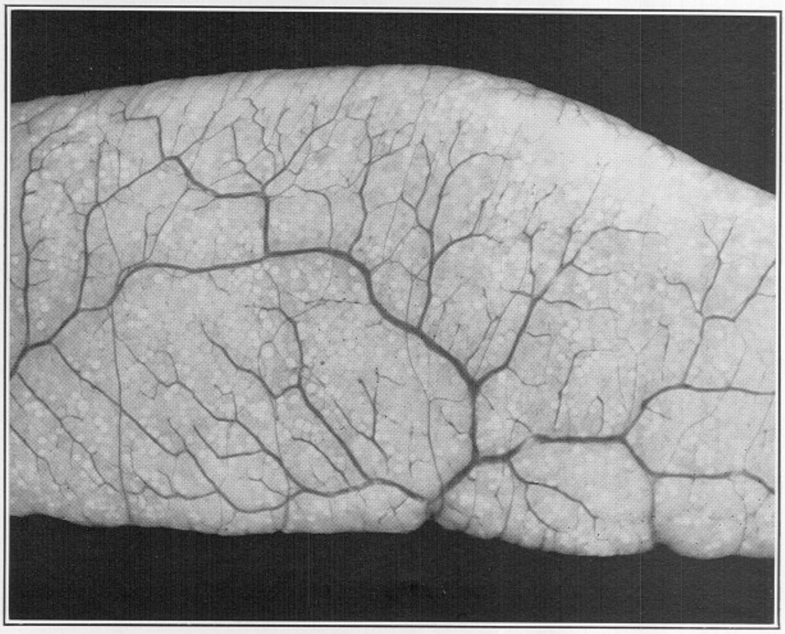


Fig. 2.

The year 1938 probably provided differences similar to 1931 and 1937.

In general we may say that the western edge of the Norwegian Channel provides temperatures 2–3° C. lower than the Hurd Deep, so that if temperature controls the time of spawning, the lag in the more northern waters should be considerable.

TABLE X

| Depth (m.) | Deficiency in temperature (° C.) | |
|---|---|---|
| | 27. ii. 30 | 29. i. 31 |
| 100 | 0·3 | 1·9 |
| 125 | 0·5 | 2·3 |
| 150 | 0·5 | 2·0 |
| 200 | 0·6 | 2·3 |

## EXPLANATION OF PLATE I

Mackerel ovary in two phases. Fig. 1, the 'plum-pudding' stage, in which the widely scattered ripe eggs appear as dark spots. Fig. 2, an ovary with ripe eggs which are not visible externally but are to be found in the lumen.

# THE LARVA OF A DIDEMNID ASCIDIAN, WITH NOTES ON THE STRUCTURE OF THE COLONY AND THE ADULT

By R. H. Millar
From the Marine Station, Millport

(Text-fig. 1)

There are few adequate descriptions of British members of the ascidian family Didemnidae and little attention has been given to the larvae. In the autumn of 1947 a didemnid was collected from the intertidal zone in the Menai Strait, North Wales. This ascidian agrees superficially with *Leptoclinum maculosum* Edwards, as figured by Milne Edwards (1842) and by Alder & Hancock (1905–1912), although differing somewhat from the diagnosis of *Didemnum maculosum* (Edwards) given by Harant & Vernières (1933). It is closer anatomically to the *D. fulgens* (Edwards) of Harant & Vernières, but differs in colour. In most features the colony and zooid closely resemble the descriptions given by Michaelsen (1923) for his species *D. helgolandicum* Michaelsen, and it is probable that this is the species to which it should be assigned. Nevertheless, the name *D. maculosum* has been retained since it is under that name that it has probably appeared in most faunistic lists.

Until recently all accounts of didemnid larvae have described three anterior adhesive organs. This was the number given by Giard (1872) for *Diplosoma gelatinosum* Edwards, and by Lahille (1890) for *Trididemnum tenerum* Verrill and *Polysyncraton lacazei* Giard. Berrill (1947), however, has described a new species of didemnid, *Trididemnum alleni* Berrill, the larva of which has only two anterior adhesive organs, a condition not previously found in any ascidian larva.

The larva (Fig. 1 A) of the colonies found in the Menai Strait resembles that of *T. alleni* in many features. The trunk is about 0·35 mm. long from the tip of the adhesive organs to the base of the tail. The sensory vesicle is prominent and contains an anterior static organ and a posterior ocellus. Four rows of stigmata in the branchial sac rudiment distinguish the larva from that of *T. alleni* which has only three rows. There are eight ectodermal ampullae in the anterior and ventral part of the trunk and, as in *T. alleni*, there are only two anterior adhesive organs, one dorsal and one ventral. The larva of *Didemnum maculosum* has therefore features in common with the larvae of most members of the family Didemnidae (four rows of stigmata), and also features in common with the larva of *Trididemnum alleni* (two anterior adhesive organs).

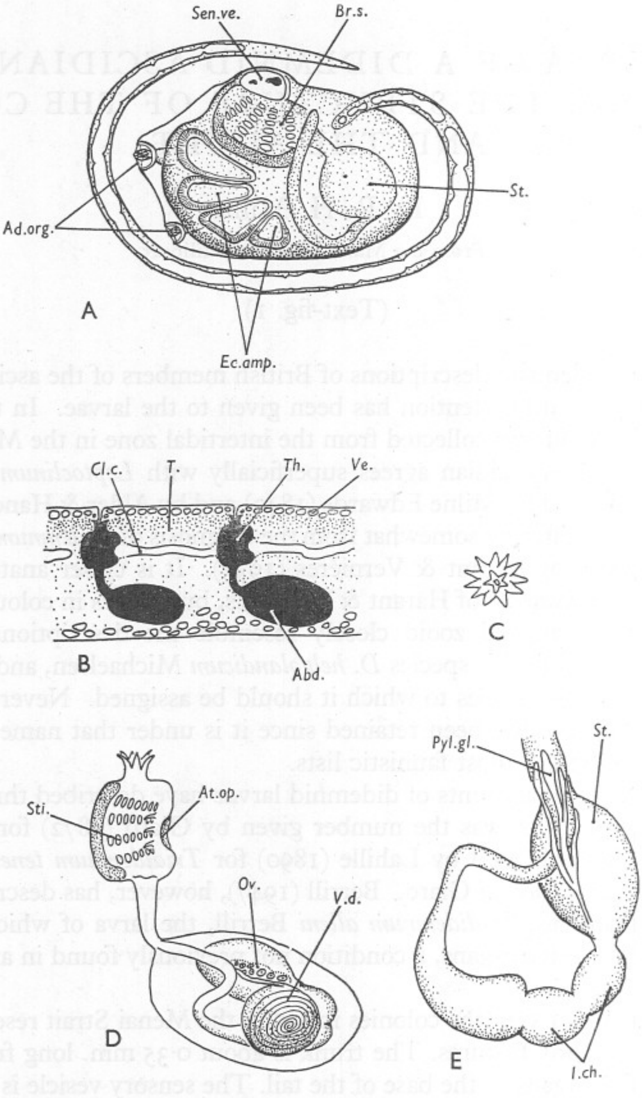


Fig. 1. *Didemnum maculosum* auctt. A, larva, seen from the left, as it appears when removed from the egg follicles. B, section through part of a colony showing the arrangement of the zooids in the common test. C, a spicule from the common test. D, zooid. E, the abdominal part of the alimentary canal.

*Abd.*, abdomen of the zooid; *Ad.org.*, anterior adhesive organs; *At.op.*, atrial opening; *Br.s.*, branchial sac; *Cl.c.*, cloacal canal of the common test; *Ec.amp.*, ectodermal ampullae; *I.ch.*, first two chambers of the intestine; *Ov.*, ovary; *Pyl.gl.*, pyloric gland; *Sen.ve.*, sensory vesicle; *St.*, stomach; *Sti.*, stigmata; *T.*, common test of the colony; *Th.*, thorax of the zooid; *V.d.*, vas deferens; *Ve.*, vesicle of the common test.

The colonies (Fig. 1B) formed large encrusting sheets about 0·5 mm. in thickness. The colour is light grey to buff, marked with streaks and spots of dark grey and purplish black. Small prominences are evenly scattered over the surface, which is also marked by deep slit-like depressions hollowed out and inhabited by the amphipod *Tritaeta gibbosa* (Bate). The dark streaks marking the colony are due to the accumulation of faecal pellets in the cloacal system of the common test, and the markings presumably become more extensive and distinct as the colony grows older. Neither oral nor atrial openings are prominent on the surface of the colony. Sections show that the most superficial part of the test is occupied by a layer of large vesicles up to 40 $\mu$ in diameter. Below these is a dense mass of white calcareous spicules (Fig. 1C) which give the colony its light colour. The spicules, which also extend in smaller numbers through the lower layers of the test, are about 25 $\mu$ in diameter, and have about 30 rays. A cloacal system of irregular channels exists within the common test, and into these channels open the atrial cavities of the zooids. In the lower part of the test there are often many large vesicles similar to those of the upper layers. In sectioned material a narrow channel is seen to lead from the upper surface of the test down to the oral siphon of each zooid, which lies a little below the surface. It is not certain whether this deep position of the oral siphon is an artefact produced in fixation.

A zooid is figured in Fig. 1D. The thorax lies approximately at right angles to the surface of the test. There are six pointed triangular lobes on the oral siphon and the atrial opening is a wide elliptical slit across the dorsal surface of the thorax, with no siphon. Four rows of stigmata lie on each side of the branchial sac and each row has about eight stigmata. The lateral thoracic organs are not conspicuous. A narrow stalk of moderate length joins the thorax to the abdomen, which is twice as long as the thorax and lies approximately at right angles to the lower surface of the test. The oesophagus is long, but not so long as that of *Trididemnum alleni*, and the large round stomach leads into the first of three chambers of the intestine. The first two of these chambers are small, ovoid and equal; the third is a large pear-shaped sac tapering to the narrow intestinal loop. Close beside the oesophagus lies the rectum, which is enveloped by a simple pyloric gland. The eight to nine coils of the spiral vas deferens lie on the side of the single testis, and the ovary is situated close to the stomach and part of the intestine.

The adult of this didemnid differs clearly enough from that of *T. alleni* to prevent confusion, especially in the possession of six oral lobes and four rows of stigmata. It belongs to the genus *Didemnum* and is almost certainly the species referred to as *D. maculosum* in most faunistic lists. This species, although common, does not appear to have been described previously in the larval stage, and there seems to be need of further investigation of the larvae of the family Didemnidae.

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# OBSERVATIONS ON THE ABSORPTION OF RADIOACTIVE STRONTIUM AND YTTRIUM BY MARINE ALGAE

By G. M. Spooner, M.A.
Zoologist at the Plymouth Laboratory

(Text-figs. 1–10)

In the autumn of 1948, when radioactive strontium (in solution) was being used as a source of $\beta$-rays for irradiating *Gammarus*, some 'tracer' experiments were undertaken to test the degree of uptake, if any, of the 'active'[1] strontium by inanimate and living objects, including marine algae. The results obtained with algae have some special points of interest, and have confirmed the belief that the use of radioactive isotopes might become a powerful tool in advancing knowledge of the chemical exchanges between marine organisms and their environment. They are therefore described as far as they have been carried to date.

The work formed part of the investigations supported by the Atomic Energy Research Establishment[2] of the Ministry of Supply, who supplied the isotopes and lent special equipment, and by whose permission this account is published.

The writer gratefully acknowledges the help given in various ways by Dr J. F. Loutit and Dr G. E. Harrison, of the Radiobiological Research Unit at A.E.R.E., Harwell. Dr Harrison has been relied on for advice on the nuclear-physics aspects of the problems investigated. The pleasantest recollections are entertained of the kindness received from them and from various members of the A.E.R.E. staff during a week's visit to Harwell in December 1947.

I am particularly grateful to the Director, Mr F. S. Russell, F.R.S., for having, in the first place, afforded me the opportunity of exploring a new field, and to him and to Dr W. R. G. Atkins, F.R.S., for their constant sympathetic interest.

The work would have been impossible without the active co-operation of Dr H. W. Harvey, F.R.S., who kept me plied with practical suggestions and devised details of technique; and of Mr F. J. Warren, who effectively main-

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[1] The terms 'active' and 'activity' used throughout this paper mean 'radioactive' and 'radioactivity'. Though these, as well as the expression 'decay', are well-established terms in the literature of the subject, they are retained in inverted commas for the benefit of readers who are not familiar with this field of research, and to distinguish them from the words used in the normal sense.

[2] Hereafter referred to as A.E.R.E.

tained the Geiger-Müller counter in working order. I am deeply grateful to them.

It was from Dr Harvey that the suggestion to investigate the larger algae originally came.

I also have pleasure in thanking Dr Mary Parke for identifications of algae, and for making up samples from the Laboratory cultures of unicellular algae, and Mr F. A. J. Armstrong for taking responsibility for disposing radioactive waste at sea.

The literature consulted on the general aspects of the subject has been mainly confined to the following books or articles:

Smyth (1945). The official White Paper on the development of atomic energy.
Lea (1946). *Actions of Radiations on Living Cells.*
Pollard & Davidson (1942, reprinted 1947). *Applied Nuclear Physics.*
Seaborg (1944). 'Table of isotopes.'
Hoag, revised by Korff (1948). *Electron and Nuclear Physics.*

Considerable delay, due to the supply situation, was experienced in securing copies of the last three mentioned.

## METHODS

The radioactive isotopes are here used in the role of so-called 'tracers', that is to say, they are regarded as a specially labelled component of the total amount of the element present. If, for example, interest is focused on the fate of 'active' $Sr^{89}$, it is not because this isotope has a peculiar chemical behaviour of its own, but because the isotope is a guide to the behaviour of the total strontium present, of which all but a negligible amount is the natural stable element. There is virtually no difference in the chemical behaviour of members of a group sharing the same Atomic Number (isotopes); and if some atoms of a new isotope are added to a previous aggregation of the element, with freedom to move, they distribute themselves at random through the aggregation. If, between its aquatic environment and an organism, the 'activity' due to $Sr^{89}$ is found partitioned in a ratio of, say, 1 : 3, it is taken to imply that all the strontium in the system is so distributed. The wording of the title (p. 587) should thus be expanded to '...absorption of strontium and yttrium as demonstrated by changes in concentration of radioactive strontium and yttrium'.

The two essential requisites in this type of investigation are: (i) the radioactive isotope, in solution or in other suitable form; and (ii) a method of measuring the 'activity' of the experimental material, or samples of it. The manipulative technique in the application of the isotope may be very simple; on the other hand, the full analysis of the collated measurements of 'activity', including 'decay' curves of specimens, may involve much labour. This is particularly true, if, as here, more than one 'active' isotope is dealt with in the same experiment.

*The Isotope Mixture*

The isotope was supplied in the form of a weak solution of strontium chloride, of which all the strontium was in the form of its two 'active' isotopes, $Sr^{89}$ and $Sr^{90}$. As time passes two stable 'decay' products accumulate, yttrium and zirconium, the latter very slowly. With the loss of an electron ($\beta$-ray), $Sr^{89}$ passes direct to stable yttrium, while $Sr^{90}$ changes first to $Y^{90}$, which in turn changes to zirconium. The processes are summarized as follows:

$$\begin{tikzcd} & \beta & \\ \mathrm{Sr}^{89} \arrow[ur] \arrow[r, "53\cdot5\text{ days}"'] & \mathrm{Y}^{89}\text{ (stable)} & \end{tikzcd}$$

$$\begin{tikzcd} & \beta & \beta \\ \mathrm{Sr}^{90} \arrow[ur] \arrow[r, "\begin{array}{c}25\text{ years or}\\ 9130\text{ days}\end{array}"'] & \mathrm{Y}^{90} \arrow[ur] \arrow[r, "63\cdot4\text{ hr.}"'] & \mathrm{Zr}^{90}\text{ (stable)} \end{tikzcd}$$

In the above formulae the periods given below the arrows are the 'half-lives' (expectation of time taken for half the original number of atoms to disintegrate, or, otherwise stated, for 'activity' to reduce to one-half). The three nuclear reactions involved proceed at very different rates, and naturally, the greater the rate of 'decay', the greater the 'activity' of the parent element. Thus, although $Sr^{89}$ and $Sr^{90}$ may originally be present in equal quantities, the 'activity' of the $Sr^{90}$ will be far less—only $53\cdot5/9130 = 0\cdot00586$, that of the $Sr^{89}$. Clearly, as time passes, the ratio of the quantities of $Sr^{89} : Sr^{90}$ steadily drops, and correspondingly the ratio of their 'activities'. Eventually the 'activity' of the $Sr^{90}$ is of comparable strength to that of the $Sr^{89}$, and later still accounts for virtually all the surviving 'activity'. But the 'activity' due to the $Sr^{90}$ is, so to speak, automatically doubled through the presence of its short-lived daughter product, $Y^{90}$. While the daughter $Y^{90}$ remains in equilibrium with the parent $Sr^{90}$, its 'activity' is identical with that of its parent; since the amount of $Y^{90}$ 'decaying' equals the amount forming, and thus equals the amount of $Sr^{90}$ 'decaying'. The fraction of the 'activity', in the mixture, due to yttrium may thus be appreciable, although the actual quantity present at any instant immeasurably small.

The presence of the daughter product, $Y^{90}$, itself a radioactive isotope, makes possible a double investigation in the experiments to be described. The absorption of yttrium can be studied in the same specimens as that of strontium.

A further physical characteristic, of which account has to be taken in making measurements, is the maximum energy of the $\beta$-rays produced by each of the reactions. Fortunately, these are not greatly dissimilar—for the rays from $Sr^{89}$ the value is given as $1\cdot5$, for $Sr^{90}$ it is $0\cdot65$, and for $Y^{90}$ it is $2\cdot2$ mev. The last have the greatest energy and are therefore the most penetrating. The screening of specimens undergoing measurement will tend to exaggerate the importance of the $Y^{90}$ component a little.

### *Chemical Effects of the Isotope Solution*

The actual concentrations of strontium and yttrium in the isotope solution, which was 'carrier-free' (i.e. free from stable strontium, which is mainly $Sr^{88}$), were so negligibly small that the chemical effects can be completely ignored. Thus, addition of some of the 'active' solution to sea water does not alter the balance of the salts originally present, or alter the pH.

Since the original solutions supplied were usually diluted with distilled water, a slight lowering of salinity was the only result. Even this effect can be obviated if desired.

Trace impurities in the original 'active' solutions were recorded as having been detected by spectrographic methods, including Ca, Ba, Al, Mg, Fe, Pb. These did not contribute to the 'activity', and were in all respects entirely negligible.

### *'Decay' and Daughter-product 'Recovery'*

The quantity of a radioactive substance present, after an interval $t$, is given by the well-known logarithmic curve

$$Q_t = Q_0 \epsilon^{-\lambda t},$$

where $Q_0$ is the quantity at the start, and $\lambda$ the specific '*decay constant*' of the substance concerned. But $\lambda = \log_\epsilon 2/H = 0{\cdot}693/H$, where $H$ is the '*half-life*', a constant which is more familiar than $\lambda$. Thus $Q_t = Q_0 \epsilon^{-0{\cdot}693t/H}$, which simplifies to

$$Q_t = Q_0 2^{-t/H}. \tag{1}$$

This form of the equation is most convenient to use in calculating theoretical 'decay' curves, and will be adopted in this paper. A logarithmic plot gives a straight line.

The measurable 'activity' 'decays' in precisely the same way:

$$A_t = A_0 2^{-t/H}. \tag{2}$$

Suppose the solution used in an experiment contained at the start a mixture of $Sr^{89}$ and $Sr^{90}$, so that the ratio of their respective 'activities' was $x : 1$. There would also be $Y^{90}$ which had accumulated as a daughter product of $Sr^{90}$, with an 'activity' ratio of 1. The triple ratio is thus $x : 1 : 1$.

After an interval of $t$ days, the respective 'activities' have become

$$x 2^{-t/53{\cdot}5} : 2^{-t/9130} : 2^{-t/9130}. \tag{3}$$

For a period of a few months the change in the last two values is negligible for most purposes, so that the values simplify to

$$x 2^{-t/53{\cdot}5} : 1 : 1. \tag{4}$$

A general 'decay' curve for mixtures of $Sr^{89}$ and $Sr^{90}$ has been worked out. For any given mixture a corresponding point on the curve is found, and the predicted subsequent history of the mixture is given by following the curve from that point.[1] This curve is frequently referred to hereafter as the 'equilibrium decay curve': it is only valid if the $Y^{90}$ remains in equilibrium with the $Sr^{90}$.

Under some conditions all, or part, of the yttrium formed may be removed from the solution: for example, it may be adsorbed on objects in contact with the solution. If the yttrium is removed at a constant rate a new equilibrium is established in which the 'activity' of the $Y^{90}$ is less than that of $Sr^{90}$.

Supposing that yttrium has been removed, and the mixture then allowed to recover equilibrium—as might happen when a drop is removed from the yttrium-deficient solution and placed on a slide for measurement. If the specimen is measured at intervals it will be observed to *increase* in 'activity' for a time, for the rate of accumulation of $Y^{90}$ will at first be greater than the combined 'decay'. If the 'activity' at first is

$$x : 1 : 0,$$

after an interval of $t$ days it becomes

$$x2^{-t/53\cdot5} : 2^{-t/9130} : \frac{9130}{9127\cdot36}\left(2^{-t/9130} - 2^{-t/2\cdot642}\right). \tag{5}$$

The more complex expression for $Y^{90}$ 'activity' is sufficiently close to $(1 - 2^{-t/2\cdot642})$ for most practical purposes. Its value increases rather rapidly from zero during the first few days, when the rate of increase of the $Y^{90}$ is greater than the rate of decrease of all three constituents combined. After a definite interval a maximum is reached. This time is easily calculated by differentiating and equating to zero. This gives

$$\frac{9130}{9127\cdot36} \times \frac{1}{2\cdot642} 2^{-t/2\cdot642} = \frac{x}{53\cdot5} 2^{-t/53\cdot5} + \left(\frac{1}{9130} + \frac{1}{9127\cdot36}\right) 2^{-t/9130},$$

or, simplifying for short periods, when the last term on the right can be ignored,

$$\frac{1}{2\cdot642} 2^{-t/2\cdot642} = \frac{x}{53\cdot5} 2^{-t/53\cdot5},$$

or

$$t = 12\cdot062 - 9\cdot2325 \log x. \tag{6}$$

When only part of the yttrium has been lost, and if the activity ratios are at first: $x : 1 : y$ ($y$ being $< 1$); then after an interval of $t$ days it becomes

$$x2^{-t/53\cdot5} : 2^{-t/9130} : \frac{9130}{9127\cdot36} 2^{-t/9130} + \left[y - \frac{9130}{9127\cdot36}\right] 2^{-t/2\cdot642}$$

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[1] Since this curve is a compound of two curves, it is not a straight line when plotted logarithmically.

The 'activity' rises to a maximum when

$$\frac{\left(\frac{9130}{9127\cdot 36}-y\right)2^{-t/2\cdot 642}}{2\cdot 642}=\frac{x}{53\cdot 5}2^{-t/53\cdot 5}+\left(\frac{1}{9130}+\frac{1}{9127\cdot 36}\right)2^{-t/9130}.$$

Again, neglecting the last term, and approximating,

$$\frac{(1-y)}{2\cdot 642}2^{-t/2\cdot 642}=\frac{x}{53\cdot 5}2^{-t/53\cdot 5},$$

or $$t=12\cdot 062+9\cdot 2325\,[\log(1-y)-\log x]. \qquad (7)$$

Equilibrium is said to be attained when the 'activity' curve approximates to the general 'decay' curve, which depends solely on the proportion of $Sr^{89}$ to $Sr^{90}$ in the sample—in other words, when the term $2^{-t/2\cdot 642}$ in expression (5) has become negligible.

Many of the curves shown in the figures are seen to start with an initial rise before reaching a maximum, and then falling to meet the equilibrium 'decay' curve. This is due, as just explained, to 'yttrium recovery', the specimen being to some degree yttrium-deficient when it was first prepared.

Other curves are seen, by contrast, to start with a steep drop (Figs. 3 and 8) and grade exponentially towards the gently downward slope of the equilibrium 'decay' curve. In these the specimen starts with an *excess* of $Y^{90}$, and nearly always contains an object or part of an object which has a special tendency to take up yttrium.

Clearly, by careful estimation of these departures from the equilibrium 'decay' curve, a calculation can be made of the degree to which yttrium had been removed or concentrated. The point at which the curve starts (the initial measurement), and the length of time taken to reach a maximum or attain near equilibrium provide critical data.

### *Composition of the Solutions Supplied*

Two separate consignments of 'active' solutions have been received and used in experiments. These are referred to, for brevity, as 'the May solution' and 'the September solution'.

The 'May solution', from investigation of its 'decay' rates at various times, is estimated to have had a $Sr^{89}$ : $Sr^{90}$ : $Y^{90}$ ratio of

39·449 : 1 : 1 on 1 April 1948
=9·443 : 1 : 1 on 21 July
=2·092 : 1 : 1 on 15 November.

The 'September solution' was similarly estimated to have given:

9·78 : 1 : 1 on 23 September 1948
=2·707 : 1 : 1 on midnight 31 December/1 January 1949
=1·250 : 1 : 1 on midnight 1/2 March.

Several dilutions of these solutions have been made, usually by addition of measured volumes of distilled water to accurately measured 1·0 or 0·5 ml. portions of the original solution.

### *Measurement of 'Activity'*

A Geiger-Müller counter, loaned by A.E.R.E., was used for measuring the 'activity' of prepared specimens. Descriptions of this excellent instrument may be found elsewhere (see Pollard & Davidson, 1942, pp. 26–30; Hoag, 1948, pp. 442–52 for the principles of construction), though doubtless much remains to be written on the subject of its occasional vagaries. It is, however, becoming a familiar object in laboratories, and can serve as an instrument of high precision.

The counter-tube was cased in a M.R.C. Castle and provided with a 'quenching' unit, which allows of precise correction for dead time. A Variac voltage control was fitted to the input of the scalar unit to ensure a steadier voltage than is supplied by the Plymouth electricity authority.

Specimens for measurement were mounted on a microscope slide. These were usually 0·05 ml. drops of a solution, carefully measured and evaporated on a warm tray. The solutions being 'activated' sea water, or at least brackish water, the evaporated drop consisted of a fine-grained crystalline patch. An optimum rate of evaporation was found which kept the crystals small and the dried patch even. Other mounts, of thin solid objects, such as pieces of the fronds of algae, or aggregates of unicellular algae, were also made. With solid objects the weight of the specimen was determined when necessary.

Of the four positions in which the tray of an M.R.C. Castle can be placed, position 1, that nearest to the counter-tube window, was used most frequently. In this position the 'efficiency' of the counter proved to be about 10·6%.[1] (A count of 100 per minute was given by $4{\cdot}2 \times 10^{-10}$ curies in an evaporated drop. See below.)

Measurements are obtained in terms of discharges, converted to impulses, per minute. When accurately calibrated, one recorded discharge in the counter represents one photon or particle absorbed by the counter (photons of X-rays, $\gamma$-rays, or cosmic rays; particles of $\alpha$- or $\beta$-rays). The counter-tube, however, does not necessarily record all potentially available radiation—that is, particles which traverse it, or photons which have a reasonable probability of giving up their energy to it. With $\beta$-rays, with which alone we are concerned here, the capacity for absorption is quite high. Not all $\beta$-rays which impinge on the counter-tube window, however, are registered, since a fraction are absorbed in the window itself (made of aluminium foil). The conversion of 'counts' per minute into absolute terms, say total $\beta$-rays discharged by the specimen, involves various complications, but for the most part the problem can be ignored, since most of the critical results involve simply computing *ratios*

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[1] In the second position the equivalent efficiency is about 3·65%.

between different readings. Results are expressed in relative terms, or related to the same arbitrary scale.

Conversion of counter readings into curie units has been made possible by A.E.R.E., who now supply a standardized solution of $P^{32}$ (giving $\beta$-rays of 1·7 meV. maximum energy). Specimen drops have been made up of such a solution in the normal manner. To these can be assigned a definite $\mu$c. value, subject to the correctness of the specification of the standard, the accuracy of the official value for the half-life of $P^{32}$ (14·30 days), and within the limits of accuracy of the measured drop. It was found that an evaporated drop of 0·05 ml. volume, on a microscope slide resting on a tray in position 1 of the castle, will give a count of 100 per minute if it contains $4{\cdot}2 \times 10^{-10}$ curies. This is equivalent to $8{\cdot}4 \times 10^{-3}$ $\mu$c. per ml.

In working the counter the chief necessary precaution has been to guard against minor fluctuations in the rate of counting. All counter-tubes used have exhibited these. Such fluctuations are made possible, apparently, by the fact that some particles entering the counter-tube cause two discharges, and others sometimes fail to cause any. An uneasy balance between these two opposite variations, which tend on the average to cancel each other out, but of which each may on occasion predominate, has to be carefully watched. The best safeguard is the use of a constant source of 'activity', preferably one not subject to measurable 'decay', such as a solid containing uranium. Such a constant source, made of uranium oxide, has been used continuously, and as far as possible the voltage supplied to the counter-tube has been adjusted so that it tended to give a certain constant reading (4930 per minute, uncorrected, on tray in position 1).

All readings have a standard 'dead time' correction[1] (see Kamen, 1948, p. 82), which has to be added, and a constant 'background' count has to be deducted. At Plymouth, values for the background of reasonable accuracy vary between 8·7 and 10·2 per minute, with 9·5 as a modal value. The latter figure is adopted as the routine correction.

Radioactive 'decay' proceeds essentially at random, though when it is producing impulses at the rate of several thousand a minute this fact is hard to grasp. One result is that variations in counts due to sampling follow the well-known Poisson distribution curve, for which the variance ($\sigma^2$) is conveniently equal to the mean. Supposing a specimen is measured for 30 min. during which period it has given a count, corrected for dead time, of 3600. This figure has a variance of 3600 ($\sigma = 60$), and so the value per minute, i.e. 120, has a $\sigma$ of $60/30 = 2{\cdot}0$. [Alternatively, $\sigma^2_{\text{mean}} = 120/30 = 4$, $\sigma_{\text{mean}} = 2$.] In practice a background value of 9·5 per minute will have to be deducted from the empirical count of 120 per minute, giving 110·5. The corresponding error must not be deducted, but added. For the $\sigma^2$ of this corrected mean is $(120+9{\cdot}5)/30 = 4{\cdot}317$, and $\sigma_{\text{mean}} = 2{\cdot}07$ (or what would normally be the

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[1] For the particular quenching unit used, the count corrected for 'dead time' was $N/(1 - 0{\cdot}000{,}005N)$, where N was the actual count per minute.

error for a mean of 129·5). Similarly, the error for $30-9·5$ is a function of 39·5, not of 20·5. It will thus be appreciated that when counts are low, say 60 per minute or less, and the background has to be deducted, the sampling error may be considerable.

Sampling errors have not been computed as a matter of routine, and it is not considered necessary to append them to all readings recorded here. They have, of course, been considered when critical comparison has been required. It is necessary to state that the accuracy of different measurements quoted is variable. Often time could not be spared to keep a specimen in the counter as long as might have been wished. Strongly active specimens are the more accurately measured, requiring less time for a given accuracy, and thus are to be recommended for economy of effort. A count of between 2000 and 6000 per minute should be aimed at, and the specimen given a run of at least 30 min.

Actual sampling errors are probably rather greater than the ideal theoretical, on account of that element of fluctuation in the performance of the counter-tube for which it is impossible to correct completely.

## Experiments with Algae

In the experiments to be described, of which the one now related in detail was the first, the technique was extremely simple. Sea water was 'activated' by the addition of a small volume of an 'active' solution. A measured volume was put into each of two or more similar glass vessels, usually boiling tubes. One vessel was kept as control, while into the other, or others, was placed a piece of healthy alga frond. The wet weight of the piece of frond, which varied from 1 to 5 g., was determined at some stage, usually after the water had been sampled. The mouths of the vessels were covered with a glass plate, or stoppered with cotton-wool plugs. They were stood near an artificial daylight source which was kept continuously lit. After an interval, varying between 2 and 5 days, the water in the vessel was tested by the drawing off of one or two measured drops. These were placed on a slide, evaporated, as described above (p. 593) and presented to the counter. The remainder of the experiment consisted in the investigation of changes in the 'activity' of these evaporated drops. Sometimes a second or third test was made a day or two later. Details of procedure varied on different occasions, and these will be mentioned as the account proceeds. Small improvements were continually being made, particularly in the accuracy with which the specimen drop was measured and mounted.

The standard quantity taken for each drop was 0·05 c.c., or, at first, an approximation to this. I am much indebted to Dr Harvey for adapting a 0·1 c.c. pipette in a simple but effective way, so that it could be manipulated accurately by hand. The liquid could be steadied and finally levelled by a screw adjustment; care being taken that the glass surface remained clean, the accuracy with which the drop was ultimately measured kept within the limits of 1% either way. In the first experiment, however, there were possibilities of a considerably greater error.

The measured drop is placed in the centre of a glass slide and allowed to evaporate. The exact shape of the drop is not important, provided the area keeps within that of the window of the counter, i.e. it must not be allowed to attenuate too much in any direction. It is well for the evaporation to take place fairly quickly, say in 10 or 15 min., when the crystals of sea salt will be small. The presence of large crystals may increase the self-absorption of the specimen and give somewhat low readings. The slides should therefore be placed on a warm tray, or over a weak bunsen flame. They should be stored in a place where deliquescence in a saturated atmosphere does not occur.

For measuring the 'activity' of the specimen, the slide is placed in the chamber of the counter so that the specimen (evaporated drop) is in an exactly defined position. It is necessary, of course, that all the microscope slides used should be of the same thickness, otherwise variations, small, but important, will arise in the distance of the specimen from the window.

As soon as a specimen is prepared its 'activity' is measured, and further measurements are made at intervals subsequently. From the nature of the 'decay' characteristics of the specimen and the relation between it and the control specimen, the degree of absorption of the 'active' ions by the weed can be accurately determined. It is not necessary to examine the weed itself further, but valuable supplementary or corroborative data can be obtained by mounting a fragment of the alga, well washed, and investigating the 'decay' characteristics of any 'activity' it may have absorbed.

The method of analysing and interpreting the 'decay' characteristics of specimen drops is best explained when the results of an actual experiment have been given.

### *An Experiment with* Fucus serratus *and* Rhodymenia palmata

In the first experiment, set out on 20 October 1948, four boiling tubes were taken and into each 25 ml. of sea water were measured, and to each 0·5 ml. of an 'active' solution added. [The 'active' solution was the May solution diluted × 114.] Into one tube (*P*) a piece of *Rhodymenia palmata* Grev. frond, 1·4 g. in weight, was added, and the second tube (*Q*) kept it as control. Into a third tube (*R*) a piece of *Fucus serratus* L., 1·2 g. in weight, was added, and the remaining tube (*S*) kept with it as control.

It may be noticed that the control solutions are not strictly identical with those of the alga-containing tubes, since the 'active' 0·5 ml. was added to each independently, and each tube was liable to a different error in the estimation of the 0·5 ml. added to it. Tubes *Q* and *S* were therefore 'similarly treated' as tubes *P* and *R*.

The *Rhodymenia* tube (*P*) was sampled 3 days later, on 23 October, together with its control (*Q*), and again on 27 October. Two drops were taken in each sampling (*P*i and *P*ii on 23 October; *P*iii and *P*iv on 27 October; *Q*i and *Q*ii on 23 October). The *Fucus* tube (*R*), with its control (*S*), was sampled on 25 October (drops *R*i, *R*ii and *S*i, *S*ii), and again on 27 October (*R*iii and *R*iv).

In working out the results of 'activity' measurements, the mean of each pair of drops is taken. Thus $\frac{1}{2}(P\text{i}+P\text{ii})=Pa$; $\frac{1}{2}(P\text{iii}+P\text{iv})=Pb$; $\frac{1}{2}(Q\text{i}+Q\text{ii})=Q$, and so on. The 'activity' curves of the various specimens are given in Fig. 1 (*Rhodymenia*) and Fig. 2 (*Fucus serratus*).

A glance at the *P* and *R* curves, the positions of which would be widely separated were they placed on the same graph, shows at once that the two algae have given entirely different results. Before, however, this difference is analysed, it is necessary to consider each graph separately, and to be clear how each alga-containing tube differs from its control.

Taking tube *P* first—it is seen that on the day the sampling was made (23 October) the water in *P* shows appreciably reduced 'activity' as compared with *Q*, though not excessively less (actually 81%). During subsequent days there is some increase in the 'activity' of the control specimen, which reaches a maximum about 27 October, after which it begins to show the expected 'decay'; but there is still greater increase in the 'activity' of the specimen of alga-treated water, as shown by the steep rise in the curve *P* (actually it is *Pa* which is plotted), which does not reach a maximum before about 1 November. The difference between *P* and *Q* steadily reduces until the two values are within 5%, or less, of each other, the final mean ratio of *P*/*Q* being 96·05%.

As explained above, an increase in the 'activity' of a specimen shows that, when it was prepared, it was deficient in yttrium. The daughter product, $Y^{90}$, has been wholly or partially removed and is below equilibrium value. In the specimen itself, the amount of $Y^{90}$ will gradually be restored to equilibrium value by the decay of $Sr^{90}$. The rate at which this occurs can be calculated as precisely as the accuracy of the values of the 'decay'-constants of $Sr^{90}$ and $Y^{90}$ permit. The greater the deficiency of yttrium, the longer is the period of 'recovery' before a maximum 'activity' is attained, and before the eventual establishment of equilibrium, when the 'decay' follows the theoretical curve determined from the ratio of $Sr^{89}$ to $Sr^{90}$ in the mixture.

The initial loss of 'activity' due to the removal of $Y^{90}$ cannot exceed a certain value at a given moment, determined by the proportion of $Y^{90}$ 'activity out of the total, itself in turn determined by the proportion of its parent $Sr^{90}$. Once the 'activity' ratio of $Sr^{89}:Sr^{90}$ has been determined for a particular hour, the expected fraction of 'activity' due to $Y^{90}$ can be worked out for any

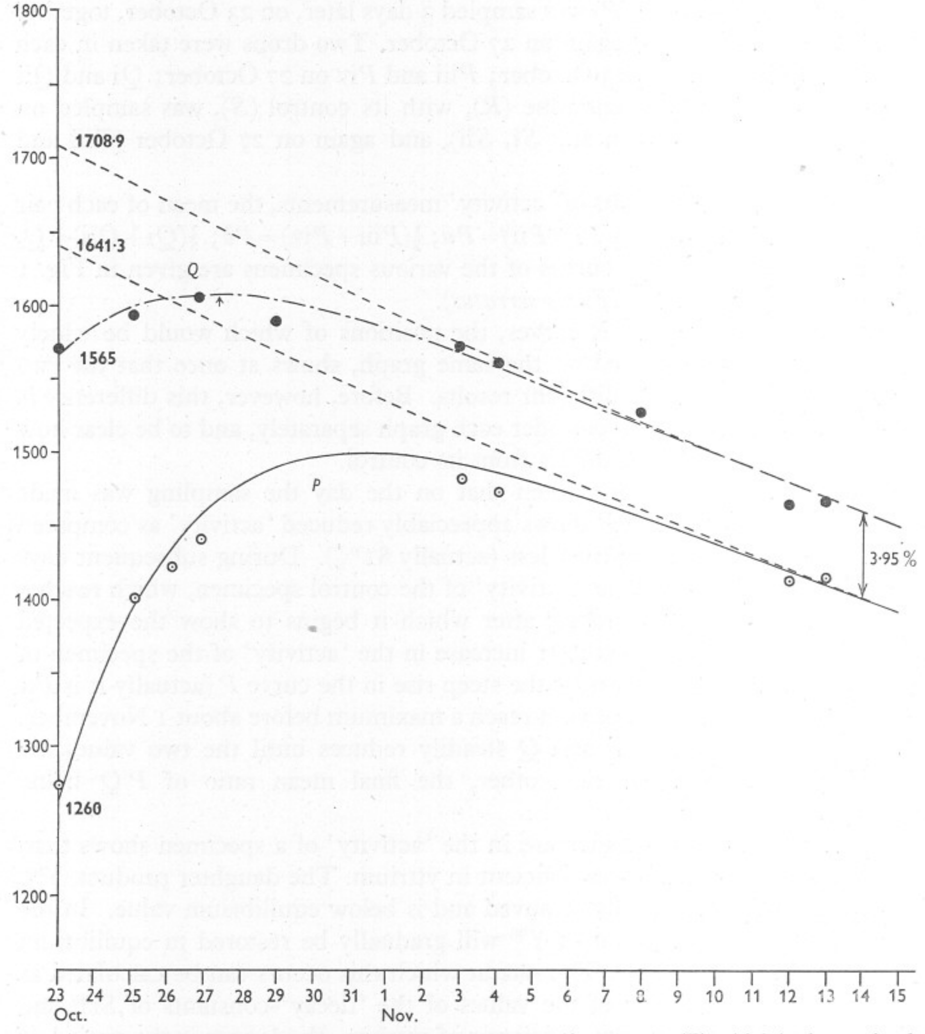

Fig. 1. 'Decay' characteristics of a specimen of 'activated' sea water (*P*) which had contained a piece of *Rhodymenia* frond; compared with a control specimen of 'activated' sea water (*Q*). Tube *P* had held 1·4 g. of alga in 25·5 ml. of sea water. Curves have been fitted to the two series of points on the assumption that the initial rise is due to recovery of an initial deficiency of $Y^{90}$. The close-pecked lines represent the two equilibrium 'decay' curves, to which the curves *P* and *Q* respectively tend. Activity in arbitrary units. The heavy numerals represent the estimated values of each of the curves at the isolation of the specimens on 23 October.

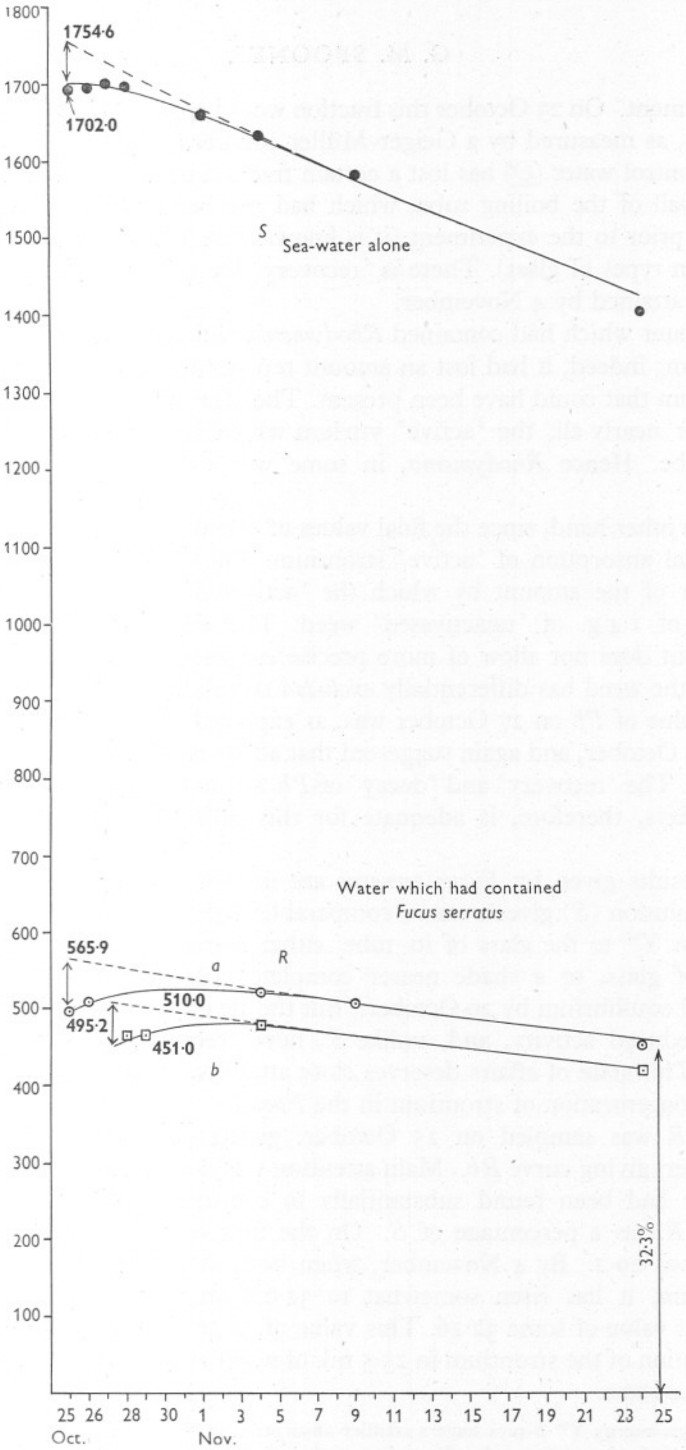

Fig. 2. Curves showing 'decay' characteristics of sea water ($R$) which had contained a piece of *Fucus serratus* frond, compared with a control specimen ($S$). Tube $R$ had held 1·2 g. of *Fucus serratus* in 25·5 ml. of sea water, and two specimens ($a$ and $b$) were examined from it. The lines with arrows on the left indicate the extent of the initial yttrium deficiency. Other particulars as in Fig. 1.

other moment. On 23 October this fraction would appear to have been 20·7%, or 22·5% as measured by a Geiger-Müller counter.[1]

The control water (*Q*) has lost a certain fraction of $Y^{90}$, no doubt adsorbed on the wall of the boiling tube, which had not been subjected to stringent cleaning prior to the experiment (it is known that Y is liable to be adsorbed on certain types of glass). There is 'recovery' for 4 days, and equilibrium is virtually attained by 4 November.

The water which had contained *Rhodymenia* had lost considerably more of its yttrium; indeed, it had lost an amount representing all, or very nearly all, the yttrium that could have been present. The alga must therefore have taken up all, or nearly all, the 'active' yttrium which had not gone on the glass of its tube. Hence *Rhodymenia*, in some way,[2] differentially concentrates yttrium.

On the other hand, since the final values of *P* and *Q* are so close, there is no differential absorption of 'active' strontium. The 4% or so reduction is of the order of the amount by which the 'activated' water is diluted by the addition of 1·4 g. of 'unactivated' weed. The accuracy of this particular experiment does not allow of more precise estimates, and it can not be said whether the weed has differentially *excluded* strontium.

The value of *Pb* on 27 October was, as expected, slightly less than that of *Pa* on 23 October, and again suggested that all, or nearly all, the $Y^{90}$ had been taken up. The 'recovery' and 'decay' of *Pb* was not studied.

Two days, therefore, is adequate for this differential absorption of $Y^{90}$ to occur.

The results given by *Fucus serratus* are in strong contrast (Fig. 2). The control solution (*S*) gives a curve comparable with *Q*, except that it had lost rather less $Y^{90}$ to the glass of its tube, either because this was of a different quality of glass, or a shade nearer complete cleanliness. It had virtually recovered equilibrium by 29 October. But the alga-treated solution (*R*) shows greatly reduced activity, and, unlike *P*, never recovers to the level of the control. This state of affairs deserves close attention, since it points to a substantial concentration of strontium in the *Fucus*.

Tube *R* was sampled on 25 October, giving curve *Ra*, and again on 27 October, giving curve *Rb*. Main attention was devoted to the former when the other had been found substantially to confirm it. It is instructive to consider *Ra* as a percentage of *S*. On the first day, 25 October, this percentage was 29·2. By 4 November, when both samples had nearly attained equilibrium, it has risen somewhat to 32·02, and subsequently settles to a constant value of some 32·26. This value of 32·26% represents the drop in concentration of the strontium in 25·5 ml. of water as a result of adding 1·20 g. of *Fucus serratus*.

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[1] The high energy $Y^{90}$ $\beta$-rays have a smaller absorption in the window of the counter.

[2] See pp. 616–18 and 620–3 for discussion of this phenomenon.

Thus, adding 1·20 g. of *Fucus* was equivalent to diluting with

$$\frac{25\cdot5}{0\cdot3226}-25\cdot5=\frac{25\cdot5\times0\cdot6774}{0\cdot3226}=53\cdot55 \text{ ml.} = 55\cdot0 \text{ g. of sea water,}$$

or $55\cdot0/1\cdot20=45\cdot8$ times as much by weight.

The slight rise in 'activity' apparent during the first few days in both the *Ra* and *Rb* specimens makes it clear that the water was even more deficient in yttrium than deficient in strontium. It is easy to calculate that only about 46% of the expected amount (i.e. of that in equilibrium with the Sr present) remains in the water.

*To sum up at this stage, it appears from deficiencies in the sea-water medium that the* Rhodymenia *has absorbed nearly all the available 'active' yttrium, but no strontium, whereas the* Fucus serratus *has taken up part of the yttrium and a good deal of strontium as well.* These deductions can be tested by direct observations on the weed itself, as will now be discussed.

A rectangular fragment of the *Rhodymenia* frond, which was found to have a wet weight of 0·012 g., was placed on a microscope slide and treated as an ordinary specimen. It had first been well rinsed in distilled water, and after mounting it had frequently been moistened with distilled water to keep it something approaching its original shape. The first counter reading, on 5 November, was 4784 per minute (Fig. 3, curve *P*). 'Decay', however, was rapid, and it was soon clear, after a few readings at regular intervals, that the rate of 'decay' was close to that of pure $Y^{90}$—that is with half-life between 60 and 70 hr., or tenth-life of just under 9 days. In 10 days (15 November), indeed, the reading had fallen to 398 per minute. After this the rate of 'decay' gradually eased, until, in early December, it had nearly attained the slow rate of a strontium mixture in equilibrium. By 10 December, when excess $Y^{90}$ must have practically disappeared, a count of 42·5 per minute remained, due to strontium (including the $Y^{90}$ in equilibrium with it). The final analysis, given in Table I, shows that, on 5 November there was (in arbitrary units of 'activity'):

4729·7 due to excess $Y^{90}$.
53·9 due to the Sr mixture, including the $Y^{90}$ in equilibrium with it.
=4743·1 due to $Y^{90}$, 40·5 due to $Sr^{89}+Sr^{90}$.

In other words, the *Rhodymenia* had taken up a very appreciable amount of 'activity', of which more than 99% is due to yttrium. Without pressing the significance of the actual figures too far, it is easy to see that the weed had not only concentrated available yttrium very heavily, but had, by contrast, taken up very decidedly less strontium than might have gone into it by free interchange. It may be said to have 'differentially' excluded strontium. The conclusions reached before are thus confirmed and amplified.

A piece of *Fucus serratus*, similarly treated (Fig. 3, curve *R*), clearly behaved quite differently. This specimen, however, was not so satisfactory for prolonged study: after a week or so it had dried too far and become strongly curled at the edges. Though it was cut into pieces which could lie together more or less flattened, the original shape could never be restored, and exact results could no longer be expected from it. However, during the first week or so the rate of 'decay' shows two things clearly: (i) the 'activity' must have been mainly derived from strontium, but (ii) it started with an appreciable excess[1] of $Y^{90}$, the 'decay' of which is apparent during the first few days.

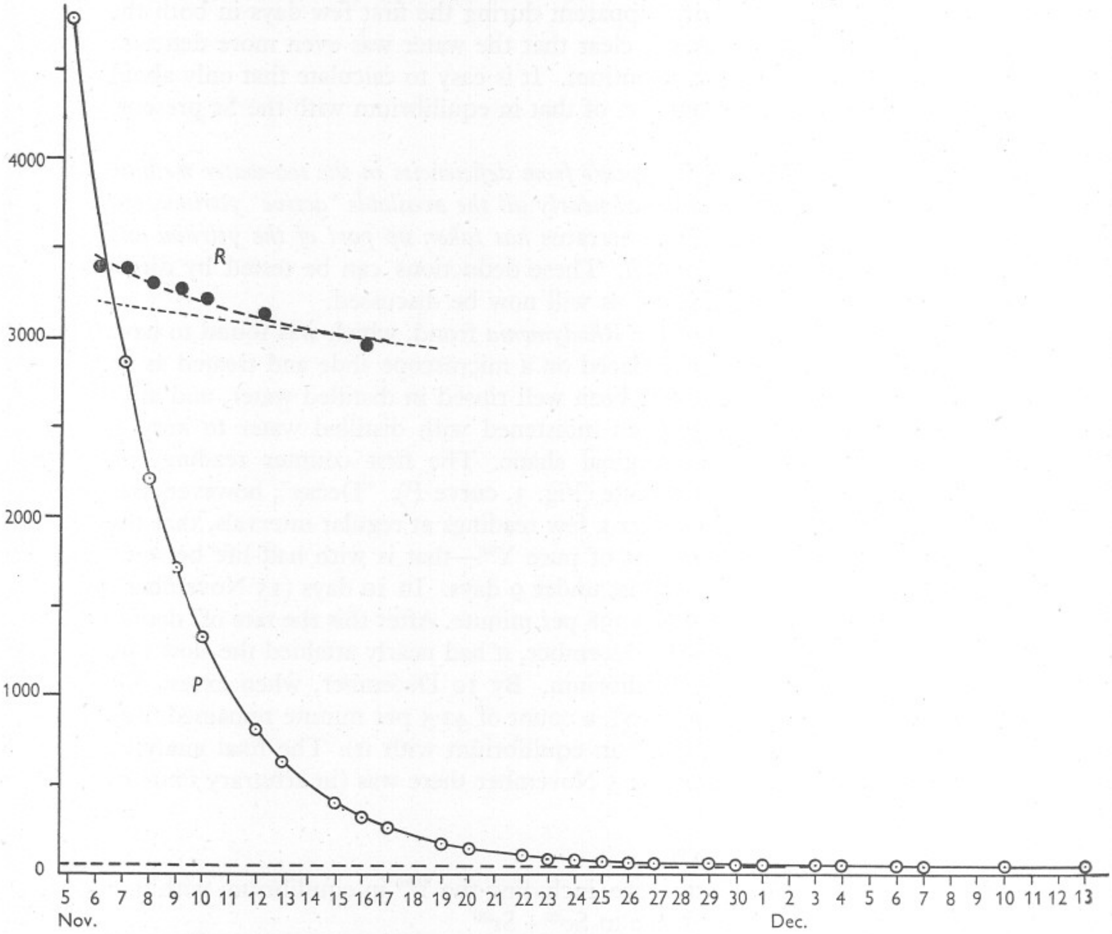

Fig. 3. 'Decay' curves of specimens of alga which had been placed in 'activated' sea water—*P*, *Rhodymenia falcata*; *R*, *Fucus serratus*. These corroborate the conclusions derived from the study of Figs. 1 and 2. *P* is seen to have acquired activity which is due almost entirely to $Y^{90}$. The activity of *R* is mainly due to 'active' Sr mixture, but it has a little excess $Y^{90}$. The units of the two curves cannot be directly compared.

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[1] I.e. excess over the equilibrium value.

About 3208 of the original count of 3442 (on 6 November) seems to have been due to the strontium equilibrium mixture and 234 to excess $Y^{90}$. The partial deficiency of $Y^{90}$ in the water has thus a counterpart of excess in the weed. Again there is corroboration of the conclusions derived from the first method.

TABLE I. 'DECAY' OF 'ACTIVATED' *RHODYMENIA* FROND (SPECIMEN *P*)

'Activity' (in arbitrary units) of a specimen mounted on 5 November and re-measured at noon on various subsequent days.

| | (1) Total 'activity' | (2) Part due to Sr equilibrium mixture | (3) Part due to excess $Y^{90}$ |
|---|---|---|---|
| 5 Nov. | 4783·6 | 53·9 | 4730 |
| 6 | 3630·2 | 53·5 | 3577 |
| 7 | 2869·0 | 53·2 | 2816 |
| 8 | 2209·0 | 52·8 | 2156 |
| 9 | 1713·2 | 52·4 | 1661 |
| 10 | 1328·8 | 52·1 | 1277 |
| 12 | 816·9 | 51·4 | 766·5 |
| 13 | 633·5 | 51·0 | 582·5 |
| 15 | 398·1 | 50·4 | 347·7 |
| 16 | 313·4 | 50·0 | 263·4 |
| 17 | 255·1 | 49·7 | 205·4 |
| 19 | 170·8 | 49·1 | 121·7 |
| 20 | 143·0 | 48·7 | 94·3 |
| 22 | 102·8 | 48·1 | 54·7 |
| 24 | 79·5 | 47·5 | 32·0 |
| 25 | 76·0 | 47·2 | 28·8 |
| 26 | 66·25 | 47·93 | 19·3 |
| 27 | 61·06 | 46·64 | 14·4 |
| 29 | 53·22 | 46·08 | 7·1 |
| 30 | 55·65 | 45·80 | 9·8 |
| 1 Dec. | 49·23 | 45·53 | 3·7 |
| 3 | 49·38 | 44·99 | 4·4 |
| 4 | 46·31 | 44·73 | 1·6 |
| 6 | 45·41 | 44·21 | 1·2 |
| 7 | 44·03 | 43·96 | — |
| 10 | 42·39 | 43·22 | — |
| 13 | 40·60 | 42·51 | — |
| 20 | 39·50 | 40·95 | — |

*Notes*. Column (1): as measured. Column (2): smoothed value. Column (3): column (1) less (2). Errors became high towards the foot of column (3). The values in column (2) are derived, knowing the decay characteristics of the 'active' solution used, to give the best fit in two respects—(i) to account for all measured 'activity' from about 10 December onwards, so that they represent a smoothed curve for column (1) after that date; and (ii) to make the logarithm of column (3) to plot as a straight line.

### *Confirmatory Experiments*

Two further tests were made with pieces of *F. serratus* (Exps. *T* and *V*), of which the results essentially confirm the foregoing.

(i) Aliquot parts of 50 ml. sea water, activated with 1 ml. of an 'active' solution on 27 October, were placed in tubes *T* and *U*. In tube *T* was then placed a piece of *F. serratus* frond 1·05 g. in weight, and *U* kept as control. Both tubes were sampled 2 days later. The 'decay' curves are given in Fig. 4,

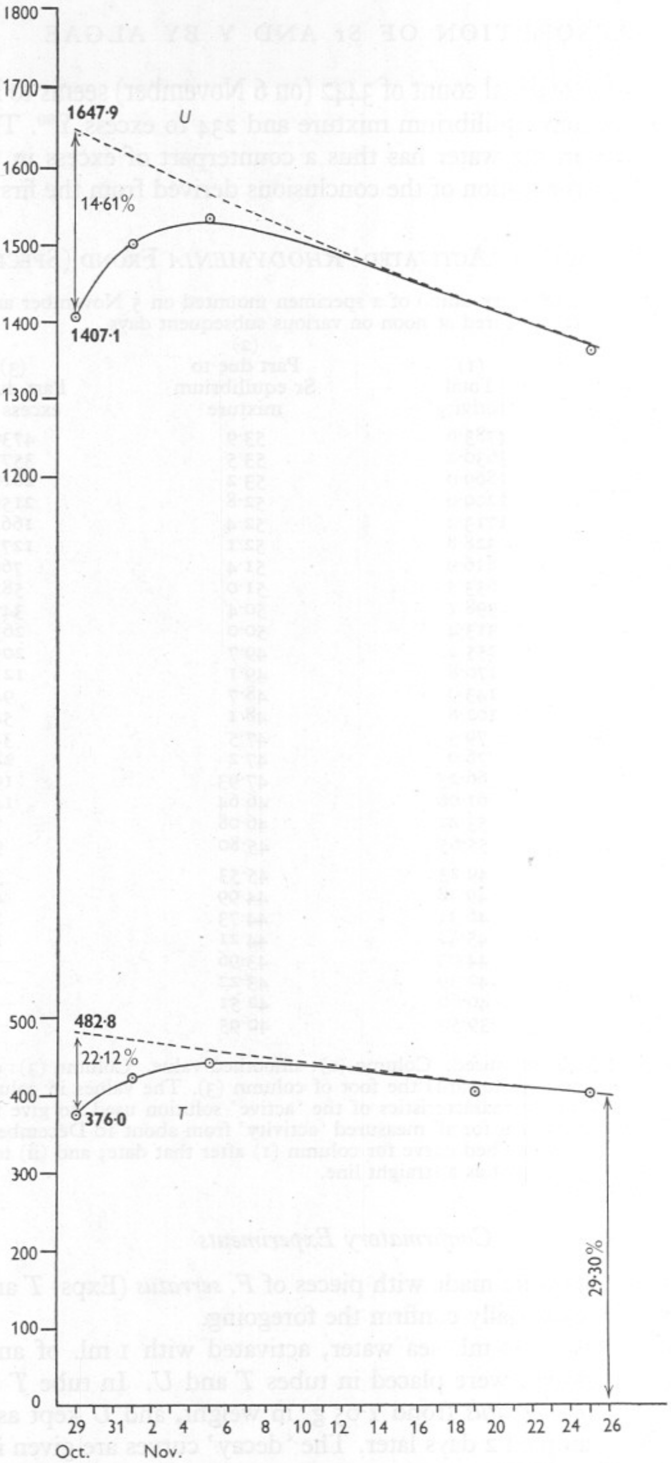

Fig. 4. 'Decay' curves of specimens of 'activated' sea water, as in Fig. 2. *T*, water which had contained a piece of *Fucus serratus* (1·05 g. in 25·5 ml. of sea water). *U*, control. 'Activity' in arbitrary units.

from which a close resemblance to Fig. 2 at once comes to notice. The value of the sample from *T* is at first 26·72% that of *U* and increases to 29·65%. Thus, reasoning as before, 1·05 g. of weed is equivalent to

$$\frac{25{\cdot}5 \times 0{\cdot}7035}{0{\cdot}2965} = 60{\cdot}5 \text{ ml. of sea water.}$$

This is a weight of 62·14 g. The degree of concentration of the strontium is thus as much as 59 times.

This experiment thus suggests an even higher concentration of strontium in the weed, but the failure, in this particular experiment, to measure the divided volumes exactly may have introduced an error of 3 or possibly 5%. There is partial yttrium deficiency in both *T* and *U*, as was found in Exp. *R*.

(ii) On 29 October another similar experiment was set up. This time the division of the 'activated' sea water was precise. The 'activity' of the water was less than before. To 50 ml. of 'outside' sea water was added 0·5 ml. of 'active solution *D*' (*D* = the September solution diluted × 560). Into tube *V* was placed 2·9 g. of *F. serratus*, and tube *W* was kept as control. The tubes had been treated with strong cleaning fluid and, probably as a result, hardly any yttrium was taken up by the control. Specimens were taken on 3 November, 5 days later. The 'decay' curves are given in Fig. 5. The final percentage of the 'activity' of the water in *V* compared with *W* is 18·80%. Thus 2·9 g. of weed is equivalent to

$$\frac{25{\cdot}25 \times 0{\cdot}812}{0{\cdot}188} = 109{\cdot}1 \text{ ml.} = 112{\cdot}0 \text{ g. of sea water,}$$

or 38·6 times the weight of the weed.

*Rhodymenia* was again tested on a later occasion (3 December). The 'activated' sea water used was that which had served as control for the previous experiment, i.e. from tube *Q*. Of this 20 ml. were drawn off and placed in tube *L*, the remaining 4 ml., or so, were kept as control. In tube *L* was placed 0·78 g. of *Rhodymenia* frond. The water was sampled on 8 December. The 'activity' curves, shown in Fig. 6, are similar to those in Fig. 1, the alga-treated water showing heavy yttrium deficiency but no strontium deficiency. As the solution is 6 weeks 'staler', there will be rather more yttrium (relatively) present at the start; and, since the ratio $Sr^{89} : Sr^{90}$ is now lower by nearly half, the 'decay' of the equilibrium mixture is decidedly slower.

The 'recovery' of the alga-treated water is so complete, as to suggest that the alga had not taken up any 'active' strontium at all. At least it seems that the weed had much less diluting effect than an equivalent weight of water. But again it has taken up almost all available yttrium (probably less had gone on the glass in the clean boiling tube containing the 20 ml. than in the control tube, the original tube *Q*, which had *not* been in cleaning fluid and had been

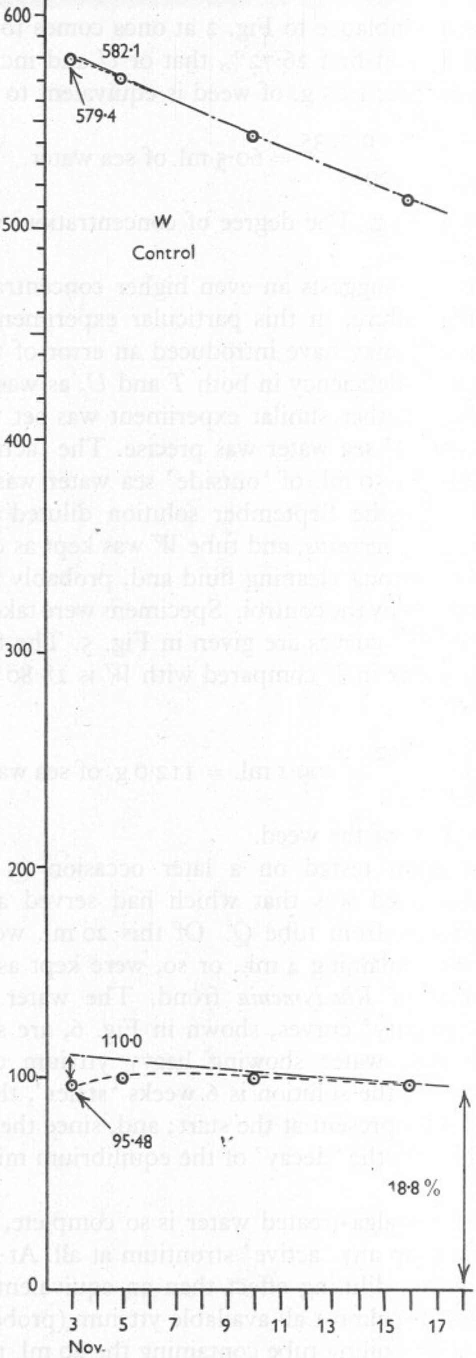

Fig. 5. Similar 'decay' curves as in Figs. 2 and 4. *V*, water which had contained *Fucus serratus* (2·90 g. in 25·25 ml. of sea water). *W*, control.

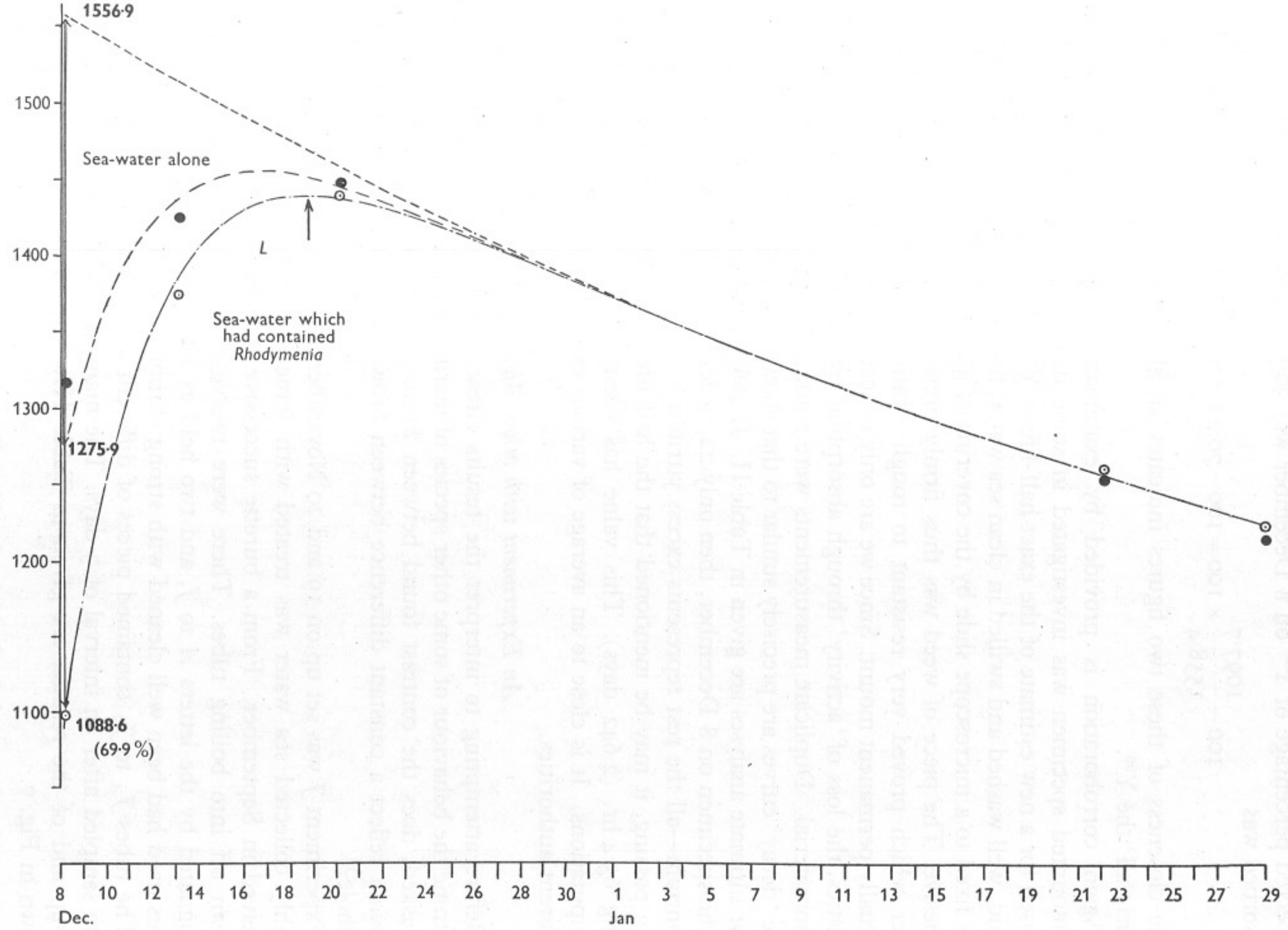

Fig. 6. 'Decay' curve ($L$) of specimen of activated sea water in which a piece of *Rhodymenia* frond (0·78 g. in 20 ml. of sea water) had been placed, as in experiment shown in Fig. 1. ⊙——⊙, specimen of alga-treated water. ●---●, control (in different type of vessel). -----, 'decay' curve of equilibrium mixture. 'Activity' in arbitrary units. Other particulars as before.

standing with sea water for some 6 weeks). Calculation shows that the expected percentage of $Y^{90}$ on 8 December was 30·59%, and the percentage absorbed was

$$100 - \frac{1097{\cdot}7}{1558{\cdot}4} \times 100 = 100 - 70{\cdot}45 = 29{\cdot}55\,\%.$$

The closeness of these two figures indicates an absorption of all or 'very nearly all' the $Y^{90}$.

Again corroboration is provided by examination of the weed itself. A mounted specimen was investigated in some detail, being one that was chosen for a new estimate of the exact half-life of $Y^{90}$. The damp fragment of frond, well washed and swilled in clean sea water, followed by distilled water, was fixed to a microscope slide by the covering of a broad strip of cellophane adhesive. The piece of weed was thus firmly pressed down by a protective layer which proved very resistant to rough treatment. It has provided a virtually permanent mount. Since we are only concerned with 'decay' characteristics, the loss of 'activity' through absorption by the cellophane covering is immaterial. Duplicate measurements were made in two counter positions. The 'decay' curves are precisely similar to that shown in Fig. 3 (curve *P*), and their ultimate analyses are given in Table II. If 4660 represents the 'activity' of the specimen on 8 December, then only 22, or less than 0·5%, was due to strontium—all the rest represents excess yttrium.[1]

In passing, it may be mentioned that the half-life of $Y^{90}$ was estimated as being 63·4 hr. (2·642 days). This value has been adopted in the present computations. It is close to an average of various estimates given to date by different authorities.

### *An Experiment with other Algae*

Before attempting to interpret the results already described it is well to examine the behaviour of some other species of marine algae. How far, it may be asked, does the contrast found between *Fucus serratus* and *Rhodymenia palmata* reflect a constant difference between brown algae and red algae as a whole?

Experiment *J* was set up on 19 and 20 November. A volume of 250 ml. of freshly collected sea water was treated with some of the 'active' solution received in September. From a burette successive fractions of 20 ml. were drawn off into boiling tubes. There were twelve of these altogether, ten designated by the letters *A* to *J*, and two held as a control. All the boiling tubes used had been well cleaned with strong chromate cleaning solution.

The tubes $J_A$ to $J_J$ contained pieces of different kinds of algae. All tubes were sampled after an interval of 3 days. The main particulars, both of the set-up and of the results, are given in Table III. The 'decay' curves are shown in Fig. 7.

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[1] Absorption of some of the $\beta$-rays by the thin cellophane covering may have somewhat favoured the $Y^{90}$ at the expense of the Sr.

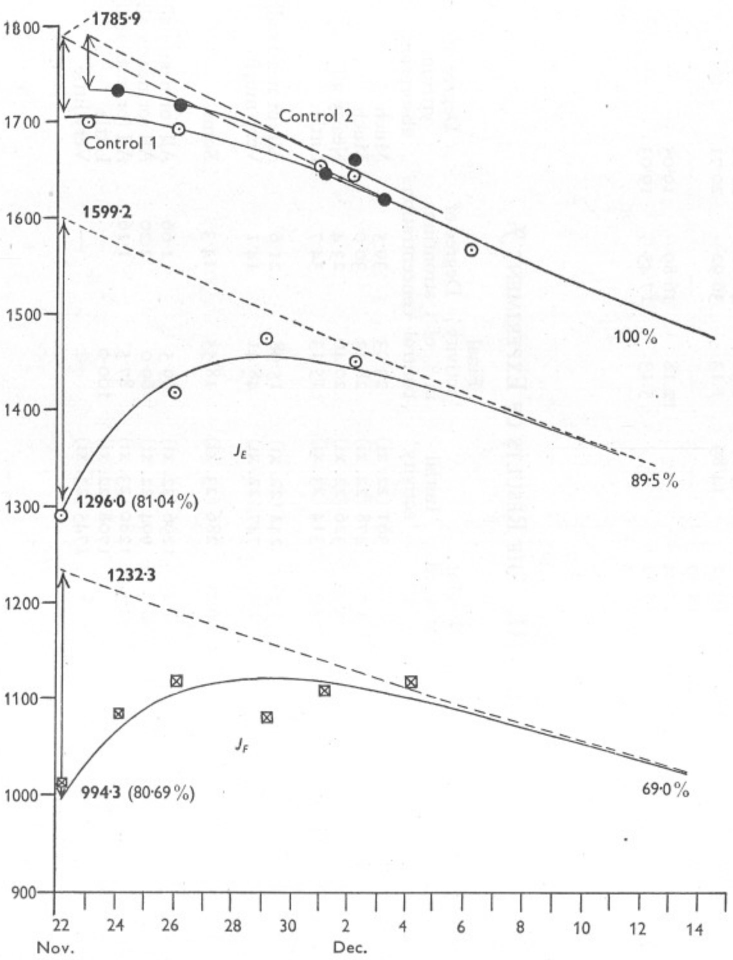
## TABLE II. 'DECAY' OF 'ACTIVATED' *RHODYMENIA* FROND (SPECIMEN *L*)

Two independent analyses at two counter positions. The 'activity' units for position 1 are reduced by a factor of 2·92 to make them very nearly comparable with the measurements for position 2. Further particulars as in Table I.

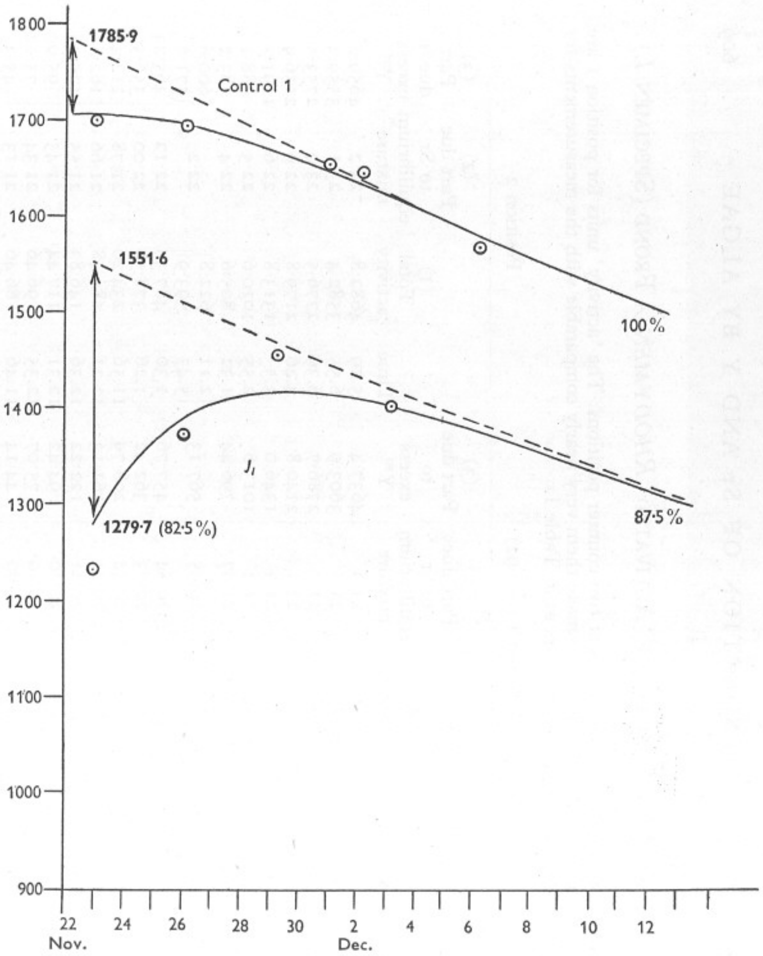
| | Position 1 (÷2·92) | | | | Position 2 | | | |
|---|---|---|---|---|---|---|---|---|
| Date | Time | (1) Total activity | (2) Part due to Sr equilibrium mixture | (3) Part due to excess $Y^{90}$ | Time | (1) Total activity | (2) Part due to Sr equilibrium mixture | (3) Part due to excess $Y^{90}$ |
| 8 Dec. | 4.54 | 4659·3 | 21·9 | 4637·4 | 5.29 | 4682·8 | 23·2 | 4659·6 |
| 9 | 5.50 | 3625·7 | 21·8 | 3603·9 | 6.55 | 3582·4 | 23·1 | 3559·3 |
| 10 | 5.50 | 2808·4 | 21·7 | 2786·7 | 6.39 | 2776·5 | 23·0 | 2753·5 |
| 11 | 3.48 | 2162·3 | 21·5 | 2140·8 | 4.46 | 2179·8 | 22·9 | 2156·9 |
| 13 | 12.22 | 1367·3 | 21·3 | 1346·0 | 3.5 | 1313·8 | 22·6 | 1291·2 |
| 14 | 1.48 | 1034·8 | 21·2 | 1013·6 | 2.55 | 1010·6 | 22·5 | 988·1 |
| 15 | 12.21 | 817·5 | 21·07 | 796·44 | 1.32 | 805·6 | 22·4 | 783·2 |
| 16 | 6.41 | 588·08 | 20·95 | 567·13 | 2.11<br>5.43 | 622·8<br>593·9 | 22·2 | 600·6<br>571·7 |
| 17 | 2.48 | 478·60 | 20·84 | 457·76 | 1.30 | 487·35 | 22·12 | 465·23 |
| 18 | 12.15 | 383·15 | 20·73 | 362·42 | 1.26 | 378·50 | 22·00 | 356·50 |
| 20 | 1.33 | 229·30 | 20·52 | 208·79 | 11.56 | 234·20 | 21·78 | 212·42 |
| 21 | 1.47 | 181·54 | 20·41 | 161·13 | 12.21 | 184·48 | 21·66 | 162·82 |
| 22 | 1.45 | 142·53 | 20·31 | 122·22 | 12.36 | 146·83 | 21·55 | 125·28 |
| 23 | 1.47 | 114·62 | 20·20 | 94·42 | 12.31 | 117·44 | 21·45 | 95·99 |
| 24 | 1.39 | 95·17 | 20·10 | 75·07 | 12.35 | 96·46 | 21·34 | 75·12 |
| 26 | 12.35 | 64·04 | 19·90 | 44·14 | 11.46 | 66·46 | 21·13 | 45·33 |
| 28 | 2.2 | 44·97 | 19·71 | 25·26 | 12.29 | 45·86 | 20·92 | 24·94 |
| 29 | 1.59 | 39·48 | 19·61 | 19·87 | 12.36 | 40·68 | 20·82 | 19·86 |
| 30 | 2.56 | 34·41 | 19·52 | 14·89 | 1.13 | 36·92 | 20·71 | 16·21 |
| 17 Jan. | 6.8 | 16·97 | 18·00 | — | — | — | — | — |
| 18 | 1.44 | 16·97 | 17·94 | — | 12.18 | 16·89 | 19·05 | — |
| 18 | 6.38 | 16·95 | 17·92 | — | 5.13 | 17·45 | 19·03 | — |

## TABLE III. THE RESULTS OF EXPERIMENT *J*

| Species | Tube no. | Weight of weed (g.) | Initial 'activity' | Final 'activity' in % of control | Degree of strontium concentration | Degree of yttrium absorption |
|---|---|---|---|---|---|---|
| *Fucus serratus* L. | $J_A$ | 1·74 | 361 (22. xi) | 23·03 | 39·5 | Much |
| *F. serratus* (in dark) | $J_B$ | 1·74 | 478 (22. xi) | 28·23 | 30·0 | Much |
| *F. vesiculosus* L. | $J_D$ | 3·41 | 326 (22. xi) | 20·46 | 23·4 | Nearly all |
| *F. vesiculosus* var. *evesiculosus* Cotton (young growth) | $J_H$ | 3·32 | 314 (23. xi) | 15·13 | 34·7 | Little |
| *Ascophyllum nodosum* Le Jol | $J_G$ | 5·01 | 242 (22. xi) | 15·98 | 21·6 | All (or nearly all) |
| *Laminaria digitata* (L.) Lamour. | $J_C$ | 1·55 | 747 (22. xi) | 48·41 | 14·1 | Very much |
| *Laminaria digitata* (L.) Lamour. | $J_J$ | 6·29 | 286 (23. xi) | 18·55 | 14·3 | Some |
| *Chondrus crispus* Stackh. | $J_E$ | 1·45 | 1296 (22. xi) | 89·5 | 1·66 | All (or nearly all) |
| *Gigartina stellata* Batt. | $J_F$ | 4·2 | 994 (22. xi) | 69·0 | 2·20 | All (or nearly all) |
| *Ulva lactuca* L. | $J_I$ | 2·54 | 1280 (23. xi) | 87·5 | 1·16 | All (or nearly all) |
| Control 1 | — | — | 1708 (22. xi) | 100·0 | — | Little |
| Control 2 | — | — | 1745 (23. xi) | — | — | Very little |



1785·9
Control 2
Control 1
1599·2
100%
$J_E$
89·5%
1296·0 (81·04%)
1232·3
$J_F$
994·3 (80·69%)
69·0%
1800
1700
1600
1500
1400
1300
1200
1100
1000
900
22
Nov.
24
26
28
30
2
Dec.
4
6
8
10
12
14



1785·9
Control 1
1551·6
100%
$J_I$
87·5%
1279·7 (82·5%)
1800
1700
1600
1500
1400
1300
1200
1100
1000
900
22
Nov.
24
26
28
30
2
Dec.
4
6
8
10
12

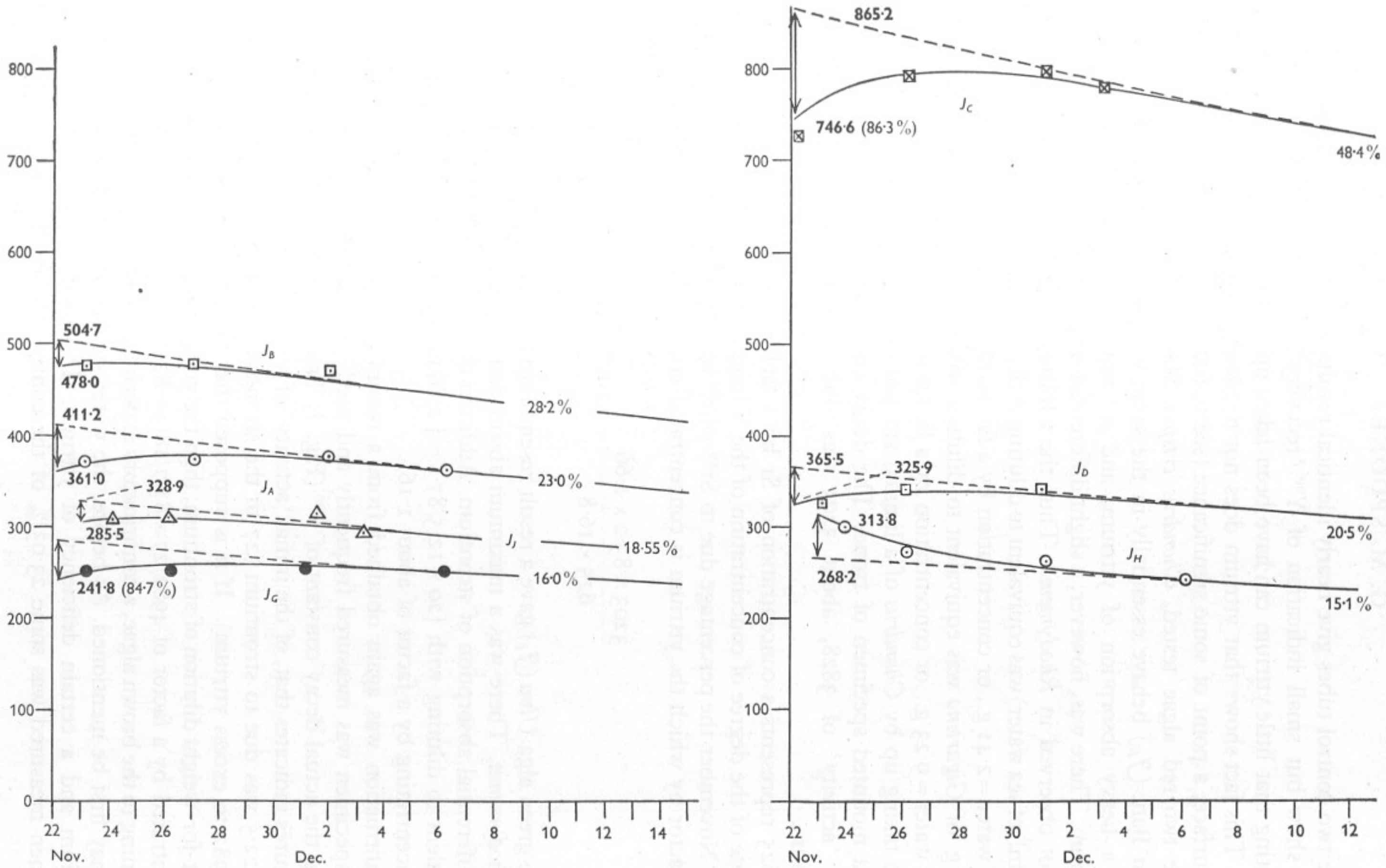


Fig. 7. Results of Exp. *J*: 'decay' curves of specimens of 'activated' sea water which had contained pieces of various Algae, compared with a control of 'activated' sea water without additions. All tubes contained 20 ml. of sea water, and the weeds were added as follows:

$J_A$, 1·74 g. of *Fucus serratus*; $J_B$, 1·74 g. of *F. serratus*; $J_C$, 1·55 g. of *Laminaria digitata*; $J_D$, 3·41 g. of *Fucus vesiculosus*; $J_E$, 1·45 g. of *Chondrus crispus*; $J_F$, 4·2 g. of *Gigartina stellata*; $J_G$, 5·01 g. of *Ascophyllum nodosum*; $J_H$, 3·32 g. of *Fucus vesiculosus* var. *evesiculosus*; $J_I$, 2·54 g. of *Ulva lactuca*; $J_J$, 6·29 g. of *Laminaria digitata*.

Final readings, critical in determining the relative equilibrium values, were made in March 1949, and are not shown (the curves are thus fitted to more points than are shown in the Figure). Other details as in Figs. 1 and 2.

The two control tubes give nearly identical results which can be combined. They show but small indication of $Y^{90}$ 'recovery', particularly Control 2, indicating that little yttrium can have been taken up by the clean glass of the tubes. This fact shows that yttrium does not necessarily adsorb on *any* available surface, a point of some significance (see p. 622).

The two red algae tested, *Chondrus crispus* Stackh. ($J_E$) and *Gigartina stellata* Batt. ($J_F$) behave essentially in the same way as *Rhodymenia*. They show a heavy absorption of yttrium, and no important concentration of strontium. There was, however, a slight differential uptake of strontium which was not observed in *Rhodymenia*. Thus the addition of 1·45 g. of *Chondrus* (to 20 ml. of sea water) was equivalent to diluting with [$20 \times 10{\cdot}5/89{\cdot}5 =$] 2·35 ml. of sea water = 2·41 g., or concentration by a factor of 1·66; while the addition of 4·2 g. of *Gigartina* was equivalent to diluting with [$20 \times 31/99 =$] 8·99 ml. of sea water = 9·23 g., or concentration by a factor of 2·20.

The taking up by *Chondrus* of a limited amount of strontium was verified from a mounted specimen of frond. The decay curve indicates that, of an initial 'activity' of 3828, about 3203 was due to yttrium and 625 to strontium.

If 625 represents a concentration of Sr by a factor of 1·66, then a rough estimate of the degree of concentration of the Y might be obtained as follows. On 22 November the percentage due to $Sr^{89} + Sr^{90}$ was 83·20 and to $Y^{90}$ 16·80. The factor by which the yttrium is concentrated could be regarded as

$$\frac{3203 \times 83{\cdot}2 \times 1{\cdot}66}{625 \times 16{\cdot}8} = 42{\cdot}1.$$

The green alga *Ulva* ($J_I$) gave a result resembling that previously described for *Rhodymenia*. There was a maximum absorption of yttrium, and scarcely any differential absorption of strontium. Addition of 2·54 g. of the frond was equivalent to diluting with [$20 \times 12{\cdot}5/87{\cdot}5 =$] 2·86 ml. of sea water = 2·93 g., or concentrating by a factor of about 1·16.

Confirmation was again obtained from a mount of a piece of the weed. This specimen was measured frequently and used for the purpose of determining the actual decay constant of $Y^{90}$ (Fig. 8, Table IV). Final analysis of the figures indicates that, of the initial 'activity' of 5009 (on 3 December) only some 22·5 was due to strontium (27 to the strontium 'equilibrium' mixture and 4982 to excess yttrium). If it is supposed that the 27 represents simple weight-for-weight dilution of strontium, then the yttrium appears to have been concentrated by a factor of $4982/27 \times 81{\cdot}7/18{\cdot}3 = 824$.

Coming to the brown algae, a confirmatory experiment with *Fucus serratus* L. ($J_A$) may first be mentioned. As before, the water showed a big deficiency of strontium and a certain deficiency of yttrium. The final 'activity' of the specimen measured was some 23·03% of the control. Thus the addition of

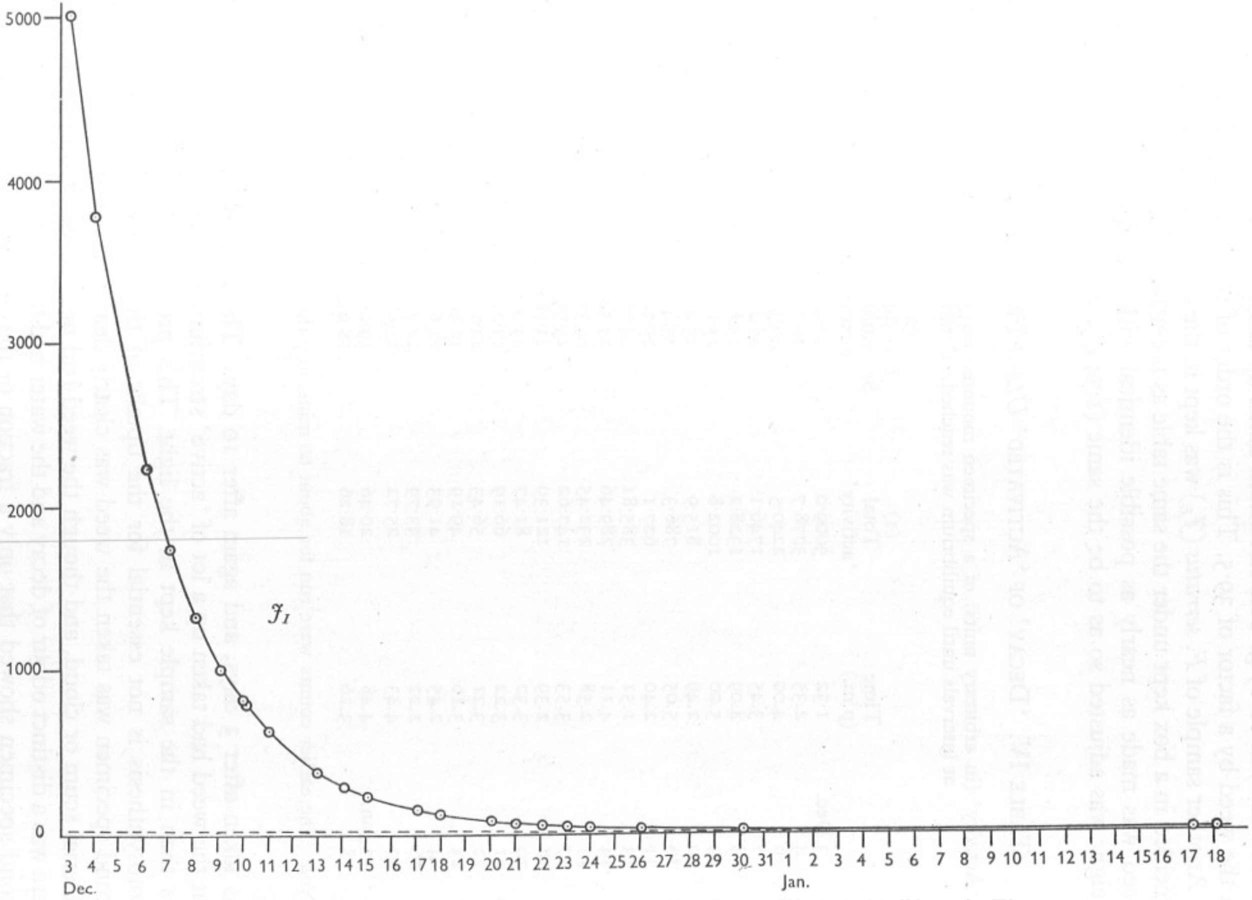


Fig. 8. ‘Decay’ curve of a mounted piece of *Ulva lactuca* (from tube $\mathcal{J}_I$), as in Fig. 3.

1·74 g. of weed was equivalent to diluting with $20 \times 77·0/23·0 = 66·87$ ml. of sea water, or 68·67 g. The strontium taken up must have been concentrated in the weed by a factor of 39·5. This is the order of result already obtained.

Another sample of *F. serratus* ($J_B$) was kept in the dark, the tube being well shielded in a box kept under the same table as the other tubes. The sample of weed was made as nearly as possible identical with the other ($J_A$), and its weight was adjusted so as to be the same (1·74 g.). A specimen of the water was taken after 3 days, and again after 10 days. The first specimen showed that the weed had taken up a lot of 'active' strontium as usual, though rather less than in the sample kept in the light. This proved at least that active photosynthesis is not essential for the uptake of the strontium. When the second specimen was taken the weed was clearly dead. Though there was no bacterial scum or cloud, and though the weed had not started to disintegrate, there was a distinct odour of decay and the water had turned bluish green. The second specimen showed that only a fraction of the 'active' Sr had returned to the sea water, the concentration factor having fallen from 30·0 to 22·5. Thus 75% of the amount originally taken up remained in the weed. Exactly the

TABLE IV. 'DECAY' OF 'ACTIVATED' *ULVA* FROND (SPECIMEN $J_I$)

'Activity' (in arbitrary units) of a specimen mounted on 3 December and measured at intervals until equilibrium was reached. Details as in Table I

| | Time (p.m.) | (1) Total 'activity' | (2) Part due to Sr equilibrium mixture | (3) Part due to excess $Y^{90}$ |
|---|---|---|---|---|
| 3 Dec. | 1·32 | 5009·0 | 27·0 | 4982·0 |
| 4 | 2.35 | 3778·7 | 26·7 | 3752·0 |
| 6 | 4.00 | 2240·5 | 26·3 | 2214·2 |
| 7 | 3.45 | 1746·1 | 26·1 | 1720·1 |
| 8 | 4.09 | 1328·2 | 25·8 | 1302·4 |
| 9 | 5.00 | 1002·8 | 25·6 | 977·2 |
| 10 | 2.49 | 815·9 | 25·4 | 790·5 |
| 10 | 5.05 | 786·3 | 25·4 | 760·9 |
| 11 | 2.40 | 627·1 | 25·2 | 601·8 |
| 13 | 1.51 | 385·81 | 24·77 | 361·04 |
| 14 | 4.11 | 289·46 | 24·54 | 264·92 |
| 15 | 2.58 | 232·45 | 24·35 | 208·10 |
| 17 | 3.53 | 147·62 | 23·96 | 123·66 |
| 18 | 2.39 | 121·39 | 23·78 | 97·61 |
| 20 | 3.32 | 81·47 | 23·40 | 58·07 |
| 21 | 3.22 | 66·19 | 23·22 | 42·97 |
| 22 | 3.21 | 56·43 | 23·03 | 33·40 |
| 23 | 3.10 | 49·19 | 22·86 | 26·33 |
| 24 | 2.45 | 41·93 | 22·68 | 19·25 |
| 26 | 2.22 | 33·79 | 22·35 | 11·44 |
| 30 | 4.43 | 25·72 | 21·66 | 4·06 |
| 17 Jan. | 4.48 | 20·46 | 19·05 | — |
| 18 | 3.16 | 18·26 | 18·93 | — |

*Note*. The earlier counts were run for about 60 mins. and the later from 60 to 90 min.

same fraction also remained in the sample $J_A$ when this was killed by heating, the concentration factor falling from 39·47 to 29·83.

Two other tubes were given to *F. vesiculosus* L. One sample, of 3·41 g., was of a well-grown typical piece of frond with a number of vesicles ($J_D$); the other, of 3·32 g., was of young fronds of a non-vesicled form (var. *evesiculosus* Cotton), growing in the upper part of the shore below the Laboratory ($J_H$).

Both took up a lot of strontium, especially the non-vesicled form. The addition of the 3·32 g. of this weed was equivalent to dilution with

$$20 \times 84{\cdot}87/15{\cdot}13 = 112{\cdot}19 \text{ ml. of sea water} = 115{\cdot}22 \text{ g.}$$

The factor for the concentration of strontium is thus 34·7. For the typical sample ($J_D$) the concentration factor is 23·4.

An unexpected difference between these two samples is seen in their relation to yttrium. The typical sample ($J_D$) appears to have taken up all, or nearly all, the available yttrium, a very marked recovery being shown by the specimen of the water. Not so, however, with the var. *evesiculosus* sample ($J_H$). The specimen of the water surrounding it was not deficient in yttrium in any way: within the limits of accuracy of the 'decay' curve it was either in equilibrium at the start, or, more probably, had a small excess of yttrium, as distinctly shown in Fig. 7 ($J_H$). The last alternative is proved to be correct, as two specimens of the actual weed from tube $J_H$ were mounted and their 'decay' characteristics observed. The 'decay' curve of both these specimens shows evident yttrium recovery at the start (the inverse, of course, to the behaviour of the water). The extent of recovery indicates that the degree of yttrium concentration in the weed, if indeed appreciable, was far less than that of strontium. Among the algae tested *F. vesiculosus* var. *evesiculosus* was the only one to behave in this way.

*Ascophyllum nodosum* Le Jol absorbs much strontium, concentrating it to the extent of some 21 times, and apparently much yttrium.

There remain the two samples of *Laminaria digitata* (L.) Lamour. One ($J_C$) consisted of a piece of frond, 1·55 g. in weight; the other ($J_J$) of a large piece of the base of the frond with some stipe of which a length, which became desiccated, protruded from the water. The submerged part of the last weighed 6·29 g.

The results of these two samples essentially agree. Much $Y^{90}$ appears to have been taken up by the *Laminaria*, best demonstrated by the 'recovery' in the $J_C$ curve. At the same time a fair amount of 'active' Sr was also taken up, the concentration factor for $J_C$ being 14·1 and for $J_J$ 14·3. The two values derived from such different weights of weed are in excellent agreement.

Thus all the four brown algae tested agreed in the general property of concentrating 'active' strontium, the effectiveness in this respect being shown in the following sequence: *Fucus serratus*, *F. vesiculosus*, *Ascophyllum nodosum*, and *Laminaria digitata*.

## INTERPRETATION IN TERMS OF IONIC EXCHANGE

How is this capacity for absorbing the 'active' strontium or yttrium to be interpreted or visualized? At the risk of over-simplification three main possibilities have to be considered: (i) adsorption, (ii) ionic exchange, (iii) extraction.

The capacity for metallic ions to become adsorbed on surfaces is well known. In sea water, elements present in very small concentrations may readily do this, as, for example, Harvey (1937, 1949) finds with iron and manganese. Mud particles, faecal pellets, and parts of organisms of all sizes, may at times provide suitable surfaces. The extent to which any element will get adsorbed will depend on the degree of previous saturation of the surface with the element. This process, it may be noted, involves active removal of the element as a whole from solution, including any radioactive isotopes which may have been added to it; and might easily go to the extent of removing all except an insignificant trace. The marine chemist has acquired the habit when dealing with an element of low concentration, of enquiring how much of it may be getting adsorbed on the apparatus with which the water is brought in contact.

The phenomenon of ionic exchange is quite different. The concentration of a given element inside an organism may not be the same as that in the water outside. For example, a much higher concentration may be maintained by the organism, which does work against osmotic forces. But, whatever the relative concentration in the organism, there may be free exchange between the ions of the outside water and those of the internal fluids. If some of the ions in the water outside are labelled in some way, after an interval these will be found distributed inside the organism as well as outside. This will happen when a radioactive isotope is introduced. At first all its ions will be outside; but after an interval these will become generally distributed at random throughout the population of the particular ion. So they will be most numerous where that element is concentrated, and vice versa. If the element is concentrated in the organism, say an alga, then the radioactive ions will be found to enter the alga, and the extent to which they aggregate in the weed will provide an exact measure of the relative concentration of the element in the weed. There is, therefore, no passage of the element as a whole into the weed, and the respective concentrations in weed and water remain unaltered (assuming the amount of active isotope is negligible). There is simply a random interchange of ions amongst the existing population. Ion exchange is only liable to reduce the amount of 'active' isotope in the external medium to a negligible quantity if there is very great difference between the concentration inside and outside the weed, and this will not frequently occur. Increasing the weight of the weed added to a given volume of water becomes increasingly ineffective: the effect is in no way additive.

The third possibility has features in common with both the preceding. Extraction resembles adsorption in that it involves removal by the organism of the element as a whole, but differs in that the ions pass into the organism where they may be 'locked up'—as, for example, calcium in skeletal tissue or mollusc shells. At the same time extraction may develop as a special case of ionic exchange when ions are progressively removed from circulation inside the organism so that fewer return to the outside solution than are taken from it. As in simple ionic exchange, passage of 'active' ions into, for example, an alga indicates that the weed has a higher concentration of the element inside. it, but where extraction is going on there is active uptake of the element as a whole, which may proceed steadily until all the element is removed from solution. The attainment of an equilibrium is less probable, and, within limits, the effect of increasing the amount of weed is likely to be additive.

With strontium which exists in comparative plenty in sea water (about 0·04% of total salts, = 14 g./m.$^3$), it is assumed that the chance of uptake by adsorption is negligible. First, all surfaces will already be saturated with the quite small quantities which may be taken up in this way. Secondly, the proportion of strontium which may be found adsorbed at any one moment is likely to be small, or very small, compared with that of ions free in solution; because of which the loss of radioactive ions by ionic exchange with surfaces already saturated may be supposed to be negligible.

As far as the red and brown algae considered here are concerned, it seems almost certain that progressive extraction can be ruled out. The consideration is likely to arise only with calcareous algae, amongst which there might be possibilities of precipitation of strontium along with the calcium carbonate. In the results obtained above it seems that the main effects occurred quickly, and the loss of 'activity' certainly did not vary directly with the weight of the weed.

Straightforward ionic exchange seems the only possible interpretation, which is positively indicated by the sort of effects obtained when the weight of the weed is increased. The two samples of *L. digitata* ($J_C$ and $J_J$) are striking in this respect from two very dissimilar weights, 1·55 and 6·29 g., and identical estimate of the degree of concentration of the strontium is obtained. As a plausible working hypothesis, therefore, the uptake of strontium is regarded as essentially a matter of ionic exchange. If, as happens, the radioactive Sr ions disappear from the water into the weed it is because the weed all along contains a heavier concentration of strontium than the water. Moreover, *the measure of the degree of concentration of the 'active' Sr ions in the weed* (as given in Table III on a weight for weight basis) *is a measure of the concentration of the weed's normal strontium content*. It is concluded, therefore, that *Fucus serratus* has about 40 times as much strontium as sea water[1], *Laminaria digitata* about 14 times, while no or very little concentration or even positive exclusion is shown by three red algae and *Ulva lactuca*.

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[1] There is now direct support for this conclusion: see p. 625.

The matter is rather different for yttrium. This element has been observed in sea water (see the chapter on the minor constituents of sea water in Harvey, 1945, pp. 31–42), and it appears to be one of many whose concentration is of the order of 1 mg./m.$^3$. It is likely, therefore, that adsorbant surfaces are far from saturated with it. Experience has shown that it quite readily adsorbs on unclean glass, from which it can only be finally removed by strong acid. Uptake by adsorption may therefore play a prominent part in the exchanges of this element, and special technique may be necessary to distinguish between adsorption and ionic exchange. This problem is further discussed below.

## Experiments with Cultures of Unicellular Algae

Certain preliminary experiments with algal cultures have not yet been developed on an adequate quantitative basis, but some qualitative results may be placed on record at this stage.

A portion of a culture was treated with some 'active' solution. It was allowed to stand until the organisms in the culture had aggregated at the bottom, or near surface, of the liquid. A drop containing the thickest aggregate obtainable of the organism was then withdrawn and compared with another drop from the main volume of the liquid, or from its clearest part. By this means it was hoped to detect differential absorption by the organisms in question, although dense aggregations were usually difficult to obtain and impossible to measure accurately in terms of weight or volume. As before, sample drops consisted of 0·05 c.c.

*Chlorella* (Exp. *M*). About 25 c.c. of a culture of *Chlorella*, reproducing at a slow rate, was treated to the extent of giving it an 'activity' of about 950 per 0·05 c.c. (measured from the first stage of the M.R.C. Castle). After standing for a day or two the *Chlorella* cells had tended to aggregate in a green ring at the bottom of the flask. A number of specimen drops were taken from this flask. All showed appreciable yttrium recovery, indicating that the glass wall of the vessel had adsorbed some, but by no means all, of the yttrium. The greatest deficiency of yttrium was each time shown by those drops taken close to the bottom (i.e. against the glass) away from the alga deposit. Drops taken from the bottom to include some of the *Chlorella* aggregate, which was dense enough to give a distinct greenish opacity to the evaporated drops, consistently showed a 5–10% higher 'activity' than other drops. It would seem that the *Chorella* definitely concentrated some of the strontium, but since the weight of alga involved was not ascertained, no estimate of the degree of concentration can be given.

*Chlamydomonas*. A series of tubes containing a *Chlamydomonas* culture was used to test lethal doses. From one of the relatively more weakly activated tubes, in which a flourishing colony of the alga had grown and aggregated at the surface, two strongly contrasting drops were obtained—one densely green, and the other clear to the naked eye (Exp. *Ch*). Rather heavy yttrium recovery took place in both drops, but more in the control than in the drop containing the *Chlamydomonas*. This indicates that some of the yttrium lost from solution had been taken up by the *Chlamydomonas*. There was an appreciably higher 'activity' remaining in the drop containing the alga, some 6% greater than the 'activity' of the clear drop, indicating that the *Chlamydomonas* had also concentrated strontium to some extent.

*Nitzschia*. On 10 November a fairly dense culture of this diatom was 'activated' with 'active solution *A*' (The September solution diluted × 14). This was done in the following way. 50 c.c. of fresh sea water was 'activated' with 0·5 c.c. of solution *A*. This was exactly halved, one half being set aside as control (flask *Y*). To the other half, 25·25 c.c., were added 10 c.c. of *Nitzschia* culture and a further 0·1 c.c. of solution *A*. This mixture, comprising 35·35 c.c. (labelled flask *X*), was stood near a fluorescent source of light.

In the course of hours the diatoms formed a layer on the bottom of the flask, and the main volume of the medium grew steadily clearer. Samples were first taken on 13 November and again on 18 November. The results of the two samples are similar, and very striking (Figs. 9–10).

The curves in Figs. 9–10 show measurements of three drops from the control flask—$Y_1$, 10 November; $Y_2$, 13 November; $Y_3$, 18 November. They show also measurements of two drops taken from the top of the liquid in the diatom flask, and containing very few, if any, diatoms—$X_2$, 13 November; $X_3$, 18 November. These drops all behave much alike: their 'activity', within experimental limits, became identical; though at the start there were definitely more signs of yttrium recovery in the *X* specimens.

In contrast to these, there were three drops taken from the bottom of the flask in an attempt to pick up as much *Nitzschia* deposit as possible—$X_1$, 13 November; $X_4$ and $X_5$, 18 November. In these the liquid looked very brown, though the actual proportional volume of diatom cannot have been great—perhaps, at a guess, one-fiftieth of the 0·05 c.c. drop.

The 'activity' of these drops was great at first—over twice that of the controls, or drops from the top of the same flask.

But 'decay' proceeded fairly rapidly, until in 3 weeks it had virtually fallen to that of the other specimens. It is plainly seen that all the excess 'activity' at the start had been due to excess $Y^{90}$ in the *Nitzschia*-containing drops. (The converse, deficiency of $Y^{90}$, is quite distinct in the clear *X* drops, as indicated above.)

*Nitzschia* cells, therefore, are capable of taking up yttrium very heavily.

It may be supposed that this phenomenon is due to the adsorption of yttrium on the diatom. These minute attenuated cells with porous or pitted surfaces present an enormous surface area.

Experimental evidence for this view is provided by the test of killing the culture. On 23 November the whole flask was heated to nearly boiling point and the cells completely killed. Similar specimens as before were taken on 25 November after settling had taken place. But the results were exactly as before—$X_6$, from the top of the flask, gave similar measurements to $X_2$ and $X_3$, and $X_7$, with bottom deposit, gave as high a reading as before ($X_1$, $X_4$, $X_5$). No yttrium had come out of the dead cells: it is certain that at least a substantial part would have returned to solution (not necessarily all—cf. *Fucus* killed in the same way) had the yttrium been held by simple ionic exchange.

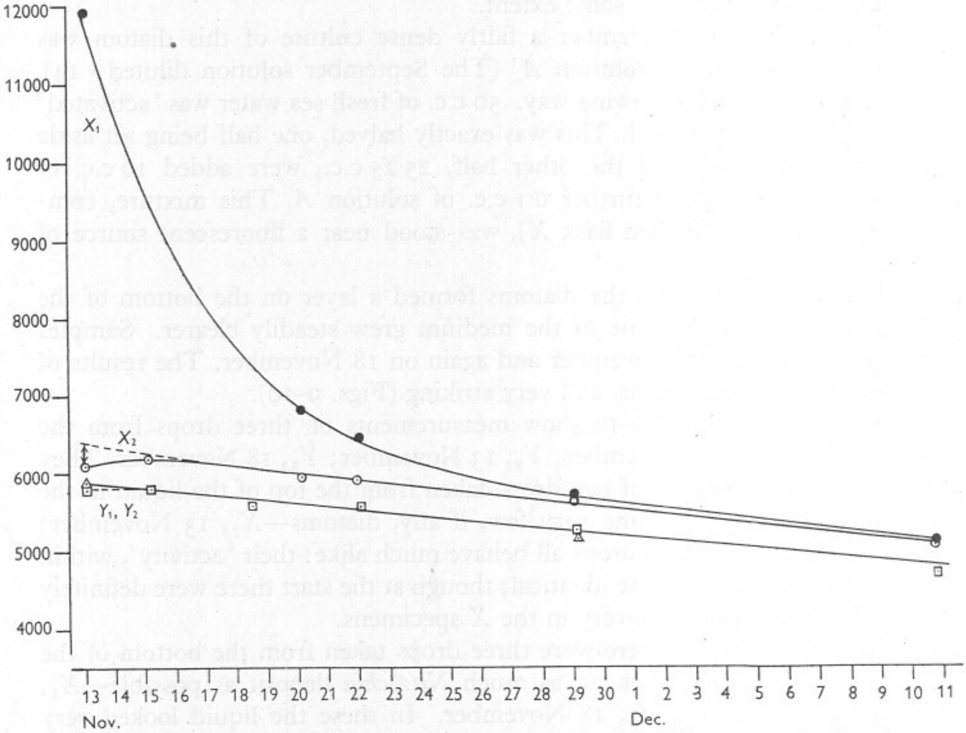

Fig. 9. 'Decay' curve of a specimen of water rich in *Nitzschia* ($X_1$), compared with culture water more or less free from *Nitzschia* ($X_2$) and with a sea-water control ($Y_2$).

This result suggests that diatoms as a whole, as well as other organisms such as sponges, are potential takers up of yttrium and other metals related to the rare earths. This possibility certainly needs pursuing further.

## DISCUSSION

The experiments described above have been essentially exploratory, and any conclusions suggested by them must, in the main, be provisional, awaiting confirmation from the many further lines of experimentation which suggest themselves.

It is, however, clear enough that at least some of the commoner brown algae have a considerable capacity for taking up 'active' strontium ions from the water around them. The provisional explanation is that the weeds have, in their normal make-up, a relatively high content of strontium, and that the 'active' strontium ions enter the alga by simple ionic exchange. It is thus supposed that there is no actual change in concentration of *total strontium* either in the weed or in the water. This is a straightforward chemical proposition, susceptible of test by direct chemical analysis. If it were not for the unusual difficulties in estimating strontium, owing to its very close affinity to calcium (see Webb, 1938), adequate information on strontium-content of different algae might have been available long ago. As it is, the scanty available

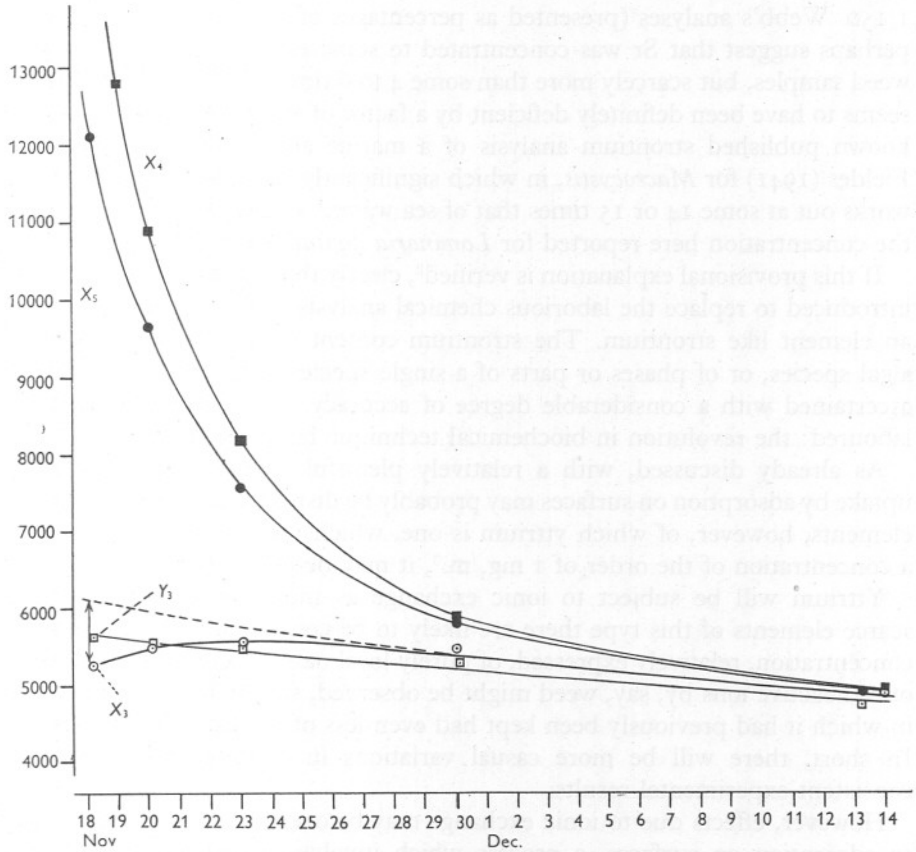

Fig. 10. Repetition of results with *Nitzschia* shown in Fig. 9. $X_4$ and $X_5$ are specimens of culture water from the bottom of the flask, rich in *Nitzschia* (cf. $X_1$). $X_3$ is a specimen of the clear culture water from the top of the flask (cf. $X_2$). $Y_3$ is a second specimen from the control flask.

data are suggestive. From Webb's (1937) spectrographically derived data, *Fucus serratus* receptacles and *Sacchorhiza bulbosa* stipe are seen to have had a high Sr/Ca content of about 1/10, three times as great as in sea water. These were the only two out of 23 analysed tissues of marine organisms (mostly animal) in which the Sr/Ca ratio was appreciably greater than that of sea water. By contrast, the ratio in *Ulva lactuca* frond is found to have been about 1/150. Webb's analyses (presented as percentages of total cations in the ash) perhaps suggest that Sr was concentrated to some extent in the two brown-weed samples, but scarcely more than some 4 to 6 times; while in *Ulva* the Sr seems to have been definitely deficient by a factor of at least $\frac{1}{2}$. The only other known published strontium analysis of a marine alga is that by Wilson & Fieldes (1941) for *Macrocystis*, in which significantly enough, the figure given works out at some 14 or 15 times that of sea water,[1] a value which agrees with the concentration here reported for *Laminaria digitata* (Table III, p. 609).

If this provisional explanation is verified[2], clearly the tracer technique can be introduced to replace the laborious chemical analysis otherwise involved with an element like strontium. The strontium content of dozens of samples of algal species, or of phases or parts of a single species, could be quite rapidly ascertained with a considerable degree of accuracy. This point need not be laboured: the revolution in biochemical technique has already set in.

As already discussed, with a relatively plentiful element like strontium, uptake by adsorption on surfaces may probably be disregarded. With numerous elements, however, of which yttrium is one, which are present in the sea in a concentration of the order of 1 mg./m.$^3$, it may be otherwise.

Yttrium will be subject to ionic exchange as much as strontium. With scarce elements of this type there are likely to be considerable fluctuations in concentration, relatively expressed, of purely local nature. Quite heavy uptake of radioactive ions by, say, weed might be observed, simply because the water in which it had previously been kept had even less of the element than usual. In short, there will be more casual variations in concentration, and less consistent experimental results.

However, effects due to ionic exchange may be overshadowed by those due to adsorption on surfaces, a process which involves actual removal of the element from the water. The tendency for glass surfaces, particularly if not well cleaned, to adsorb yttrium is easily demonstrated. It is likely that the observed affinity of *Nitzschia* for yttrium (p. 619) is the result of adsorption on the surface of this diatom. Perhaps, too, the marked concentration of yttrium by the three red algae and *Ulva* might be purely a matter of adsorption on a surface: the almost complete removal of 'active' yttrium from solution by these weeds, which would otherwise imply an enormous concentration in the

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[1] Wilson & Fieldes give values for parts per million of air-dried weed. It is assumed that air-dried weed is one-fifth the wet weight, and wet weight is compared directly with sea water.

[2] See Postcript, p. 624.

weed compared with the sea water, suggest this explanation. But other considerations must be taken into account before a decision is made.

First, yttrium is not automatically adsorbed on to all surfaces. If glass is well cleaned with strong cleaning solution, there is very little yttrium uptake (Fig. 2(*s*), Fig. 5(*w*)). Secondly, the brown algae did not take it up anything like to the same degree as the red algae, and that, indeed, *Fuscus vesiculosus* var. *evesiculosus* took up very little. Though it is always possible that the yttrium loss on the glass of the vessel is variable and difficult to allow for exactly, the uptake by brown algae also seems variable and not readily predictable. It is possible therefore that uptake of $Y^{90}$ in the brown algae is chiefly a matter of ionic exchange, while in the red algae and *Ulva* surface adsorption is predominant, and in *Nitzschia* adsorption virtually the sole cause. Further experiments are necessary to clear this matter up.

Of all elements, yttrium is one which has a minimum of biological significance. It plays no special part, as far as is known, or can be visualized, in the chemical exchanges of animals and plants. What purpose, therefore, is served in putting the observations on this element on record? In answer the following points may be brought to notice.

(i) However unimportant yttrium itself may be, its properties and behaviour are probably typical of a number of elements which occur very sparingly in the sea, and of which some are of proved biological importance. Facts derived from yttrium may prove equally applicable to iron, manganese, cobalt, etc., particularly with regard to adsorption phenomena.

(ii) Opportunity has been taken, while yttrium happened to be available for study, of developing technique which can be readily adapted to other elements. Not the least interesting point is that a good deal of information, partly quantitative, can be secured from an element which is (*a*) present in minute quantities, and (*b*) not deliberately chemically separated. Yttrium is not easily obtained in pure chemical form, free from the related 'rare earth' elements, etc.; yet, when $Y^{90}$ occurs as a daughter product of $Sr^{90}$, it is pure and free from contamination of other elements which have similar chemical properties. (Its parent and daughter products are both in different columns of the periodic table.) The technique of using *daughter isotopes* as tracers opens up interesting possibilities.

(iii) It may be a matter of interest when a biological experiment proves capable, unexpectedly, of making a contribution to pure chemistry or physics. The discovery that some red algae and *Ulva* were able to concentrate $Y^{90}$ at the expense of its parent, $Sr^{90}$, enabled specimens to be prepared from which it is possible to make an apparently accurate estimate of the half-life of $Y^{90}$. The attempt made by the present writer could no doubt easily be improved on by the same technique, yet it appears to be as reliable as any made hitherto, judging by the small margin of error which the figures obtained seem to allow.

### *Postscript*

Since the above was written the result has become known of an estimate of the strontium content of a sample of *Fucus serratus* ash, determined by the Analytical Group Chemistry Division of A.E.R.E. The ash was prepared at Plymouth by Mr F. A. J. Armstrong from a known weight of weed, and the Sr determination at A.E.R.E. made, after various difficulties had been overcome, by the technique of flame spectrometry.

The strontium content was reported as 0·9 % of the ash, the ash originally representing 5·26 % of the wet weed. The weed therefore contained 0·04734 % of Sr, as compared with the 0·00135 to 0·00140 % believed to be characteristic of sea water. This difference represents a concentration of Sr in the weed by a factor of 34 or 35, and is in excellent agreement with the values derived above for *Fucus serratus*, supporting both the assumption that Sr is concentrated in this and other brown algae, and the validity of employing the tracer technique to provide quantitative assessments of the degree of this concentration.

## SUMMARY

Certain marine algae were treated with sea water containing carrier-free radioactive strontium (mixture of $Sr^{89}$ and $Sr^{90}$), to test whether these ions were taken up by the weeds.

At the same time the behaviour of radioactive yttrium ($Y^{90}$), which occurred as a short-lived daughter-product of $Sr^{90}$, was investigated by the expedient of studying the 'decay' characteristics of specimens of water and weed. Promising possibilities of this technique, by which an isotope is made available for study by applying its parent substance, are pointed out.

Radioactive strontium is extracted from sea water by the brown sea-weeds, in particular by *Fucus serratus*.

It is held that this effect is simply a result of ionic exchange, and that the algae regularly contain many times as much strontium in their cell fluids as exists in sea water.

On the ionic exchange hypothesis, it appears that *Fucus serratus* has about 40 times as much strontium as sea water, *F. vesiculosus* about 30, *Ascophyllum nodosum* about 20, and *Laminaria digitata* about 14.

By contrast, red algae and green algae such as *Ulva* extract 'active' strontium only to a small or negligible extent. On the above hypothesis, in *Gigartina* the strontium is concentrated by a factor of about 2, while in *Rhodymenia* it may be less than in the sea.

Radioactive yttrium is heavily taken up by the red algae (*Rhodymenia*, *Gigartina*, *Chondrus*) and by the green alga *Ulva*, even to the extent of depleting the water of this element, or very nearly so.

The yttrium, however, is not usually heavily taken up by the brown algae,

and may (as with a sample of *Fucus vesiculosus* var. *evesiculosus*) be taken up only to quite a small degree.

The diatom *Nitzschia* takes up 'active' yttrium very heavily.

The extraction of yttrium appears to be a matter partly of ionic exchange and partly of *adsorption* on surfaces. It is suggested that both processes may be important with red algae, the former primarily with brown algae, and the latter primarily with *Nitzschia*.

From the 'decay' characteristics of mounted pieces of frond of the red algae and *Ulva*, estimates of the true half-life of $Y^{90}$ were made. The value derived is 63·4 hours (or 2·642 days).

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# THE DISTRIBUTION OF LUGWORMS (*ARENICOLA MARINA* L.) OVER THE FLATS AT WHITSTABLE

By Garth Chapman, M.A., Ph.D. and G. E. Newell, B.Sc., Ph.D.

From the Department of Zoology, Queen Mary College, University of London

(Plate I and Text-figs. 1–2)

## INTRODUCTION

It has been noted at Whitstable that lugworms (*Arenicola marina* L.) on the Flats are not uniformly scattered (Newell & Chapman, 1948). This is clearly seen in the distribution of castings which tend to be more numerous along straight lines of up to 60 yd. in length. That this effect is not a subjective one is clearly shown by photographs (Pl. I, figs. 1 and 2), by the visibility of the lines to unprejudiced observers as well as by counts of castings in and around the lines, whilst the permanence of the lines (see. p. 630) indicates that they are not due to chance. It also appears that the 'line distribution' is a purely local phenomenon since it occurs only over a restricted area of the Whitstable Flats and has not, apparently, been noticed elsewhere in similar situations. This view has received some confirmation from the late Mr R. Elmhirst and Mr E. M. Venables (private communications).

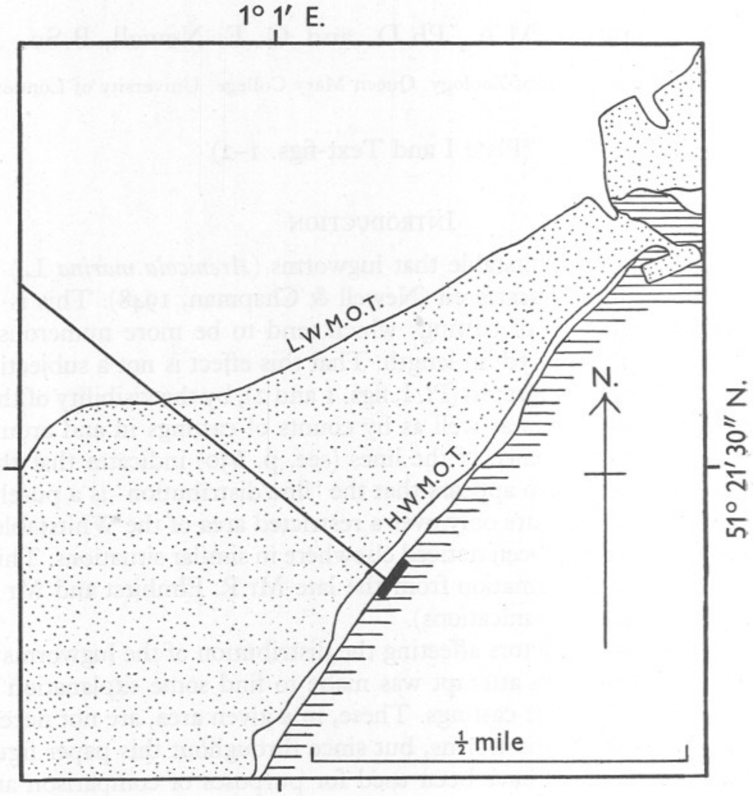
Since a study of the factors affecting the distribution of the lugworms might be of general interest, an attempt was made to find some explanation of the grouping displayed by the castings. These, in a given area, are not necessarily the same in number as the worms, but since throughout this paper figures of the numbers of castings have been used for purposes of comparison and the observations on which the comparisons were made have been done at the same time, it is fair to use the population of castings as an indication of the population of worms.

Experiments carried out on the burrowing of the lugworm (Chapman, 1949) tended to show that the 'hardness' of the marine soil might affect the distribution of these animals, since they seemed to be completely unable to burrow into soil which was made more resistant by the withdrawal of water from it.

It seemed important, therefore, to determine first of all if there were any significant differences in hardness of the soil in different areas of the Flats which might cause patchy distribution. The hardness at different stations was therefore tested by means of the penetrometer used on previous occasions.

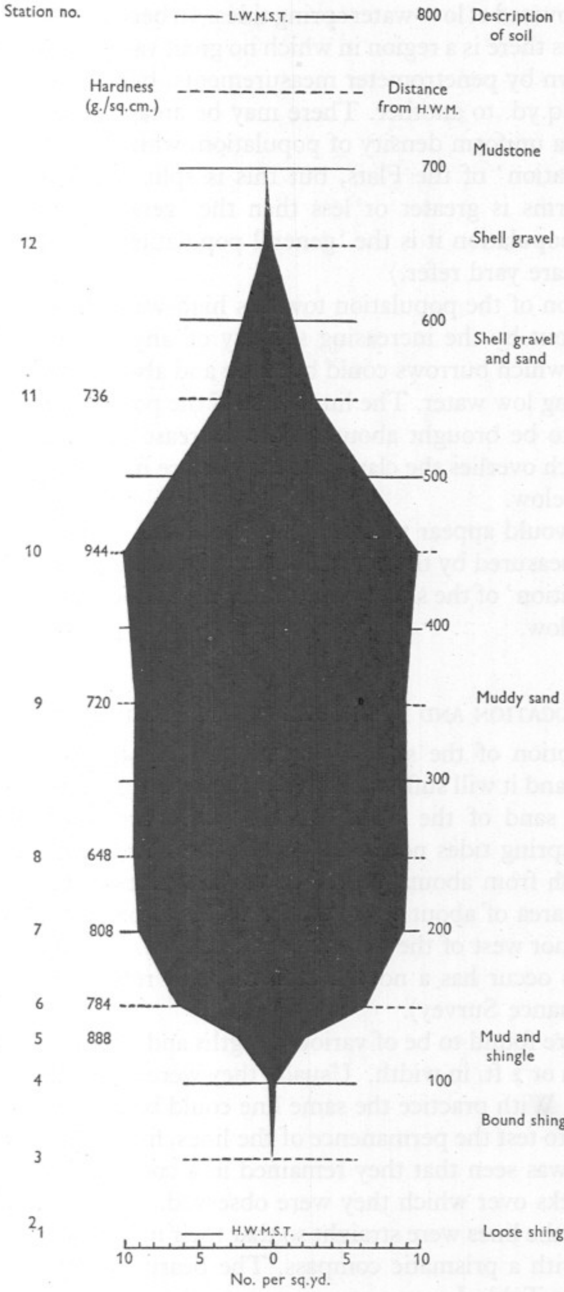
### VARIATION IN NUMBERS OF WORMS FROM HIGH TO LOW WATER

The number of worms per square yard was counted at selected intervals on a transect of the Flats shown in Text-fig. 1. At each station areas of 1 sq.yd. were dug over and examined for lugworms after they had been well broken by the fork. Although the method may be described as 'rough and ready' it is quite adequate for the task involved and capable of yielding consistent results as Newell (1948) has shown. The hardness of the soil in the proximity of the sample was tested with the penetrometer. The results are set out pictorially in Text-fig. 2 in which the hardness of the sand, the mean population of lugworms, and the position on the shore of each station is shown.



Text-fig. 1. Transect of intertidal zone at Whitstable along which the lugworm population was determined.

It can be seen from Text-fig. 2 that the lugworms are most numerous in the region of the Flats that can be described as muddy sand and that they fall off rapidly in numbers in the shingle bank towards high water and towards the



Text-fig. 2. Diagram showing the numbers of lugworms per sq.yd. in intertidal zone at Whitstable. The hardness, in g./sq.cm., is the mean of twenty readings at each station. The numbers of worms per sq.yd. is a mean of not less than three samples. H.W.M.S.T., high-water mark spring tides; L.W.M.S.T., low-water mark spring tides.

clay that is uncovered at low-water spring tides. In between these two less thickly populated zones there is a region in which no great variation in hardness occurs, at least as shown by penetrometer measurements, but in which the population varies from 1 sq.yd. to another. There may be areas of many square yards in which there is a uniform density of population, which can be described as the 'general population' of the Flats, but this is split up by areas in which the number of worms is greater or less than the 'general population'. (In this survey of the population it is the 'general population' to which the figures of worms per square yard refer.)

The limitation of the population towards high-water mark would appear to be brought about by the increasing scarcity of any soil of sufficiently small particle size in which burrows could be made and also, probably, by the drying of the soil during low water. The limitation of the population towards low-tide mark appears to be brought about by the decrease in depth of the sand and fine gravel which overlies the clay. Other evidence in favour of this hypothesis will be given below.

In short, it would appear that there is insufficient variation in the hardness of the soil, as measured by the penetrometer, to cause any great variation in the 'general population' of the shore. The cause of such local variations as do occur is discussed below.

## THE LOCATION AND DISTRIBUTION OF THE LINES OF CASTINGS

A brief description of the shore zonation at Whitstable has been given by Newell (1948), and it will suffice to mention here that the lines of castings occur on the muddy sand of the Flats which stretches from within about 100 yd. of high-water spring tides nearly down to low-water mark, the lugworm belt varying in width from about 400 to 800 yd. The lines of lugworm casting are confined to an area of about 0·5 square mile, none being found east of Whitstable harbour nor west of the clay cliffs at Seasalter. The centre of the area in which the lines occur has a normal national grid reference of 097662 (sheet 173, 1 in. Ordnance Survey).

The lines were found to be of various lengths and widths but rarely exceeded 60 yd. in length or 2 ft. in width. Usually they were about 40 yd. in length and 18 in. in width. With practice the same line could be recognized on successive occasions, but, to test the permanence of the lines, five of them were marked by stakes when it was seen that they remained in a constant position during the period of 5 weeks over which they were observed.

Almost all of the lines were straight so that their magnetic bearings were easy to determine with a prismatic compass. The bearings of 50 lines were taken and are given in Table I.

Unaided observation gave the impression that the lines run at random in all directions, but it can be seen from the compass bearings recorded that there is not an *equal* number of lines in all directions. More, in fact, occur with bearings of about 45° and about 165° than in other directions. The predominating direction of the lines of castings seems to be roughly parallel with the coastline.

### Table I. Bearings of Lugworm Lines

Number of lines recorded in each 5° of arc, magnetic bearings.
Number of lines recorded in each 20° of arc is also indicated.

| Bearing | No. of lines | | Bearing | No. of lines | | Bearing | No. of lines | |
|---|---|---|---|---|---|---|---|---|
| 0 | 1 | | 60 | 2 | | 120 | 0 | |
| 5 | 2 | | 65 | 0 | | 125 | 1 | |
| 10 | 1 | | 70 | 1 | | 130 | 1 | |
| 15 | 3 | 7 | 75 | 1 | 4 | 135 | 0 | 2 |
| 20 | 3 | | 80 | 0 | | 140 | 3 | |
| 25 | 0 | | 85 | 0 | | 145 | 1 | |
| 30 | 2 | | 90 | 1 | | 150 | 2 | |
| 35 | 0 | 5 | 95 | 1 | 2 | 155 | 1 | 7 |
| 40 | 4 | | 100 | 1 | | 160 | 3 | |
| 45 | 5 | | 105 | 0 | | 165 | 2 | |
| 50 | 1 | | 110 | 0 | | 170 | 0 | |
| 55 | 4 | 14 | 115 | 0 | 1 | 175 | 3 | 8 |

### Population Density of the Lines and Adjacent Areas

The number of castings in the lines is greater than the number per square yard forming the general population of the shore. For example, castings on the shore which are not in lines vary in numbers from minima of 1 or 2 to maxima of 30 to 40 per sq.yd. The population of the lines may rise above 40 per sq.yd., whereas the areas adjacent the lines generally contain about 5 or 6 casts per sq.yd. To obtain these results areas of $\frac{1}{2}$ by 2 yd. were marked off, one on either side and one along the lines and the number of castings in each area was counted. The results are shown in Table II.

### Table II. Population of Lines and Adjacent Areas

| Worms per sq.yd. flanking line | Worms per sq.yd. in line | Worms per sq.yd. flanking line |
|---|---|---|
| 0 | 42 | 4 |
| 3 | 45 | 5 |
| 6 | 46 | 8 |
| 6 | 28 | 4 |
| 3 | 38 | 10 |
| 0 | 45 | 1 |
| 0 | 43 | 6 |
| 3 | 29 | 6 |
| 2 | 36 | 9 |
| 14 | 43 | 8 |

### Variations in Soil Depth and Type

As has been mentioned in previous papers, the soil of the Flats consists of muddy sand underlain by impervious clay. This stratum is almost certainly London clay (Dr J. F. Kirkaldy and Mr C. D. Ovey, private communications), and is found at different depths on different parts of the shore, being exposed near low-water mark but being elsewhere overlain by a thickness of sand which varies from about 1 to 12 in. It has been noted that lugworms, which appear to be able to burrow and live in gravelly soil seem unable to penetrate the clay (Wells, 1945), or at least are not normally found living in it. Accordingly, the depth of the sand (or topsoil as it may well be called) was measured along the lines of casting by means of an auger and was compared with that in the less densely populated areas.

In each of four prominent lines a series of borings was made in order to record the depth of the topsoil (*a*) along the middle of the line, (*b*) at distances of 6 in. from the middle of the line, (*c*) at distances of 12 in. from the middle of the line, and (*d*) at distances of 18 in. from the middle of the line. A selection of these results is given in Table III, from which it can be seen that the topsoil is much deeper along the line than at its flanks.

TABLE III. DEPTH OF SAND IN AND NEAR LUGWORM LINES

Depth of sand in inches.

| 18 in. from centre | 12 in. from centre | 6 in. from centre | Centre of line | 6 in. from centre | 12 in. from centre | 18 in. from centre |
|---|---|---|---|---|---|---|
| 8 | 9 | 10 | 12 | 9·5 | 6 | 8·5 |
| 7·5 | 8 | 12 | 12 | 10·5 | 7·5 | 6 |
| 4·5 | 7 | 11 | 12 | 5·5 | 3·5 | 3·5 |
| 5 | 10·5 | 15 | 12 | 11 | 10 | 4·5 |

## THE GENERAL EFFECT OF THE DEPTH OF TOPSOIL ON THE NUMBERS OF WORMS

A close correlation between the dense population of lugworms and the depth of the topsoil along the lines of castings having been established it seemed of interest to find out if this principle were of wider application. Fortunately, a small area was found which showed patchy distribution of a different kind from that previously examined. In 1942 a large bomb fell on the Flats just seaward of the *Fucus* and shingle zone and, its crater subsequently filling with muddy sand, its presence was no longer detectable except for the extreme density of the lugworm population. The centre of the former crater had a great depth of topsoil, but was surrounded by a rim of clay covered merely by a few inches of sand. Within the margins of the crater the lugworm population had a density of 42 per sq.yd., that of the marginal zone being only 4 per sq.yd., whilst the undisturbed area outside the crater rim had a density of 28 per sq.yd. So sharp was the separation of an area rich in worms from an area practically devoid of castings that the counts from which the figures were quoted were made only a yard or so apart.

The evidence from the bomb crater and from a study of the lines of castings is strongly in favour of the view that one of the main factors influencing the density of the lugworm population is the depth of the topsoil overlying the clay rather than the admixture with the topsoil of even a large proportion of shingle or shell gravel.

## MIGRATIONS OF THE LUGWORM POPULATION

There is some evidence in favour of the view that lugworms can change their burrows and that the population of a given area is not determined solely by the original settlement of the larvae. There are reasons for believing that movement to new burrows takes place through the water, that is by swimming. To test this view two pits, each a square yard in area, were excavated in the clay forming the rim of the former bomb crater, the clay being removed to a depth of 10 in. The pits were filled with topsoil from which an attempt had been made to remove all lugworms and were then examined occasionally for the presence of worm castings. The number of castings found on visits made from the beginning of the experiment in August 1948 to April 1949 are shown in Table IV, from which it can be seen that the pits became repopulated gradually until the spring when there was a rapid immigration of worms. It is inconceivable that the worms could have burrowed through the very dense clay forming the walls of the pits. Neither were there, in fact, any worms to be found in the soil immediately adjacent to the pits, so that it must be concluded that they had repopulated the areas by swimming and burrowing from the surface.

TABLE IV. REPOPULATION OF AN ISOLATED AREA OF DEEP SOIL

| Date | No. of casts in marked square yard 1 | No. of casts in marked square yard 2 |
|---|---|---|
| 18 Aug. 1948 | Pits dug in clay and filled with fine sand | |
| 20 Aug. 1948 | 0 | 2 |
| 24 Aug. 1948 | 0 | 3 |
| 24 Sept. 1948 | 1 | 4 |
| 24 Oct. 1948 | 0 | 3 |
| 21 Nov. 1948 | 0 | 4 |
| 5 Dec. 1948 | 0 | 5 |
| 16 Jan. 1949 | 4 | 6 |
| 18 Feb. 1949 | 4 | 9 |
| 16 Apr. 1949 | 15 | 12 |
| 24 Apr. 1949 | 16<br>13 headshafts | 13<br>11 headshafts |

From this it would seem that the patchy distribution of the worms, whether in lines or in other areas is due to the dynamic effect of a shifting population, the worms tending to aggregate in areas of deep topsoil most suitable to their burrowing and feeding activities. The explanation of the trenching in the clay, however, which allows of a deeper layer of topsoil is far from clear, but its solution must probably be sought in the geological history of the Flats. It is, nevertheless, interesting to find that the lugworm is a fairly reliable indicator of the depth of soil suitable to its (and probably to other animals') way of life, and that its discontinuity of distribution shows up, quite clearly, unsuspected discontinuities in what at first sight appears to be a very uniform habitat.

## SUMMARY

It has been shown that the main factor which influences the local distribution of the lugworm at Whitstable is the depth of the muddy sand overlying the clay stratum below.

In places this clay is furrowed by straight channels which are revealed only by the arrangement of the lugworm castings. These are more numerous along the channels.

Migration of adult lugworms has been shown to occur, most freely in the spring.

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## EXPLANATION OF PLATE 1

Figs. 1 and 2. Photographs of the muddy Flats at Whitstable showing lines of lugworm castings.

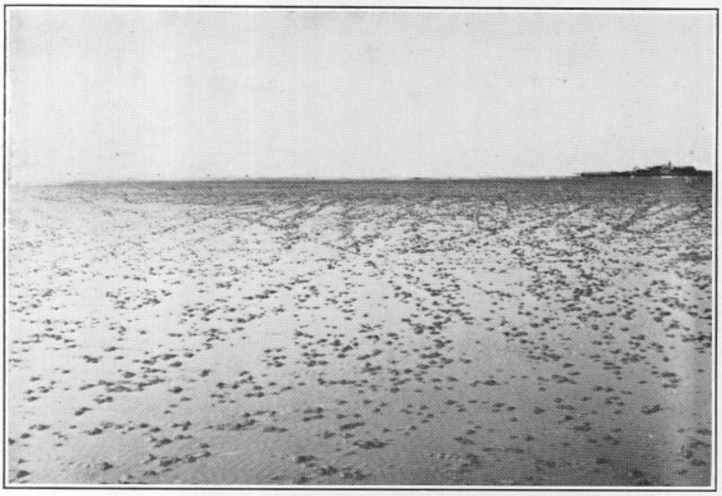

Fig. 1.

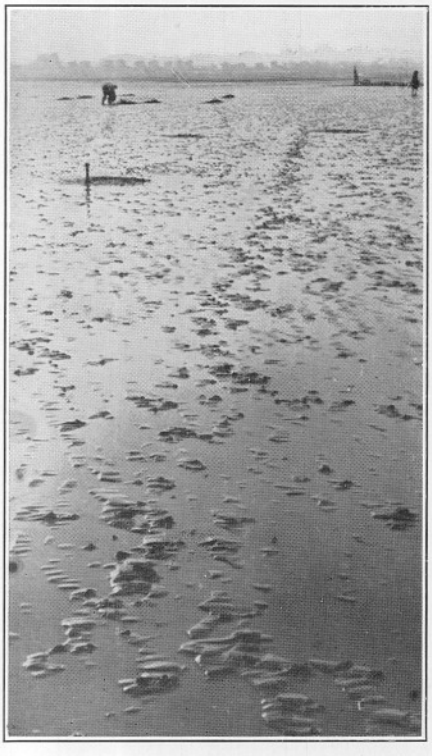

Fig. 2.

# THE LATER LARVAL LIFE OF *ARENICOLA MARINA* L.

By G. E. Newell, B.Sc., Ph.D.

From the Department of Zoology, Queen Mary College, University of London

(Plate I and Text-figs. 1–3)

## Introduction

The literature dealing with the life history of the common lugworm has been reviewed in a previous paper (Newell, 1948), and it will suffice to mention that, until recently, the earliest larval stages that had been identified were the so-called 'Benham larvae' which are really post-larval in the sense that they resemble the adult worms in most essentials except size. These Benham stages were for a long time believed to represent the end of a pelagic developmental series of unknown duration, but both Thorson (1946) and Newell (1948) brought forward strong evidence for the belief that all stages from the fertilized egg up to the fully metamorphosed worm were bottom-dwelling. Thorson was uncertain as to the true explanation of the Benham larvae in the spring plankton but suggested that either they were bottom stages that had been accidentally stirred up, or else they were abnormalities due to larvae metamorphosing in mid-water. Newell, on the other hand, believed that the lugworm larvae at all stages of development dwelt in the top layers of the sand and shingle in the *Fucus* zone until they become to all intents and purposes miniature adults, when they migrate to the habitats of the adults by swimming, and that their presence in the spring plankton is therefore not accidental but an essential and regularly occurring phase in the life history. This view receives support from the finding during the winters of 1947–48 and 1948–49 of bottom-dwelling larval stages intermediate in size between the larvae with two chaetigerous segments and the post-larval stages of Benham.

## Methods

Although extremely simple, the method of collecting the larvae is thought to be worthy of mention since it is applicable to the larvae of other animals and could, if so required, be made the basis of a quantitative method for sampling the microbenthonic fauna.

First, a small pit was dug and then shallow channels were made so as to drain into it from an area of from 20 to 30 sq.yd. The shingle and sand in this area were then stirred up by means of a garden fork to a depth of a few inches. By these means water containing a proportion of the small animals and organic debris in suspension was caused to drain into the pit. The water in the pit was then poured, a pint or so at a time, through a small plankton net whose contents were then transferred at intervals to a jar of sea water. Usually about 20 gallons or so of sea water were filtered in this way, and the resulting suspension was then examined in Petri dishes for polychaete larvae. These were removed by means of a pipette and reserved for further examination. Trial and error soon showed that it was only in the pebbly *Fucus* zone that lugworm larvae were to be found and, it may be remarked, that it was only in this zone that the larvae of other polychaetes were at all plentiful.

## DESCRIPTION OF LARVAE

*Larva with three chaetigerous segments* (Text-fig. 1)

On 17 November 1947, and 29 November 1948, larvae with three chaetigerous segments were found. Otherwise they differed but little in general appearance from larvae with two chaetigers previously described. Although able to swim by means of their cilia, they were usually enclosed in a layer of dense mucus. The prostomium was the largest division of the body and bore an apical tuft and one pair of eyes. A broad prototroch encircled the greater part of the prostomium and peristomium. The three segments behind the achaetous peristomium each bore a pair of dorsal chaetae and a minute crotchet. The dorsal chaetae were of two kinds; a capillary chaeta and a shorter one which was broadly winged or spatulate. Both neurotroch and telotroch were still prominent. The total length of the larva was 0·33 mm.

*Larva with four chaetigerous segments*

This was found on 14 November 1948. It measured 0·35 mm. in length and much resembled the three segment larva.

*Early post-larval stage* (Text-fig. 2 and Pl. 1, fig. 1)

An early post-larval stage was collected on 14 February 1949. Its total length when alive varied between 2·5 and 3·2 mm. and when fixed was 2·8 mm. with a diameter of about 0·4 mm. in the thoracic region. The tail was about half the length of the thoracic region from which it was sharply distinguishable by being narrower and achaetous. The prostomium, still a prominent lobe, bore six eyes, two of which were larger than the others and probably represented the single pair of eyes persisting from earlier stages. The otocysts in the peristomium were clearly visible in transparency and contained minute particles of sand.

Behind the peristomium were twenty segments bearing chaetae, but in the first chaetiger the chaetae, of which there was but one on each side, were difficult to detect. The next nineteen segments bore both notopodial and neuropodial chaetae. The notopodial chaetae (Text-fig. 3A) were of two kinds: (*a*) capillary with narrow wings, and (*b*) shorter ones with broad wings.

The neuropodial chaetae (Text-fig. 3B) were minute crotchets with a curved rostral hook and one (possibly two) smaller hooks. The number of crotchets varied from five in the second chaetiger to nine in the twentieth chaetiger.

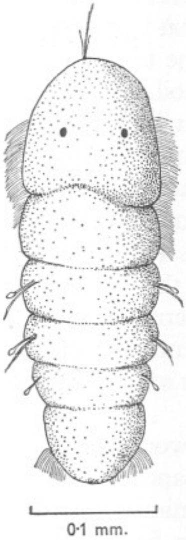

Fig. 1

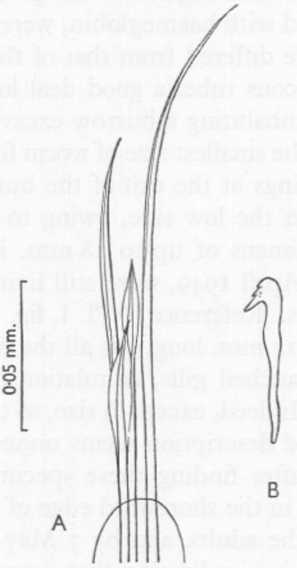

Fig. 3.

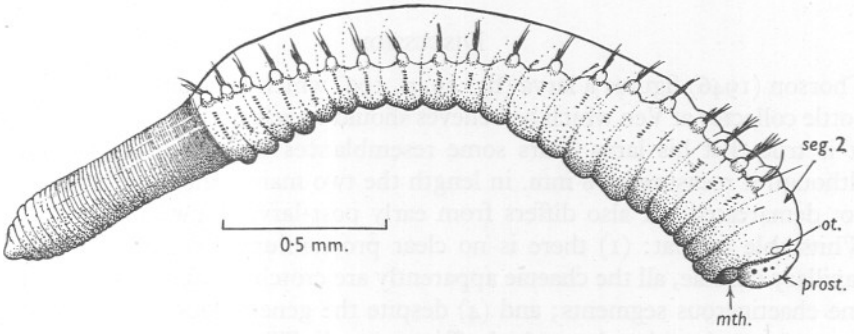

Fig. 2.

Text-fig. 1. Larva with three chaetigerous segments, dorsal view. × *c.* 175.

Text-fig. 2. Early post-larval stage 2·8 mm. in length, side view. × *c.* 43. *mth*, mouth; *prost.*, prostomium; *ot.*, otolith; *seg.* 2, segment 2 (first chaetigerous segment).

Text-fig. 3. Notopodial chaetae from third chaetigerous segment (A) and crotchets from third chaetigerous segment (B) of 2·8 mm. post-larval stage. × *c.* 400.

The tail consisted of about fifty segments and ended in a cone-like pygidium still bearing a trace of a telotroch. None of the segments of the body was as yet divided into annuli; neither were there any traces of gills. The gut was fully functional and the worm seemed to feed by means of its eversible proboscis which engulfed food in much the same way as does that of the adult. Faecal matter was seen in the intestine and the food probably consisted of fine organic debris. The main regions of the gut, as well as the blood vessels, which contained blood with haemoglobin, were already differentiated. Nevertheless, the mode of life differed from that of the adult in that the larva was enclosed in a thick mucous tube, a good deal longer than the total length of the worm, instead of inhabiting a burrow excavated in the soil.

In fact, the smallest size of worm found living in the adult manner, as shown by the castings at the exit of the burrow, was 8 mm. in length. This figure is probably on the low side, owing to shrinkage during preservation and even larger specimens of up to 18 mm. in length, which were collected between 19 and 30 April 1949, were still living in mucous tubes like the earlier post-larval stages. Reference to Pl. I, fig. 2, will show that one of these specimens, which was 12 mm. long, has all the main adult features including the thirteen pairs of branched gills, annulation of the segments and papillae on the tail segments. Indeed, except in size, so closely does it resemble the mature worms that detailed description seems unnecessary.

Shortly after finding these specimens young worms began to make their appearance in the shoreward edge of the muddy sand flats which are the main habitat of the adults, and by 7 May 1949 their minute castings were seen in great profusion, indicating that seaward migration from the shore took place somewhat later in 1949 than in 1947.

## Discussion

Thorson (1946) figures a larva (fig. 59, p. 109) which he found in a mid-water bottle collector at Ven which he believes should be referred to *Arenicola marina*. It is true that his larva bears some resemblances to a young lugworm, but although it measured 2·8 mm. in length the two main regions of the body are not demarcated. It also differs from early post-larval lugworms collected at Whitstable in that: (1) there is no clear prostomium; (2) in the absence of capillary chaetae, all the chaetae apparently are crotchets; (3) there are twenty-one chaetigerous segments; and (4) despite the general lack of differentiation the segments are already marked off into annuli. When it is remembered that this larva was collected in the bottle between 27 July and 13 August, that is, at a time when Thorson states that the gametes are far from mature in the adult worms, it becomes reasonably certain that the larva was not that of *Arenicola marina* and may not even have been that of any species of *Arenicola*.

The 2·8 mm. post-larval stage from Whitstable also differs in several important respects from Benham's larva. Among these differences may be listed: (1) the general appearance; (2) the fact that Benham figures considerably fewer segments (about 30) in the tail region; (3) only two capillary chaetae are

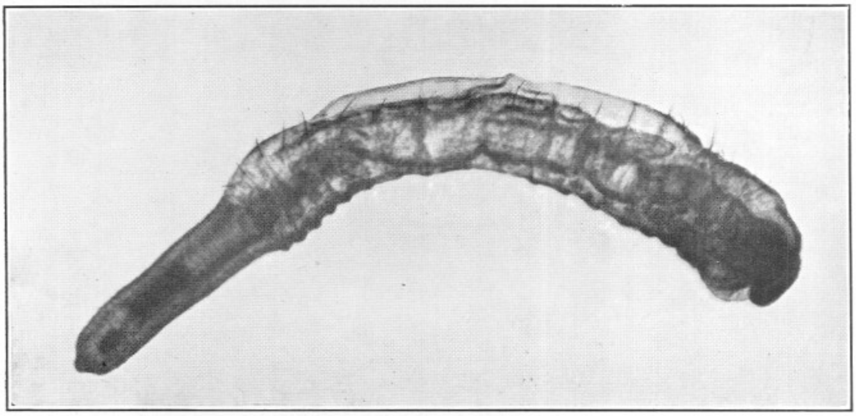

Fig. 1. Photomicrograph of 2·8 mm. post-larval stage after clearing in cedar-wood oil. × *c*. 37·5.

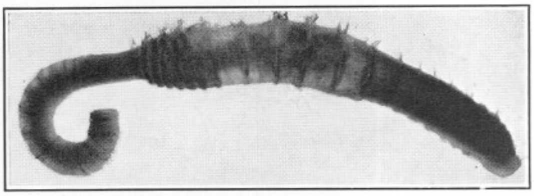

Fig. 2. Photomicrograph of late post-larval stage (12 mm. in length). × *c*. 7·5.

figured in the anterior dorsal bundles, whereas, since Benham's larvae is much larger, even more bristles would be expected, not less; (4) the absence of notopodial lobes; (5) apparently the notopodial bristles are all of one kind, and (6) the smaller number of crotchets in the neuropodial regions.

Ashworth (1904) also succeeded in obtaining post-larval stages of *Arenicola*, but only when they were in the plankton. Reference to his descriptions and figures shows that they agree well with the older post-larval stages collected at Whitstable.

## SUMMARY

Larvae with three and four chaetigerous segments and also an early post-larval stage of *Arenicola marina* are described with figures. These are all bottom-dwelling stages enclosed in mucous tubes and were collected from the pebble and *Fucus* zone at Whitstable.

The finding of these larvae furnishes additional evidence for the view that, except when migrating in the water to new habitats, the lugworm possesses no pelagic larval stage in its life history.

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# THE MECHANISM OF OPENING AND CLOSING OF *CALLIACTIS PARASITICA*

By Garth Chapman, M.A., Ph.D.

From the Department of Zoology, Queen Mary College, University of London

(Text-figs. 1–4)

## INTRODUCTION

In a previous paper Chapman & Newell (1947) described the part played by the body fluid in the burrowing of the lugworm, and recorded the hydrostatic pressure occurring in the fluid contents of the coelom. The fluid-muscle system of this animal is completely closed, except for six pairs of nephridia which do not leak under pressures higher than those which occur naturally in the body of the worm.

It was considered of interest to inquire if the fluid-muscle system functions in the same way in an animal whose body cavity opens to the exterior by a wide aperture. *Calliactis parasitica* Couch was chosen as a large active animal whose normal or resting position is 'open'.

On the movements made by anemones, Hyman (1940) gives a few details of the method of working of the fluid-muscle system, but is obliged to quote Faurot's (1895) account of the burrowing of anemones into sand. Faurot describes only the outward appearance of the process in *Peachia* and says that 'il parait evident que le liquide qu'elles renferment est soumis à une compression'. Jordan (1935) gives an analysis of the properties of *Metridium* body wall, but does not describe the working of the muscular system as a whole. He demonstrates that 'muscle preparations' can be stretched by very small forces and that they do not spontaneously regain their original length when the forces are removed, but he does not distinguish clearly between the properties of muscle and those of mesogloea. Pantin (1940) states that 'on stimulation most anemones cover the disk by contraction of the longitudinal retractors and the parietal muscles of the mesenteries. The mouth, disk and tentacles are pulled in, and during this process some water is squirted out of the mouth. Full re-expansion subsequently requires the gastral cavity to be filled again with sea water. This is done by ciliary action of the stomodaeum and is a slow process. In *Calliactis*, closure is due primarily to the contraction of a powerful sphincter at the edge of the column just under the tentacles. There is little loss of contained water and re-expansion depends simply on the comparatively rapid relaxation of this muscle'. According to Stephenson (1928), water may be lost at the cinclides, through which the acontia are carried by water currents.

He considers that the cinclides may function as safety valves in preventing rupture of the body wall.

From the foregoing it can be seen that there is room for an investigation into the mechanism controlling the volume of contained water and the origin of the restoring force which brings about the 'rapid relaxation' of the sphincter during the movements of *Calliactis*. It would seem that some light could be thrown on the way in which anemones move by the measurement of internal hydrostatic pressure during various phases of movement coupled with observation of their movements and some knowledge of the distribution of their muscular tissues.

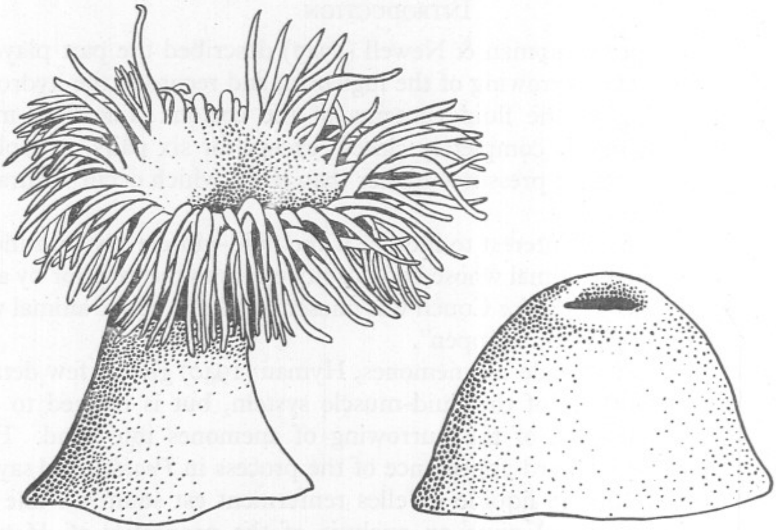

Fig. 1. *Calliactis parasitica* fully open and fully closed.

## Observations of Movements

When open, the tentacles of *Calliactis* are large, numerous, and well distended with water, and the disk is clearly displayed (see Fig. 1). On strong mechanical stimulation the animal can close rapidly and completely until its external surface is that of the column only (see Fig. 1). At the beginning of the contraction the tentacles diminish in size as their contents are expelled into the main gastral cavity, while the disk is retracted by the parietal muscles. A little later the powerful sphincter muscle at the edge of the disk just below the tentacles begins to contract so that the sides of the column are, as it were, drawn over the retracted disk until only a shallow depression indicates that the body wall is not continuous. The animal is now the shape of a bee skep and is firm to the touch, as if made turgid by the pressure of the muscular walls on the contained fluid. Even after strong stimulation this contracted posture is not long maintained, the sphincter usually beginning to relax in less than 2 min. Relaxation of the sphincter is followed by the expansion of the tentacles which are inflated by the inrush of fluid from the enteron of the column.

It seems unlikely that expansion as rapid as that shown by *Calliactis* could be accomplished by means of water pumped into the enteron by ciliary action. As mentioned by Pantin (1940) there is little loss of contained fluid, as was seen by putting a few drops of carmine suspension on to the opening of the stomodaeum of an expanded anemone and stimulating it to contract. Only when the sphincter had nearly closed was there any suggestion that water had been ejected from the animal, and at that stage of the contraction it might well have come from the liquid squeezed out from between the retracted disk and the enveloping sphincter. Conversely, carmine applied to a closed anemone showed that very little water, if any, was taken in during opening.

In addition, carmine suspension was placed near to the cinclides at the base of the column. Neither on normal contraction, nor on contraction strong enough to extrude the acontia, was any water seen to leave the apertures, even as the acontia were being expelled. It is unlikely that *no* water escapes during the extrusion of the acontia, but the amount must be very small.

A test was made to see if water was lost at each contraction by an amount small enough to escape observation but sufficient, when lost repeatedly, to affect the speed of opening and closing. A small anemone was stimulated mechanically twenty-two times in the course of 1 hr. 40 min., and at the end of the period was opening and closing rather more rapidly than at the beginning. The creature was stimulated strongly enough to cause complete closure but not sufficiently to cause the expulsion of the acontia.

Since the animal appears to behave as a closed system analogous to that of *Arenicola*, the stomodaeum being closed during movement, it might well be expected that there would be some considerable variations in pressure during different phases of muscular activity.

## THE INTERNAL HYDROSTATIC PRESSURE

An inclined capillary tube manometer filled with sea water was used to estimate the internal hydrostatic pressure, and was connected to the animal by a hypodermic needle of large bore. In use, the anemone formed the left-hand, and the capillary tube the right-hand, limbs of a manometer (see Fig. 2). Estimations were made by connecting the reservoir to the capillary tube until the level of the sea water in it rose to about 10 cm. above the level in the aquarium jar containing the animal. The tap was then turned so as to connect the anemone with the capillary tube and to cut off connexion with the reservoir. As preliminary tests had shown that less than 1 min. was required for the pressure in the animal and manometer to become balanced as shown by a stationary meniscus, scale readings were made 1 min. after the animal was connected to the manometer tube. Control tests, made with the needle free in the water of the aquarium jar, gave a correction to be deducted from the scale reading which allowed for the height of the water in the jar and for the small capillary rise of liquid in the manometer tube above the level in the aquarium. Finally, the scale reading, made to the nearest mm., was halved, since the slope of the manometer was such as to give a multiplication factor of 2.

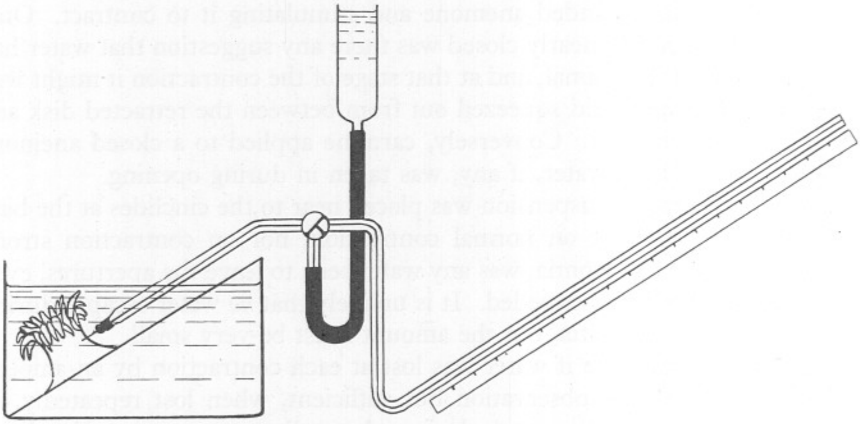

Fig. 2. Inclined capillary manometer.

TABLE I. MEAN PRESSURE IN CM. OF SEA WATER IN *CALLIACTIS*

| Test no. | Expanded | Contracted |
|---|---|---|
| 1 | 1·0 | 2·4 |
| 2 | 2·2 | 1·8 |
| 3 | 1·0 | 3·3 |
| 4 | 0·2 | 1·0 |
| 5 | 1·2 | 2·0 |
| 6 | 3·3 | 2·7 |
| 7 | 0·3 | 1·1 |
| 8 | 1·5 | 3·1 |

Several measurements were made on each animal both in the open and in the contracted state. Contraction was brought about and maintained by mechanical stimulation of the base of the column with a glass rod. Difficulty was sometimes experienced in keeping the animals contracted for a minute. The mean pressures measured by this method on the stock of eight animals are set out in Table I; detailed results are given in the Appendix.

The striking feature of Table I is the inconsistency of the readings, in spite of the fact that each figure represents a mean of between four and thirteen readings. Whilst, in general, the pressure in the closed animal is higher than it is in the open one, the amount of the difference is not constant, nor is the pressure in the open animals constant. A manometer was therefore made to give a continuous indication of the pressure changes inside the animal without, however, providing an exact measure of the pressures recorded, in order to show whether the instantaneous pressures previously recorded are representative of the normal pressure range.

## VARIATIONS OF THE INTERNAL PRESSURE

The apparatus, by which variations of internal pressure were shown (Fig. 3), consisted of a xylene-filled manometer connected to a very thin-walled rubber teat ($T$) at the end of a glass tube which could be manipulated and clamped with the teat in place in the enteron of the anemone. The air enclosed between the manometer and the teat could be put into communication with the exterior by a three-way tap, one position of which enabled the pressure within to be raised by blowing into it through a mouthpiece ($M$). The teat was made of rubber sufficiently thin to collapse when immersed in even 1 cm. depth of water, and hence was collapsed when it was quickly inserted into the stomodaeum of an open anemone. The glass tube bearing it was clamped into place and the teat was inflated by blowing gently into the mouthpiece until, at a pressure of 4 or 5 cm. of xylene, communication with the outside was cut off and the teat was left in communication with the manometer only. The apparatus was left for 5 min. to ensure that the air within the teat assumed the temperature of the water and hence remained practically constant during the course of the experiment. A scale was adjusted so that, at the beginning of the readings, the meniscus of the right-hand limb lay at zero. Readings of the pressure recorded by the manometer were made at 15 sec. intervals over

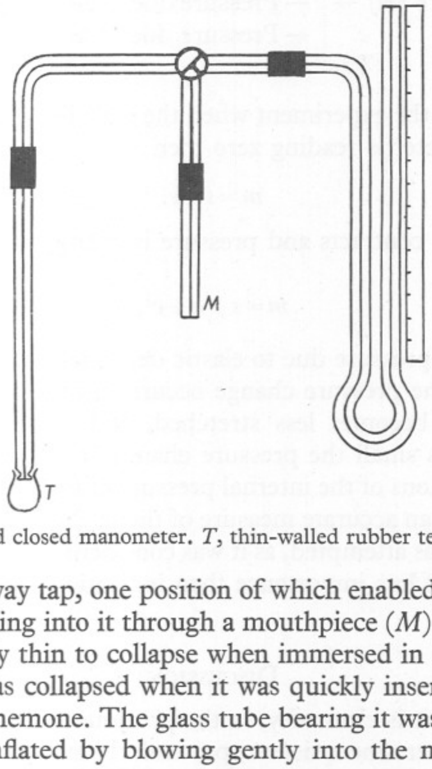

Fig. 3. Xylene-filled closed manometer. $T$, thin-walled rubber teat; $M$, mouthpiece.

periods of up to 40 min. duration. From time to time the animal was stimulated by prodding the column with a glass rod, and throughout the experiment its state, whether open or closed, was recorded with the manometer readings. The times at which mechanical stimulation was applied, together with a line representing the state of opening of the animal, were marked on the records. The results of three typical tests are represented graphically in Fig. 4.

It will be realized that the pressures recorded by the manometer are not equal to the pressures occurring in the animal, but are the reaction of the resultant of three pressures acting on the wall of the teat. They can be represented diagrammatically:

| ← Pressure due to depth of submergence ($s$)
Manometric pressure ($m$) → | ← Pressure due to elastic deformation of teat ($e$)
| ← Pressure due to anemone ($a$)
Teat wall

At the beginning of the experiment when the scale is set so that the right-hand limb of the manometer is reading zero then

$$m = s + e.$$

When the anemone contracts and pressure is exerted on the teat due to that contraction then

$$m = s + a + e^1,$$

where $e^1$ is the new pressure due to elastic deformation at the new size of teat brought about by the pressure change occurring in the anemone. As $a$ rises, therefore, the teat becomes less stretched, and $e$ is therefore diminished. Since, however, $e$ is small the pressure changes recorded by the manometer serve to show variations of the internal pressure of the anemone, even although they do not provide an accurate measure of them. No calibration or correction of the manometer was attempted, as it was considered that accuracy of pressure measurement was of less importance than indication of pressure change.

## DISCUSSION

From these records it is clear why, in the previous tests, measurements of the internal pressures were inconsistent, particularly in the closed animal.

From inspection of the graphs, and from observations made during the course of the experiments, it would appear that, on mechanical stimulation followed by closure, pressure rises rapidly, generally attaining a maximum within 15 sec. This maximum pressure is developed only momentarily and immediately begins to fall, during which time the anemone may remain contracted or may begin to open again. With the beginning of opening either the rate of fall of pressure is briefly arrested or a small rise in pressure may

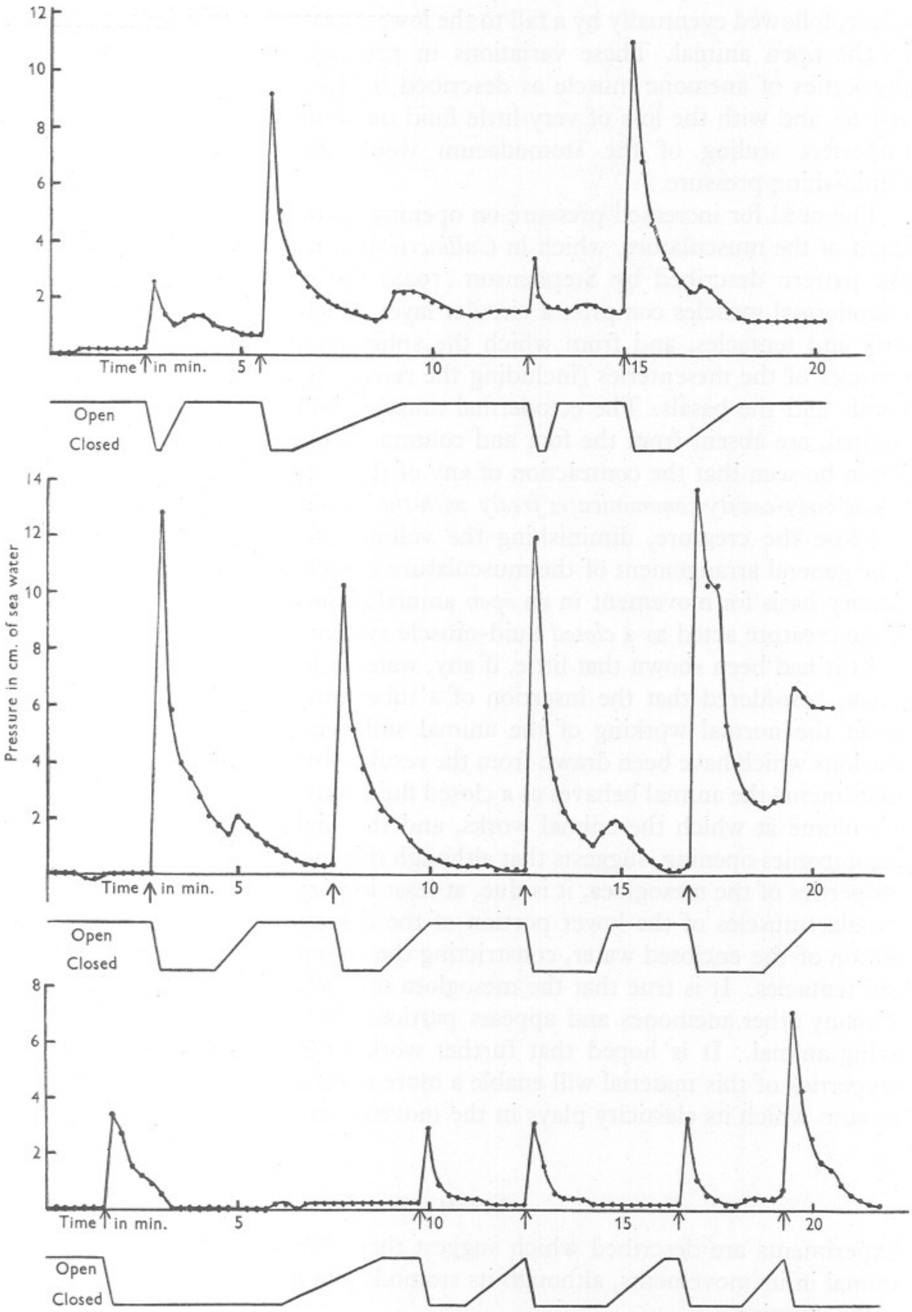

Fig. 4. Three records of the internal hydrostatic pressure changes in *Calliactis parasitica*. The animals were stimulated mechanically at the base of the column at the times marked by arrows; the line below each graph represents the opening and closing of the animal.

occur, followed eventually by a fall to the lowest pressures, which are recorded in the open animal. These variations in pressure are consistent with the properties of anemone muscle as described by Jordan (1935) and by Bozler (1936), and with the loss of very little fluid on contraction. Any loss through imperfect sealing of the stomodaeum would be reduced by a rapidly diminishing pressure.

The need for increased pressure on opening is connected with the arrangement of the musculature, which in *Calliactis* does not differ appreciably from the pattern described by Stephenson (1928) for anemones in general. The endodermal muscles comprise a circular layer which covers the foot, column, disk and tentacles, and from which the sphincter is derived as well as the muscles of the mesenteries (including the retractors of the disk), the parietobasals and the basals. The ectodermal muscles, which are, in general, longitudinal, are absent from the foot and column (Pantin, 1935). On inspection, it can be seen that the contraction of any of these muscle layers, *in an animal whose body-cavity communicates freely with the outside*, would be to contract or to close the creature, diminishing the volume of water which it contains. The general arrangement of the musculature is such as would provide a satisfactory basis for movement in an *open* animal if the mesogloea were elastic, *or* if the creature acted as a *closed* fluid-muscle system.

As it had been shown that little, if any, water is lost on normal contraction, it was considered that the insertion of a tube into the stomodaeum did not upset the normal working of the animal sufficiently to invalidate the conclusions which have been drawn from the results obtained, namely, that during movements the animal behaves as a closed fluid-muscle system. The constancy of volume at which the animal works, and the slight rise in pressure which accompanies opening, suggests that although this may be aided by the physical properties of the mesogloea, it is due, at least in part, to the contraction of the circular muscles of the lower portion of the column. These alter the distribution of the enclosed water, constricting the column and expanding the disk and tentacles. It is true that the mesogloea of *Calliactis* is stronger than that of many other anemones and appears particularly so when cut out from the living animal. It is hoped that further work on the structure and physical properties of this material will enable a more exact estimate to be made of the amount which its elasticity plays in the movements of the animal.

## SUMMARY

Experiments are described which suggest that *Calliactis* behaves as a closed animal in its movements, although its stomodaeum appears to be widely open to the exterior.

Observations of the movements of the animal are correlated with variations of the internal pressure. It is shown that expansion is not merely 'passive

relaxation', but is generally accompanied by a rise in pressure which is, however, much lower than that which accompanies rapid closing.

It is concluded that the fluid-muscle system of *Calliactis* behaves in a similar way to that of other soft-bodied invertebrates, but that the system works at a much lower pressure.

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## APPENDIX

### Details of Pressure Measurements in *Calliactis*

Pressures are given in cm. sea water to nearest 0·1 cm.

All readings made 1 min. after connecting animal with manometer tube.

All readings are corrected for capillary rise, height of water in aquarium jar and for slope of manometer.

| | Anemone 1 | | Anemone 2 | | Anemone 3 | | Anemone 4 | |
|---|---|---|---|---|---|---|---|---|
| | Open | Shut | Open | Shut | Open | Shut | Open | Shut |
| | 1·4 | 1·2 | 2·9 | 0·5 | 0·7 | 2·3 | 0·3 | 0·6 |
| | 2·3 | 3·1 | 3·0 | 1·5 | 0·9 | 5·0 | 0·2 | 1·1 |
| | 1·5 | 1·6 | 1·0 | 1·6 | 0·9 | 2·1 | 0·2 | 0·4 |
| | 0·8 | 3·7 | 2·9 | 2·0 | 1·1 | 3·7 | 0·1 | 0·9 |
| | 0·8 | 2·5 | 0·9 | 1·7 | 0·8 | 4·5 | 0·2 | 1·4 |
| | 0·5 | — | 3·4 | 1·9 | 2·1 | 1·9 | — | 1·0 |
| | 0·3 | — | 0·7 | 3·2 | 1·3 | — | — | 1·5 |
| | 0·3 | — | 3·6 | — | 0·7 | — | — | — |
| | — | — | 1·2 | — | 0·6 | — | — | — |
| | — | — | — | — | 0·9 | — | — | — |
| Mean pressure | 1·0 | 2·4 | 2·2 | 1·8 | 1·0 | 3·3 | 0·2 | 1·0 |

| | Anemone 5 | | Anemone 6 | | Anemone 7 | | Anemone 8 | |
|---|---|---|---|---|---|---|---|---|
| | Open | Shut | Open | Shut | Open | Shut | Open | Shut |
| | 1·7 | 3·1 | 1·7 | 3·8 | 0·8 | 1·0 | 1·6 | 3·0 |
| | 1·3 | 1·3 | 1·6 | 3·2 | 0·9 | 1·2 | 1·8 | 4·4 |
| | 1·3 | 1·3 | 2·1 | 1·2 | 0·4 | 0·7 | 1·7 | 3·7 |
| | 0·8 | 2·3 | 2·6 | 4·0 | 0·0 | 0·7 | 1·2 | 2·1 |
| | 0·6 | — | 4·3 | 1·5 | 0·0 | 1·9 | 1·8 | 4·5 |
| | 1·1 | — | 3·3 | — | 0·0 | — | 1·7 | 1·7 |
| | 1·3 | — | 3·0 | — | 0·0 | — | 1·1 | 1·5 |
| | 1·2 | — | 2·3 | — | 0·0 | — | 1·2 | 4·0 |
| | — | — | 4·7 | — | — | — | — | — |
| | — | — | 4·4 | — | — | — | — | — |
| | — | — | 6·5 | — | — | — | — | — |
| | — | — | 4·7 | — | — | — | — | — |
| | — | — | 2·3 | — | — | — | — | — |
| Mean pressure | 1·2 | 2·0 | 3·3 | 2·7 | 0·3 | 1·1 | 1·5 | 3·1 |

# ON THE VOLUME MEASUREMENT OF WATER FILTERED BY A PLANKTON PUMP, WITH SOME OBSERVATIONS ON THE DISTRIBUTION OF PLANKTONIC ANIMALS

By H. Barnes
The Marine Station, Millport

## Introduction

Winsor & Walford (1936) have suggested that variations in replicate vertical plankton hauls can be explained on a random distribution of the population which is affected by variations in the volume of water filtered, and the results of Silliman (1946) and Barnes (1949) are in apparent agreement with this suggestion. It might be expected that the use of a pump would eliminate such volume errors. Further, in view of the increased attention now being paid to the use of pumping methods for obtaining plankton samples, it is desirable to know the accuracy, under various conditions, of the volume estimation in such samples. The use of the pump has been described by Gibbons & Fraser (1937). Comparison of nets, pumps and the Clarke-Bumpus sampler has been given by Wiborg (1948).

## The Accuracy of Filling a Tank

Various methods have been used for estimating the volume of water pumped, the simplest technique consisting of filtering the water through a net into a calibrated tank to a series of marks. This method has been used in this laboratory. An ex-National Fire Service pump fitted with 2½ in. armoured hose has been used, the water being pumped into a galvanized iron tank of dimensions 60 × 60 × 100 cm., i.e. a total capacity of approximately 400 l.

The volume of water pumped into this tank in any experiment was determined in the following way. After taking the sample a known volume of concentrated dye solution was added to the water and, after thoroughly mixing, a sample of the coloured liquid was taken and its transmittancy determined using the appropriate filters. The dilution was then obtained by reference to a calibration curve for dilution and transmittancy. The transmittances were determined by means of the Spekker Absorptiometer using 20 cm. cells. It was necessary to construct a calibration curve each day using the water pumped on that occasion since the amount of suspended matter and organisms in the water, contributing to the absorption, varies from day to day. The accuracy of such volume determinations was approximately ± 1 l.

The procedure was as follows. Having adjusted the pump throttle and valve (see p. 654) to deliver water at an approximately known rate, the person in charge of the delivery hose filled the tank to a mark and removed the hose. As the water level approached the mark the hose was raised so that it could be quickly moved clear of the tank when the desired level was reached. At the same time the water delivered at the pump by-pass was collected and measured in a measuring cylinder (see later for discussion). After filling up to a mark in this way, the concentrated dye solution was added to the water in the tank, and after stirring a subsample was taken. This was repeated several times, the tank being carefully washed out with the hose between each experiment. The transmittances of the samples were then determined and the volumes of water taken in the tank calculated. Results of the first series are given in Table I. (The results given in Tables I–III were obtained with the engine running continuously throughout each series.)

TABLE I. FIRST PUMP SAMPLES TAKEN ON PIER

Nominal volume taken, 200 l.; weather rather cold, little wind; pumping speed approximately 200 l./min.

| | Volume (l.) | Volume, by-pass (ml.) |
|---|---|---|
| | 204 | 3543 |
| | 206 | 3510 |
| | 205 | 3517 |
| | 192 | 3548 |
| | 200 | 3591 |
| | 191 | 3638 |
| | 190 | 3600 |
| | 201 | 3622 |
| | 190 | 3641 |
| Mean | 197·7 | 3579 |
| Standard deviation | 6·8 | 51 |
| Coefficient of variation (%) | 3·4 | 1·4 |

The factors influencing the accuracy with which the required volume is obtained, when attempting to fill a tank up to a mark in this way, are the judgement of the person manipulating the hose, particularly in relation to movement of water in the tank, and his efficiency in removing the hose after the mark has been reached. With practice one tends to allow for the small amount added during the removal of the hose. Any change in the speed of pumping will affect the accuracy by its effect on these two factors. It is evident from the results that under these working conditions the volume of water by this method can be taken with reasonable precision and that the variations are very much less than those encountered in plankton sampling.

In the second experiment the pumping speed was increased and the same number of samples taken.

The greater pumping speed increases the motion of the water in the tank and gives more foam on the surface, both factors tending to make the estimation of the point at which the mark has been reached more difficult. The error due to water being added whilst removing the hose is also increased. However, even with these possible sources of increased errors and under slightly more adverse weather conditions the accuracy of the volume measurement is unchanged. It should be noted that high pumping speeds are undesirable in collecting plankton since they may lead to the washing of material through the net, and to damage of the collected material.

TABLE II. SECOND PUMP SAMPLES TAKEN ON PIER

Nominal volume taken, 330 l.; weather, cold with some wind; pumping speed approximately 350 l./min.

| | Volume (l.) | Volume, by-pass (ml.) |
|---|---|---|
| | 332 | 1569 |
| | 331 | 1589 |
| | 324 | 1573 |
| | 324 | 1572 |
| | 344 | 1579 |
| | 340 | 1567 |
| | 340 | 1581 |
| | 326 | 1559 |
| | 306 | 1547 |
| Mean | 330 | 1571 |
| Standard deviation | 11·5 | 12·4 |
| Coefficient of variation (%) | 3·5 | 0·8 |

The above experiments were repeated on board ship.

Here judgement in filling up to the mark is very considerably hampered by any movement, which if the tank is filled to the higher marks may even result in loss of water.

TABLE III. PUMP SAMPLES TAKEN ON BOARD SHIP

Nominal volume taken, 200 l.; weather, some wind, fairly cold; pumping speed approximately 150 l./min.

| | Volume (l.) | Volume, by-pass (ml.) |
|---|---|---|
| | 219 | 3375 |
| | 199 | 3380 |
| | 195 | 3295 |
| | 195 | 3420 |
| | 197 | 3380 |
| | 181 | 3440 |
| | 186 | 3350 |
| | 200 | 3375 |
| | 206 | 3425 |
| Mean | 197·6 | 3382 |
| Standard deviation | 11·0 | 43·8 |
| Coefficient of variation (%) | 5·6 | 1·3 |

Although the error in the measurement of the volume is still quite small it is greater than at double the pumping speed on shore, and with increasing adversity of weather conditions the error of volume measurement on board might be expected to increase rapidly. It should also be noted that during the experiments described no net was used and no material was collected; attention could therefore be focused entirely on filling the tank.

### Calibration of the By-Pass

On ship, however, even under good weather conditions, the use of tanks can hardly be said to be a convenient technique of volume measurement, since for continuous work two rather cumbersome tanks taking up considerable deck space must be employed, one to be emptying whilst the other is in use. Consideration was given, therefore, to other possible methods of volume measurement. With a pump running at constant speed the timing of the delivery, once it was calibrated (and if checked at intervals) would be satisfactory when using a constant length of hose. However, even with constant hose length, this is not possible with the type of pump in use here, since the rate of delivery is determined both by the position of the main valve and by the engine speed, the latter being controlled by a throttle whose setting cannot be accurately reproduced from day to day.

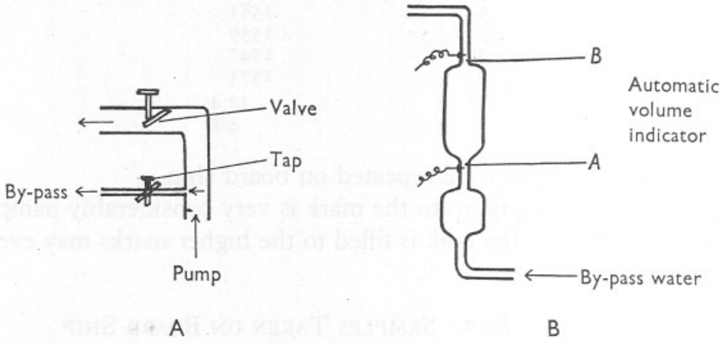

Fig. 1.

It was therefore decided to determine whether the volume of water going through the by-pass (used to cool the engine) could be used as a measure of the volume pumped. This by-pass water is taken through a filter fitted with a cock which can be conveniently used to take a sample. The amount of water forced into the by-pass depends both upon the position of the main valve (which as it is closed causes considerable back pressure) as well as upon the engine speed. At a given engine speed the volume of by-pass water increases as the valve is closed and therefore as the volume pumped decreases. The arrangement is indicated in Fig. 1 A.

The results already given (Tables I–III) show that at a given engine speed and main valve position the amount of water delivered from the by-pass was constant for a constant volume collected (within the limits of error of the latter), and under these conditions the error in the volume of by-pass water is not greater than the error in filling the tank. The factors contributing to the errors of the two estimates of volume pumped are not identical; in taking the by-pass water co-ordination with the person working the hose is of importance for accurate work. That the coefficient of variation of the by-pass volume is less than that of the tank volume suggests that the co-ordination between the two workers was excellent and that much of the error in taking the tank volume is due to the water added when putting in and taking out the hose, since the by-pass water was taken when the person working the hose gave a shout at the beginning of the experiment and when the mark had been reached, and since manipulation of the vessel collecting the by-pass water was simpler than removal of the hose.

That a constant by-pass volume was obtained for other valve positions and engine speeds is shown by the results in Table IV. The actual volume delivered was not measured in these experiments, but the tank was filled up to a mark.

TABLE IV. BY-PASS VOLUMES FROM PUMP SAMPLES AT DIFFERENT VALVE POSITIONS

Samples taken on pier; nominal volume taken, 330 l.; weather, cold with some wind; pumping speed approximately 330 l./min.

| Main valve postion... | 2 turns | 3½ turns | 4 turns |
|---|---|---|---|
| | Volume (ml.) | | |
| | 1361 | 1366 | 1465 |
| | 1273 | 1340 | 1475 |
| | 1304 | 1356 | 1528 |
| | 1356 | 1354 | 1453 |
| | 1354 | 1338 | 1396 |
| | 1352 | 1326 | 1394 |
| | 1264 | 1311 | 1360 |
| | 1273 | 1320 | 1406 |
| Mean | 1317 | 1339 | 1435 |
| Standard deviation | 44·5 | 19 | 55 |
| Coefficient of variation (%) | 3·4 | 1·4 | 3·8 |

*Note.* These experiments were not done on the same day. The engine speeds would be different, which accounts for similar volumes being obtained with different values of cock position used.

Under given working conditions of fixed valve position and fixed running speed a satisfactory calibration could therefore be obtained between volume of water pumped and by-pass volume. The main valve position is readily reproduced and maintained but a given engine speed is difficult to reproduce. However, with fixed valve position it might be expected that for *small* changes in engine speed the by-pass water would be constant for a constant volume pumped, i.e. changes in engine speed would affect both volumes of water in the same proportion. Table V gives some results of experiments with varying engine speeds at two fixed valve positions.

For small changes in engine speed, at fixed positions of the valve, the delivery at the by-pass is a satisfactory measure of the volume pumped. A calibration of the pump is therefore possible in terms of the by-pass water. After calibration it would then only be necessary to measure the by-pass water in order to compute the volume of water pumped at a given valve position and engine speed. This by-pass water could be collected in a measuring cylinder.

In order to ensure that the engine speed is approximately constant throughout any given series the preliminary adjustments have been made with the aid of a simple pressure-measuring device, utilizing the pressure developed in an upright tube at right angles to the direction of flow. As a pressure meter an ex-R.A.F. rate-of-climb indicator has been used. As supplied it records rate of change of pressure, but if the air escape is blocked then actual pressures are recorded in arbitrary units and the instrument is then far more sensitive than the similarly constructed altimeters or air speed indicators. This was attached to one of the two similar paired cocks on the by-pass filters (only one of these cocks can be used at the same time; a simple valve allows transfer from one to the other), the second being used to collect the water. A fixed position is necessary and metal tubing and metal unions were used for connexions both to the cock and to the pressure meter.

TABLE V. BY-PASS VOLUMES AT DIFFERENT ENGINE SPEEDS (AT TWO VALVE POSITIONS)

Samples taken on pier; nominal volume taken, 330 l.; weather, good; pumping speed approximately 330 l./min.

| Main valve... | 2 turns | | 4 turns | |
|---|---|---|---|---|
| Throttle | Volume (ml.) | Mean volume | Volume (ml.) | Mean volume |
| (*a*) | 1955<br>1937<br>1938<br>1928 | 1940 | 1392<br>1391<br>1405<br>1406 | 1399 |
| (*b*) | 1886<br>1920<br>1931<br>1919 | 1914 | 1396<br>1389<br>1401<br>1377 | 1391 |
| (*c*) | 1918<br>1910<br>1932<br>1930 | 1923 | 1348<br>1333<br>1344<br>1343 | 1342 |
| (*d*) | 1826<br>1846<br>1835<br>1836 | 1836 | 1282<br>1295<br>1280<br>1289 | 1287 |
| | 1919<br>1898<br>1889<br>1925 | 1908 | 1170<br>1181<br>1220<br>1215 | 1197 |

(*a*), (*b*), (*c*) and (*d*) represent very considerable successive increases of engine speed which are, however, different in the two separate experiments since the position of the main valve varied (2 turns and 4 turns).

It was shown that when the pressure was adjusted by means of the throttle to a given value as indicated by this meter a constant volume of water was pumped (at constant main valve position, which is readily reproduced). That this is so is indicated by the results given in Table VI.

Collection of the by-pass water, followed by measurement of its volume in a cylinder, is not very convenient, although a good deal more so than the use of two large tanks, and a device has therefore been made which gives a signal when a known volume of water has been delivered. This consists of a vessel (Fig. 1 B) with a large and small section connected to the by-pass cock and having platinum electrical contacts at the entrance and exit of the main bulb. The small lower bulb serves to delay the first contact after the by-pass water has been turned on, thus giving the person working the hose time to get ready. The contacts are connected to a thermionic relay in circuit with a bell. Contact is made immediately the water reaches *A* and the bell rings; the circuit is then broken by means of a switch, which puts the second contact in circuit, and the bell rings again when the water reaches the second contact at *B*. The person working the hose collects water between the ringing of the first and second bells.

TABLE VI. BY-PASS VOLUMES AT DIFFERENT PRESSURES

Samples taken on pier; nominal volume taken, 330 l.; weather, good; constant main valve position; pressure changed by changing engine speed.

| Pressure (arbitrary units) | Volume (ml.) | Mean volume (ml.) |
|---|---|---|
| 5·2 | 2526 | 2537 |
| | 2527 | |
| | 2558 | |
| 6·6 | 2760 | 2768 |
| | 2775 | |
| 7·8 | 3586 | 3585 |
| | 3543 | |
| | 3626 | |
| 5·2* | 2480 | 2492 |
| | 2512 | |
| | 2483 | |
| | 2495 | |
| | 2514 | 2511 |
| | 2508 | |
| | 2512 | |
| | 2504 | 2528 |
| | 2458 | |
| | 2565 | |
| | 2618 | |
| | 2493 | |

* Between these three series the cock was moved and readjusted and the pressure meter taken down and reassembled.

Using this device the volume of water in the tank can be accurately and conveniently taken. The volume pumped for a fixed volume of the by-pass (i.e. volume of large bulb) with fixed valve position and approximately constant engine speed (adjusted by pressure meter) can be varied by inserting a tap at the inlet to the lower bulb. However, in view of the possibility of such a tap slipping and since in general only a small number of different units of volumes are likely to be required at one period in this type of work, a series of interchangeable tubes of varying bore have been used between the by-pass delivery (kept with cock fully open) and the entrance to the apparatus.

Using this method the results in Table VII were obtained. The apparatus was dismantled between the three runs which were done at intervals of several days, the volume being measured by the method already outlined. Once calibrated (which can be done on shore) the apparatus may be used to collect known volumes of water without the use of large tanks. A small vessel into which the collecting net can be held is used, the net being kept under the water during filtration.

TABLE VII. VOLUMES IN TANK FOR FIXED BY-PASS VOLUME

Nominal volume taken 200 l.; weather, good on shore, only moderate on ship; pumping speed approximately 170 l./min.; separate days' experiments.

| Pump standing on pier, volume (l.) | | Pump on ship, volume (l.) |
|---|---|---|
| 197 | 190 | 190 |
| 191 | 186 | 187 |
| 189 | 200 | 189 |
| 189 | 196 | 192 |
| 194 | 197 | 195 |
| 196 | | 191 |

| | |
|---|---|
| Grand mean | 192·3 |
| Standard deviation | 4·0 |
| Coefficient of variation (%) | 2·1 |

## THE RESULTS

If the assumptions of Winsor & Walford are correct, samples taken by a calibrated pump should show considerably less variation than net samples. So far only a small number of samples have been taken and analysed. In the first series of experiments approximately 1000 l. were pumped for each sample and four consecutive samples were taken. The total time to take one sample was of the order of 6 min. (170 l./min.), and allowing for the time taken in changing the nets and bottling off the catch the whole collection occupied about $\frac{3}{4}$ hr.

The net was a small fine net (200 meshes to the inch) held in a tank of water with the whole of the filtering surface immersed whilst the water being pumped was, as far as possible, not directed on to the net surface.

Four samples were taken, and since the collections took a considerable time they have been grouped in two pairs and the results of the analysis of variance

TABLE VIII. COMPOSITION OF PLANKTON SAMPLES FROM FOUR CONSECUTIVE PUMP HAULS

| | Haul | | | |
|---|---|---|---|---|
| Group | 1 | 2 | 3 | 4 |
| Nauplii | 2662 | 2142 | 2200 | 2166 |
| Copepodites | 485 | 466 | 565 | 833 |
| Lamellibranchs | 608 | 882 | 1118 | 1279 |

are given below. In each sample three groups of organisms were counted, namely, copepods (adult stages), copepods (nauplius stages) and lamellibranch larvae (Table VIII).

Analysis of the variance[1] of these data gives the following results:

| | Degrees of freedom | Sum of squares | Mean squares |
|---|---|---|---|
| Main effects: | | | |
| Groups | 2 | 0·7441 | 0·3721 |
| Hauls | 1 | 0·0062 | 0·0062 |
| Times | 1 | 0·0370 | 0·0370 |
| First-order interaction: | | | |
| Groups-hauls | 2 | 0·0142 | 0·0071 |
| Groups-times | 2 | 0·0351 | 0·0176 |
| Hauls-times | 1 | 0·0025 | 0·0025 |
| Second-order interaction: | | | |
| Groups-times-hauls | 2 | 0·0109 | 0·0055 |
| Totals | 11 | 0·8500 | |

The values for the times, group-haul, group-time and haul-time interaction are not significant. There is, therefore, no significant change in population, and the analysis can be simplified and regrouped as follows (this is equivalent to treating the data as four consecutive hauls):

| | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Groups (G) | 2 | 0·7441 | 0·3721 |
| Hauls (H) | 3 | 0·0457 | 0·0152 |
| Residual | 6 | 0·0602 | 0·0100 |

The mean square for the hauls is not significant.

$\sigma^2_{\mathrm{GH}}$ is a measure of the within-haul variance

$$\sigma^2_{\mathrm{GH}} = 0{\cdot}0100.$$

Standard deviation $= \sigma_{\mathrm{GH}} = 0{\cdot}1000 = \log 1{\cdot}259$, corresponding to a coefficient of variation of 25·9%.

A further pair of hauls gave 21% as the coefficient of variation of a single observation, the conditions being similar to those of the first series.

These results indicate that little improvement has been effected by the use of the pump, and a third pair substantiated these results. It was thought that the manipulation of the catch on board was a possible source of error, and in a fourth series a pair of nets was used for the filtration. Two samples were taken of 220 l., the total time between beginning the first haul and completing the second being less than 10 min. These nets were new and 'identical' and were soaked for some time before use. After filtering the pumped water, the nets were carefully transferred to buckets without removing the collecting bucket and taken to the laboratory where the catch was removed with extreme

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[1] Logs of catches have been used. The hauls have been separated into Haul 1 and Haul 2 since there is some evidence that the first haul of a series is different from the second, due to the state of the net. The above results do not substantiate this suggestion.

care using a fine jet to wash down the catch. A large number of species were counted and thanks are due to Dr S. M. Marshall for counting this set. The analysis of the variance of the data yields the following:

| | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Hauls (H) | 1 | 0·1122 | 0·1122 |
| Species (S) | 54 | 56·2223 | 1·0412 |
| Interaction | 54 | 0·6787 | 0·0126 |

Thus $$55\sigma_{\mathrm{H}}^2+\sigma_{\mathrm{HS}}^2=0{\cdot}1122,$$

and $$\sigma_{\mathrm{HS}}^2=0{\cdot}0126.$$

Hence, $$\sigma_{\mathrm{H}}^2=0{\cdot}0018,$$

corresponding to a standard deviation of $0{\cdot}0424=\log 1{\cdot}103$, giving a coefficient of variation of 10·3%.

Further, $$\sigma_{\mathrm{HS}}^2=0{\cdot}0126,$$

or a standard deviation of $0{\cdot}1123=\log 1{\cdot}295$, corresponding to a coefficient of variation of 29·5%.

The standard deviation of a single observation is

$$\sqrt{(\sigma_{\mathrm{H}}^2+\sigma_{\mathrm{HS}}^2)}=\sqrt{0{\cdot}0144}=0{\cdot}12=\log 1{\cdot}318,$$

corresponding to a coefficient of variation of 31·8%.

TABLE IX. THE DISTRIBUTION OF $\chi^2$ DERIVED FROM POISSON SERIES (AS EXPECTED ON A RANDOM DISTRIBUTION), AND NET AND PUMP SAMPLES FOR ALL ORGANISMS

| $\chi^2$ value | Poisson | Nets | Pump |
|---|---|---|---|
| 0–0·0039 | 5 | 4·5 | 5·5 |
| –0·0158 | 5 | 1·5 | 3·6 |
| –0·0642 | 10 | 3·7 | 3·6 |
| –0·148 | 10 | 5·2 | 9·1 |
| –0·455 | 20 | 10·4 | 9·1 |
| –1·074 | 20 | 11·2 | 5·5 |
| –1·642 | 10 | 9·0 | 12·7 |
| –2·706 | 10 | 11·9 | 7·3 |
| –3·841 | 5 | 11·2 | 3·6 |
| > 3·841 | 5 | 31·3 | 40·0 |

## DISCUSSION

The results from this small series of pump samples do not show any less variability than found with the net samples, and their similarity is confirmed on comparing the values of $\chi^2$ for the two series. In the distribution of $\chi^2$, and in the relation between $\chi^2$ and sample size, the two series show similar trends as shown in Tables IX and X, in particular the fact that even with pump samples the large values of 'sample size', i.e. population density high, contribute a very large proportion of the abnormally high discrepancies. Doubt is therefore cast upon the assumption that the variability of net hauls is due to variation in the volumes of water filtered, since this was controlled in the pump samples, and it seems desirable to re-examine the assumption that the animals are randomly distributed, since it was upon a random population that variable volume filtered was supposed to act. Work designed to investigate the distribution of the organisms, using a new method of sampling, is already in progress.

TABLE X. SUM OF $\chi^2$ BY SAMPLE SIZE (POPULATION DENSITY)

Numbers in brackets indicate number of samples in each group.

| | Net | Pump |
|---|---|---|
| 5–40 | 128·928 (50) | 8·598 (12) |
| 40–170 | 100·513 (44) | 65·401 (19) |
| 170–400 | 69·076 (19) | 51·699 (7) |
| 400–1000 | 161·507 (9) | 128·690 (11) |
| > 1000 | 1726·151 (12) | 227·718 (6) |

I wish to thank Dr R. Robb for his criticisms and to acknowledge the help of Mr R. Kerr and Mr C. Davidson in the experimental work.

## SUMMARY

The accuracy of volume estimation in filling a marked tank by means of a plankton pump has been determined. The method even in its simplest form is satisfactory under good conditions. Further refinements, in which the plankton was filtered off, after filling a modified tank (for example with an overflow device) would no doubt increase the accuracy.

A device is described by which, using an ex-N.F.S. pump, a constant (but variable by selection) volume of water can be taken without the use of large tanks.

A small number of sets of samples taken with adequate volume control indicate the same order of variability as net hauls. Comparison of the distribution of $\chi^2$ for paired samples with nets and pumps also indicates variation of a similar type.

These results suggest that the variability of net hauls is not entirely due to the variations in the volume of water filtered. Further work is in hand to elucidate this question.

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# AN APPARATUS FOR PRODUCING ARTIFICIAL TIDES

By Anwar Abdel Aleem, M.Sc., Ph.D.
(Farouk University, Alexandria)
From the Plymouth Laboratory

(Text-figs. 1–2)

It is often desired to grow animals and plants of the intertidal zone in the laboratory, under conditions as far as possible simulating those in nature and with the least trouble and expense. This need was felt by the writer during an ecological study of the diatoms inhabiting the mud-flats at Whitstable, Kent. It was found necessary to maintain such diatoms in the laboratory in London in a healthy condition for several days so as to study the effect of light and tides on their movements. The apparatus described in this paper was therefore devised. It has an advantage over other tidal systems (Bracher, 1919; Martin & Reid, 1935) in that the substratum could be automatically alternately flooded and drained at regular intervals by a much simpler mechanism. Besides, it is more handy and can be operated with only a small supply of sea water, a matter of some importance in localities remote from the sea.

It consists of a tidal chamber, *T*, and a reservoir, *R* (Fig. 1). The former is an inverted bell-jar fitted with a rubber bung through which passes a long glass tube, *g*, which extends to the base of the reservoir. At the upper end of the tube is a small funnel by which sea water enters the apparatus. A T-tube, *t*, serves to connect the tidal chamber and reservoir, its horizontal arm being connected to the siphon *S*.

The wide-mouthed bottle constituting the reservoir is fitted with a stopcock, *v*, which is useful for expelling air when setting up the apparatus.

The mud with the diatoms, *m*, is held in a container, *w*, of fine-meshed wire gauze covered with a few layers of muslin to prevent the mud from slipping through. The tube, *g*, passes through the centre of this container which rests on supports so that the upper surface of the mud is at a level about half-way up the bell-jar. The chamber *T* can be covered with a sheet of glass, and fitted with a thermometer, but this must of course not make an air-tight fit.

When in use, sea water is allowed to drip into the funnel from the jet of the constant delivery device shown in Fig. 2. This ensures that the rate of delivery shall be the same irrespective of the level of the water in the aspirator since the pressure head remains constant, being determined only by the height, *x* (Fig. 2). Any air-bubbles remaining after the reservoir has been filled are allowed to escape through the stopcock, *v*, which is then closed. The water now passes up the tube, *t*, simultaneously in the tidal chamber and the siphon-tube. When it reaches and covers the surface of the mud in the chamber a condition somewhat comparable with that of high tide is realized and persists until the water reaches the level *l*. The siphon then commences to discharge water from the tidal chamber much more rapidly than it flows in and this continues until the chamber and siphon are emptied. Water then rises again in the tidal chamber and the same succession of events is repeated. This will go on automatically for an indefinite period.

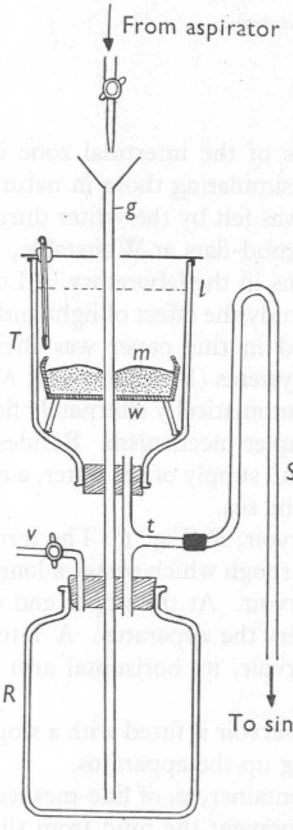

Fig. 1. Tidal apparatus (for description see text).

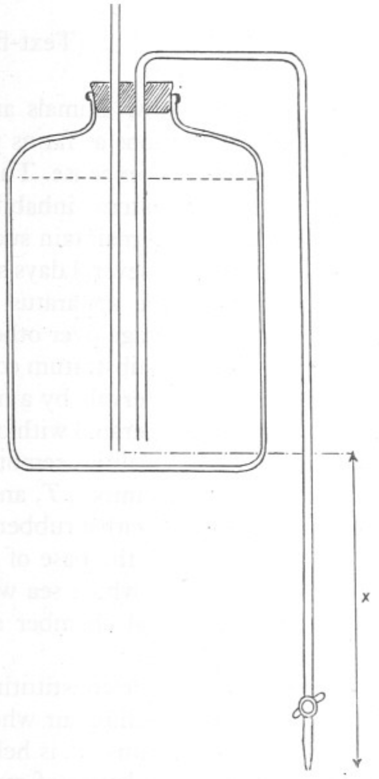

Fig. 2. Aspirator supplying the apparatus with a constant flow of sea water.

The rate of dripping, the position of the wire container holding the mud, the height of the level *l*, and the rate of discharge through the siphon can all be adjusted so that the mud surface is subjected to two periods of submergence and two periods of exposure in each 24 hr., with an interval of 6 hr. between successive phases. The bore of the siphon-tube is such that the discharge of water from the chamber occupies only a minute or so. The rate of supply can be adjusted by means of a tap so that longer or shorter periods of exposure or submergence of the mud can be obtained. Moreover, the effects of different factors on the movements of the diatom community can be compared by using several similar pieces of apparatus fed from a common supply of sea water.

The apparatus could be used for maintaining animals and plants of the intertidal zone in the laboratory or for studying the effects of exposure on the growth of algal germlings (*Fucus*, *Laminaria*, etc.). The mud would then be replaced by an appropriate substratum.

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# THE LAST LARVA AND POST-LARVA OF *TYPTON SPONGICOLA* FROM PLYMOUTH (CRUSTACEA DECAPODA)

By Marie V. Lebour, D.Sc.

From the Plymouth Laboratory

(Text-figs. 1–4)

The first larva of *Typton spongicola* was described in 1925 from the eggs carried by the parent (Lebour, 1925). No later stages are known; therefore it was interesting to find a last larva in the plankton from 2 miles north-east of the Eddystone (21 August 1946), which changed to the post-larva in the laboratory. There seems to be no doubt that the identification is correct although, surprisingly, the antennal scale, rudimentary in the adult, is still large. The agreement in colour of the last larva and post-larva with the newly hatched first larva, and the great similarity in the structure, in most ways, of post-larva and adult, makes it practically certain that we are dealing with *T. spongicola*.

A specimen of a post-larval *Typton*, almost certainly *T. tortugae*, was found in one of Dr Hilary Moore's hauls from Bermuda in 1940. This is much smaller than the Plymouth post-larva, but a good deal further advanced, having no antennal scale, and is interesting for comparison with *T. spongicola*.

## **Typton spongicola** Costa (Figs 1–3)

### *The Last Larva*

The last larva measured *c.* 4·8 mm. in length, but it is difficult to be exact because of the internally bent body, the abdominal hump coming up close to the head and the legs bent up parallel to the body, the antennules and antennae held straight out. This is distinctly of the *Mesocaris* type (see Gurney, 1938; Gurney & Lebour, 1941), with the body doubly flexed and legs 3–5 equal or sub-equal and not elongated. The colour is deep orange with red spots, most of the sixth abdominal somite, telson and uropods colourless, agreeing with the colour of the first larva. The animal makes sideway leaps in much the same way as do so many of the hump-backed larvae of similar form, so numerous in the Bermuda plankton. There are setose exopods on legs 1–4, but not on 5, leg 5 being very slightly longer than legs 2 and 3. This larva changed to the post-larva in the laboratory (26 August 1946), and the following description is taken from the cast skin. The rostrum is short and pointed with one spine dorsally. The carapace has a small supra-orbital spine and a short spine probably to be regarded as antennal, and there is a point at the outer anterior angle. The abdominal somites are rounded, the sixth being very long, longer than 2–5 combined, the uropods slightly pointed, the telson long with one pair of lateral spines and 8 terminal setae, the outermost the longest, the third from the outside next in length, the inner setae very short. The antennule has two short branches, a tooth on the outer margin of the base and a small tooth near the centre of the basal segment. The antenna has a short segmented flagellum and a well-developed scale. The mandible has a grinding and

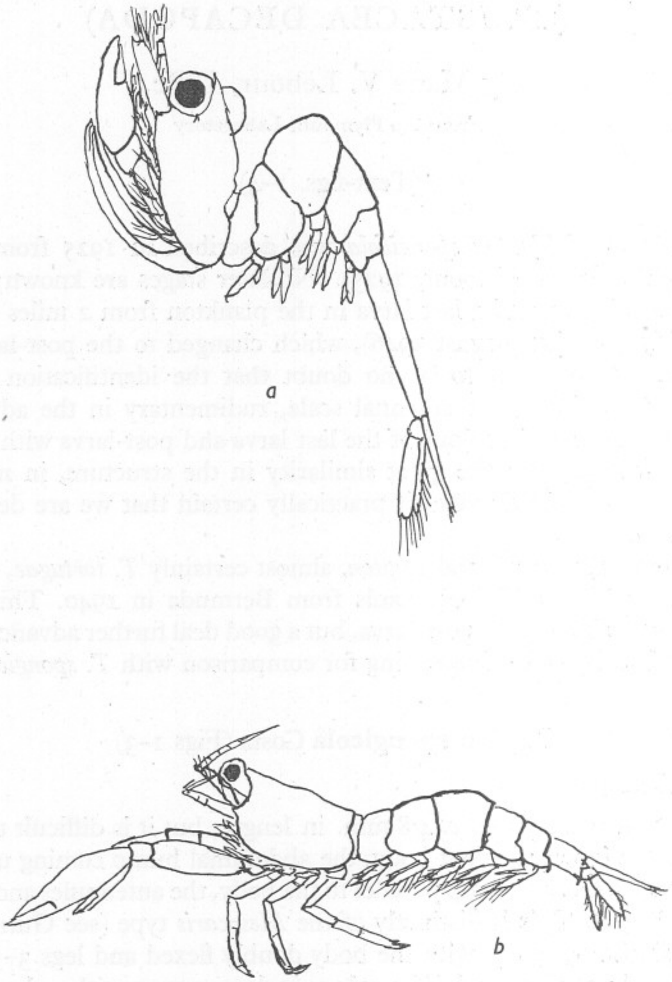

Fig. 1. *Typton spongicola*. Sketch from life of (*a*) the last larva, (*b*) the post-larva from last larva.

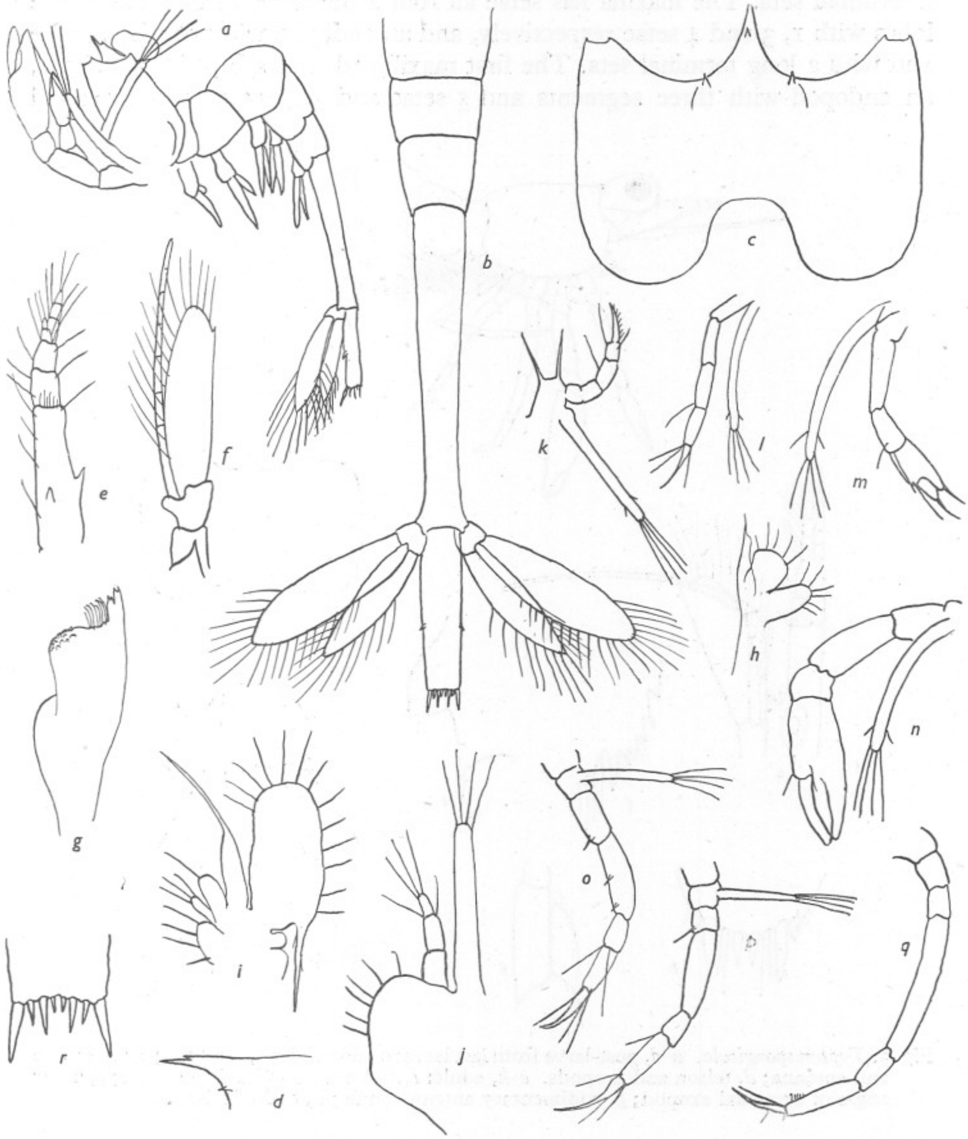

Fig. 2. Last larva of *Typton spongicola*: *a*, cast skin of body; *b*, abdomen and tail fan; *c*, carapace; *d*, rostrum; *e*, antennule; *f*, antenna; *g*, mandible; *h*, maxillule; *i*, maxilla; *j*, first maxillipede; *k*, second maxillipede; *l*, third maxillipede; *m*, first leg; *n*, second leg; *o*, third leg; *p*, fourth leg; *q*, fifth leg; *r*, end of telson.

cutting edge, the maxillule with two inner setose lobes and an endopod with a terminal seta. The maxilla has setae all round the exite, three inner setose lobes with 1, 3 and 4 setae respectively, and an endopod without a basal lobe and with a long terminal seta. The first maxillipede has a broad setose base, an endopod with three segments and 5 setae and an unsegmented exopod with 4 setae. The second maxillipede has a broad base with 2 strong setae, a 4-segmented endopod ending in a strong hook and an unsegmented exopod with 6 setae. This strongly resembles the second maxillipede in the first stage, as does also the third maxillipede, the endopod of which ends in a strong claw with stout setae at the base. The first leg has an exopod with 6 setae and a chelate endopod; the second leg is similar but longer with a larger chela;

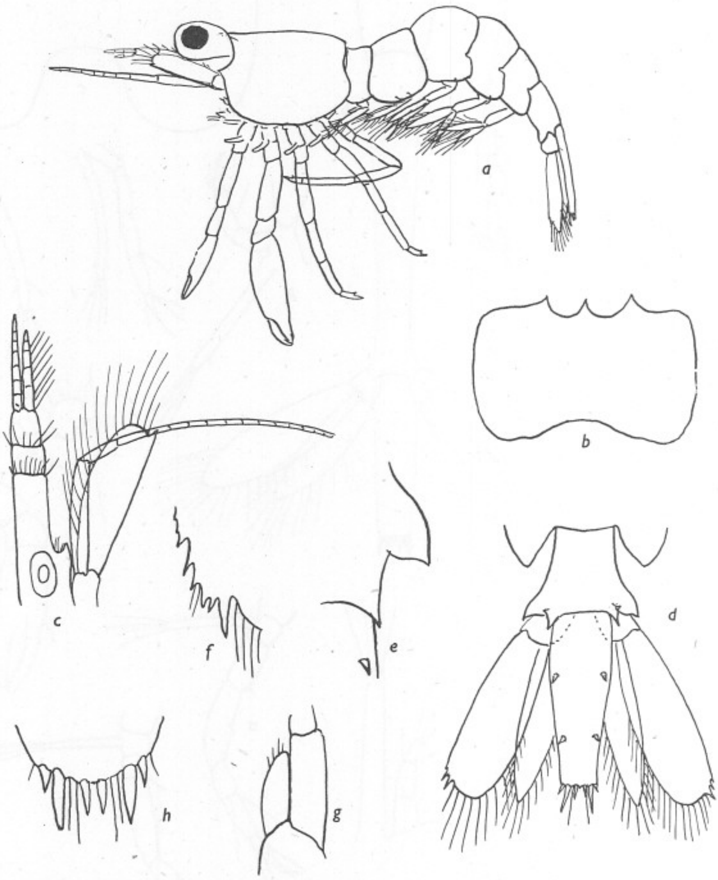

Fig. 3. *Typton spongicola*. *a–d*, post-larva from last larva: *a*, side view; *b*, carapace; *c*, antennule and antenna; *d*, telson and uropods. *e–h*, adult: *e*, end of last abdominal somite; *f*, outer angle of uropodal exopod; *g*, rudimentary antennal scale; *h*, end of telson.

the third and fourth legs are sub-equal with 4 setae on the exopod, the endopod ending in a long pointed dactyl; the fifth leg is slightly longer and without an exopod. There are no setae on the pleopods.

### *The Post-Larva*

The Post-larva from the last larva measures 3·8 mm. long and is no longer doubly flexed, but the abdomen is held out nearly straight with a slight dorsal hump (Fig. 1*b*). The colouring is much the same as in the last larva, but the orange extends on to most of the abdominal somites, the telson and uropods still being colourless. There is a short unarmed rostrum and an antennal spine, the other spines having disappeared. The antennule does not differ much from the last larva and there is still an antennal scale, although it is somewhat shorter, the breadth being greater compared with the length. The flagellum is about twice as long as the scale. The abdomen is similar in shape to that of the adult, the ends of somites 4 and 5 ending in rounded points. The sixth somite is very much shorter than in the last larva and bears two broad spines, each side posteriorly very much as in the adult. The telson is straighter and narrower than in the adult, but is similarly armed with two pairs of lateral spines and three pairs of stout spines at the end with a minute central tooth. There is also a pair of hairs in the post-larva and more in the adult between the spines. The outer angle of the uropodal exopod in the adult has a main spine and seven small spines outside it; these latter are represented in the post-larva by two spines outside the main one. Except for the continued presence of the antennal scale the post-larva agrees very well with the adult. The mouthparts were not examined. There are remains of exopods on legs 1–4, and the first and second legs are much the same as in the last larva, the second legs being about equal and not as in the adult of unequal length. Legs 3–5 end in short dactyls as in the adult. The second legs are held straight in front of the body in life and the antennules and antennae stick up in front with the flagella doubled back. It appears to be likely that the post-larva swims about before entering the sponge and perhaps undergoes several moults before entering a sedentary life. No young stages have so far been found in the sponge.

### **Typton tortugae** Smith (Fig. 4)

The post-larva was found in one of Dr Moore's Bermuda hauls in 1940. It is only 2·9 mm. in length, and there is no antennal scale, thus differing conspicuously from *T. spongicola*. The legs agree very well with Schmitt's figure and there seems to be no doubt that it belongs to this species. There are remains of exopods on legs 1 and 2 only, and not on legs 3–5. Gurney and Lebour (1941) have described a larva (*Mesocaris* A) from Bermuda which they suggest might belong to *T. tortugae*. This has exopods on legs 1–4, which seem to exclude it from this species whose larva is thus still to be found.

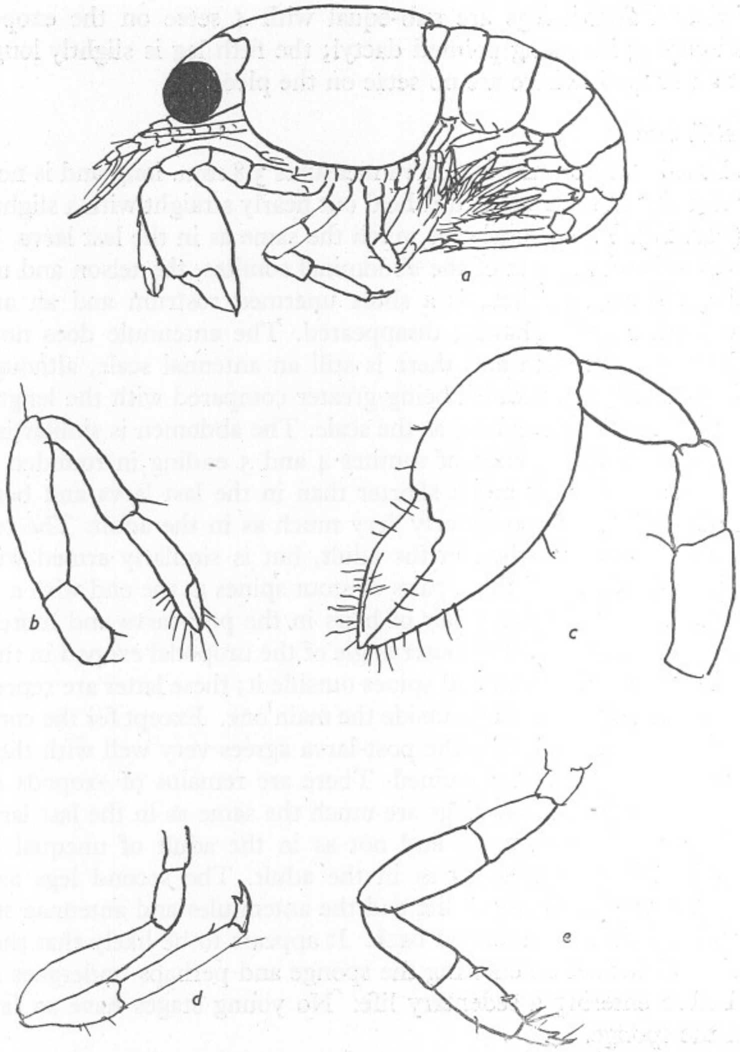

Fig. 4. *Typton tortugae*, post-larva: *a*, side view; *b–e*, legs 1–4.

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# CORRELATION OF SOME OF THE PHYSICAL AND CHEMICAL PROPERTIES OF THE SEA WITH THE CHEMICAL CONSTITUTION OF THE ALGAE

By W. A. P. Black, B.Sc., Ph.D., F.R.I.C.
and E. T. Dewar, B.Sc., Ph.D.
Scottish Seaweed Research Association, Musselburgh

(Text-figs. 1–14)

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## PART I. THE SEASONAL VARIATION IN TEMPERATURE, pH, SALINITY, DISSOLVED OXYGEN, PHOSPHATE, AND NITRATE IN THE INSHORE WATERS AT THREE POSITIONS ON THE ARGYLLSHIRE COAST

### Introduction

Although reliable data are available for the seasonal variation of the nutrient salts of surface off-shore waters in various parts of the world (Harvey, 1945, pp. 75–8, 85–6), information on inshore coastal waters is scanty. In North

America, however, extensive investigations have been carried out within the last 20 years on the coastal waters bordering on the states of Washington and British Columbia. These waters are cut off from the Pacific Ocean by Vancouver Island, and thereby possess certain characteristic properties. Hutchinson, Lucas & McPhail (1929) have described the seasonal variations in the waters of the Strait of Georgia. The phosphate figures are much higher than in the open sea, and these authors attribute the high nutrient content to the inflow of water from the Fraser River.

The waters of Puget Sound are also particularly rich in phosphates, nitrates and silicates. Thompson & Robinson (1933) believe this to be due to upwelling off the entrance to Juan de Fuca Strait and to vigorous mixing and agitation of the waters. Phifer & Thompson (1937) give the results of 5 years' study of the inshore conditions at Friday Harbour, on the San Juan Channel. In general, the nitrate and phosphate figures are about four times higher than those reported in our waters, and they are not subject to the same marked seasonal variation, while dissolved oxygen saturations rarely exceed 80 %. In this channel strong tidal currents throughout the year create turbulent conditions, which are responsible for the high nutrient and low oxygen contents of these waters.

Newcombe, Horne & Shepherd (1939) have studied the waters of Chesapeake Bay, in the region of Solomons Island, Maryland, U.S.A., during the period 1936–38. Conditions in Chesapeake Bay, however, are typically 'estuarine', surface chlorinities being low (5·8–10·2 ‰) and summer temperatures high (25° C.). The phosphate content of the Bay waters in summer commonly ranges about $0{\cdot}23 \times 10^{-3}$ mg. atom P/l. at the surface, while the river waters may contain $1{\cdot}0 \times 10^{-3}$ mg. atom P/l. Minimum concentrations are obtained during the winter period, when the abundance of phytoplankton organisms is maximum. Estuarine waters are rich in ammonium and silicate.

Marshall & Orr (1927) obtained a close relation between the growth of diatoms and chemical changes in the Clyde Sea Area in 1924, 1925 and 1926 and again in 1927 and 1928 (1930). In 1926 the seasonal variation in temperature, density, pH, salinity, dissolved oxygen and phosphate were determined for two points in Loch Striven. The two localities visited were Clapochlar (depth *c.* 60 m.) and Loch Striven head (depth *c.* 28 m.), and samples were taken at 0, 10, 20, 40 and 60 m. at weekly intervals from the end of January till the end of November. Loch Striven is not polluted to any extent by the Clyde, although the surface water is often affected by drainage from the hills, which give rise to erratic salinity values.

No other work, at least to the writers' knowledge, appears to have been carried out on the seasonal variation in the nutrient content of the Scottish inshore waters, and it seemed possible that lack of nutrients during the summer months might influence the growth of algae.

This investigation was undertaken, therefore, in order to determine the seasonal variation in the nutrient content of our sea water and to ascertain if any correlation existed between the composition of the sea water, in particular, nitrate, and that of the algae growing in it.

## LOCATION AND METHODS OF SAMPLING

The three positions selected were Eilean Coltair (at the entrance to Loch Melfort), Rudh-an-Aoil (Shuna Island) and Cullipool (Luing Island). Eilean Coltair is the most sheltered of the three positions, being situated in a loch with the water cut off to a certain extent. Shuna Island is more exposed, with strong tidal currents running, but it is protected from the open sea by the Island of Luing. Cullipool, situated on the north-west coast of Luing Island, is open to the Atlantic and is the most exposed position.

The upper waters pass in general direction from the Irish Sea, through the North Channel and up the west coast of Scotland, through the Minch and round the north coast to the Orkney region. The water at the three positions selected can therefore be regarded as typical coastal inshore water, practically free from oceanic water.

Samples from the three localities were taken monthly for 13 months from March 1948 to March 1949 by means of a Nansen-Pettersson water bottle at a depth of 4–5 m. (low water), just above the weed bed. Temperatures were recorded with a reversing thermometer and the transparency of the waters measured with a standard Secchi disk.

The samples of water, carefully protected from light, were transported to Inveresk Gate and the chemical analysis carried out within 24 hr.

## EXPERIMENTS AND RESULTS

The usual methods for the various determinations were utilized, and the results are summarized in Tables I and II and Figs. 1–6.

The pH was measured with the Marconi pH meter, and the observed readings corrected for the rise in temperature since sampling. The pH values for the three localities are given in Table I but, because of the relative constancy for any given month during the period, only the Shuna Island figures are reproduced in Fig. 5. Dissolved oxygen was estimated only in the Shuna Island waters and the results are given in Table II and Fig. 3.

Nitrate was determined by the diphenylbenzidine method of Atkins (1932), which was modified slightly, as outlined below, to allow the colour intensities to be measured by the Spekker Photoelectric Absorptiometer. The intensity of the blue colour which develops does not bear a linear relationship to the nitrate content, but the graph of colour intensity plotted against nitrate concentration gives a smooth curve. The slope of this curve increases with increased nitrate content, so that the higher nitrate figures are more accurate than the lower figures. The accuracy of the method, however, increases from

TABLE I. SEASONAL VARIATION IN TEMPERATURE, pH AND TRANSPARENCY

| Month | Temperature (°C.) | | | pH *in situ* | | | Secchi disk (m.) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Eilean Coltair | Shuna Island | Culli-pool | Eilean Coltair | Shuna Island | Culli-pool | Eilean Coltair | Shuna Island | Culli-pool |
| 1948 | | | | | | | | | |
| March | 7·5 | 7·5 | — | 8·03 | 7·96 | — | — | — | — |
| April | 8·2 | 8·1 | 7·8 | 8·09 | 8·11 | 8·11 | 9 | 9 | 5 |
| May | 9·8 | 9·8 | 9·0 | 8·17 | 8·13 | 8·10 | 7 | 7 | 9 |
| June | 12·4 | 11·1 | 10·6 | 8·13 | 8·13 | 8·10 | 7 | 8 | 9 |
| July | 12·2 | 12·3 | 11·7 | 8·11 | 8·12 | 8·11 | 9 | 7 | 5 |
| August | 13·0 | 13·0 | 12·7 | 7·91 | 7·95 | 7·96 | 9 | 9 | 7 |
| September | 12·5 | 11·9 | 12·2 | 7·86 | 7·91 | 7·90 | 7 | 9 | 7 |
| October | 12·2 | 11·9 | 12·1 | 8·01 | 8·06 | 8·06 | 7 | 6 | 5 |
| November | 10·5 | 10·9 | 11·0 | 8·01 | 8·04 | 8·06 | 5 | 7 | 7 |
| December | 9·7 | 10·0 | 10·2 | 7·96 | 8·02 | 8·05 | 8 | 7 | 7 |
| 1949 | | | | | | | | | |
| January | 6·5 | 7·0 | 8·1 | 8·04 | 8·07 | 8·07 | 7 | 7 | 7 |
| February | 7·8 | 7·7 | 8·0 | 8·01 | 8·03 | 8·05 | 7 | 7 | 5 |
| March | 6·1 | 6·9 | 6·9 | 8·04 | 8·05 | 8·07 | 7 | 7 | 7 |

TABLE II. SEASONAL VARIATION IN SALINITY, OXYGEN, PHOSPHATE AND NITRATE

| Month | Salinity (g./kg.) | | | Oxygen. Shuna Island | | Phosphate (mg. atoms P/m.$^3$) | | | Nitrate (mg. atoms N/m.$^3$) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Eilean Coltair | Shuna Island | Culli-pool | ml./l. at N.T.P. | % saturation | Eilean Coltair | Shuna Island | Culli-pool | Eilean Coltair | Shuna Island | Culli-pool |
| 1948 | | | | | | | | | | | |
| March | 34·05 | 34·12 | — | — | — | 0·55 | 0·55 | — | 6·4 | 6·1 | — |
| April | 33·56 | 33·81 | 33·94 | 6·24 | 93·5 | 0·35 | 0·52 | 0·41 | 0·7 | 3·1 | 5·0 |
| May | 33·78 | 33·86 | 34·02 | 6·14 | 95·4 | 0·19 | 0·26 | 0·33 | 1·0 | 2·6 | 4·6 |
| June | 33·90 | 33·93 | 33·93 | 5·94 | 94·9 | 0·16 | 0·20 | 0·18 | 1·4 | 2·4 | 1·6 |
| July | 33·83 | 33·72 | 33·92 | 6·02 | 98·2 | 0·16 | 0·16 | 0·20 | 0 | 0 | 0·9 |
| August | 34·01 | 34·02 | 34·05 | 5·73 | 94·9 | 0·19 | 0·19 | 0·20 | 0·5 | 1·0 | 1·5 |
| September | 33·61 | 33·06 | 33·76 | 5·83 | 93·9 | 0·30 | 0·23 | 0·30 | 3·0 | 3·1 | 4·9 |
| October | 33·63 | 33·57 | 33·65 | 5·71 | 92·4 | 0·37 | 0·31 | 0·31 | 5·0 | 5·4 | 4·8 |
| November | 33·34 | 33·67 | 33·83 | 5·86 | 93·0 | 0·40 | 0·50 | 0·42 | 4·9 | 5·6 | 5·7 |
| December | 33·16 | 33·59 | 33·83 | 5·85 | 90·4 | 0·75 | 0·65 | 0·50 | 5·5 | 6·1 | 5·7 |
| 1949 | | | | | | | | | | | |
| January | 32·92 | 33·26 | 33·44 | 6·41 | 92·8 | 0·57 | 0·53 | 0·53 | 6·3 | 6·5 | 6·9 |
| February | 33·45 | 33·62 | 33·56 | 6·40 | 94·3 | 0·51 | 0·53 | 0·53 | 6·5 | 6·7 | 6·5 |
| March | 33·62 | 33·83 | 34·03 | 7·00 | 101·5 | 0·48 | 0·53 | 0·52 | 5·5 | 5·8 | 5·9 |

± 10 mg. at 0–30 mg. nitrate – N/m.$^3$ to ± 4 mg. at 90 mg. N/m.$^3$. This method cannot compete with Harvey's strychnidine method at low nitrate concentrations, for the latter gives a linear relation between colour intensity and nitrate content. It was not used, however, in these investigations, because of the difficulty of preparing a satisfactory reagent.

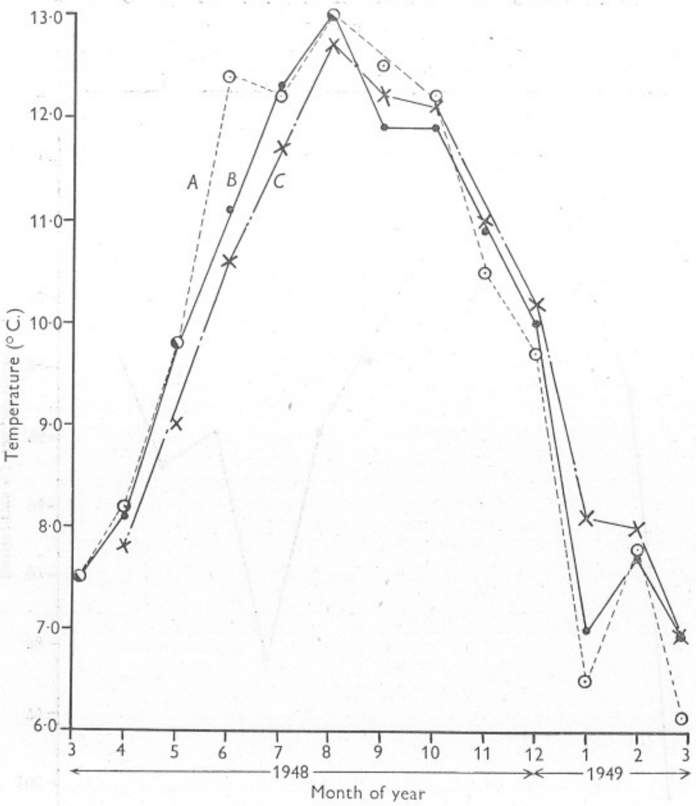


Fig. 1. Seasonal variation in temperature. (*A*) L. Melfort; (*B*) Shuna Island; (*C*) Cullipool.

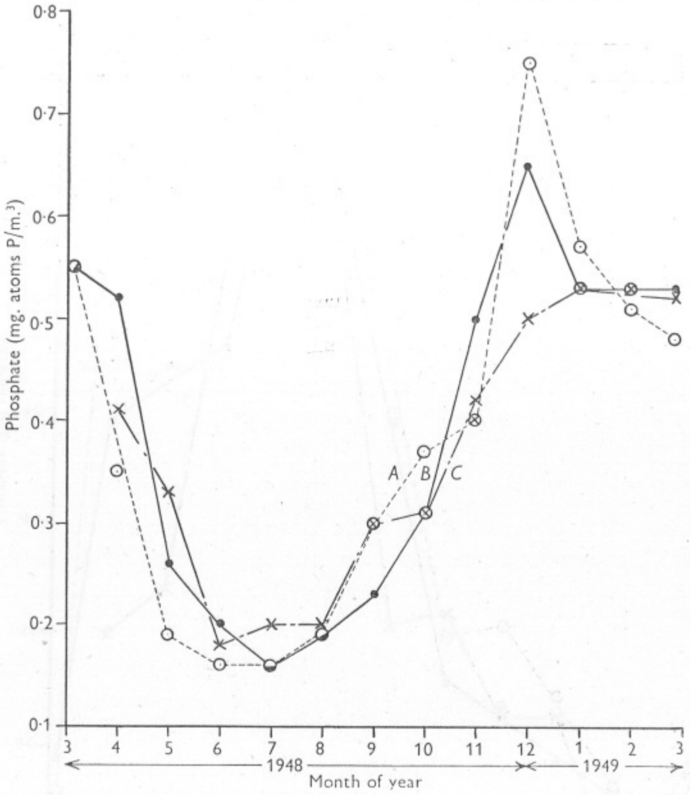


Fig. 2. Seasonal variation in phosphate. (*A*) L. Melfort; (*B*) Shuna Island; (*C*) Cullipool.

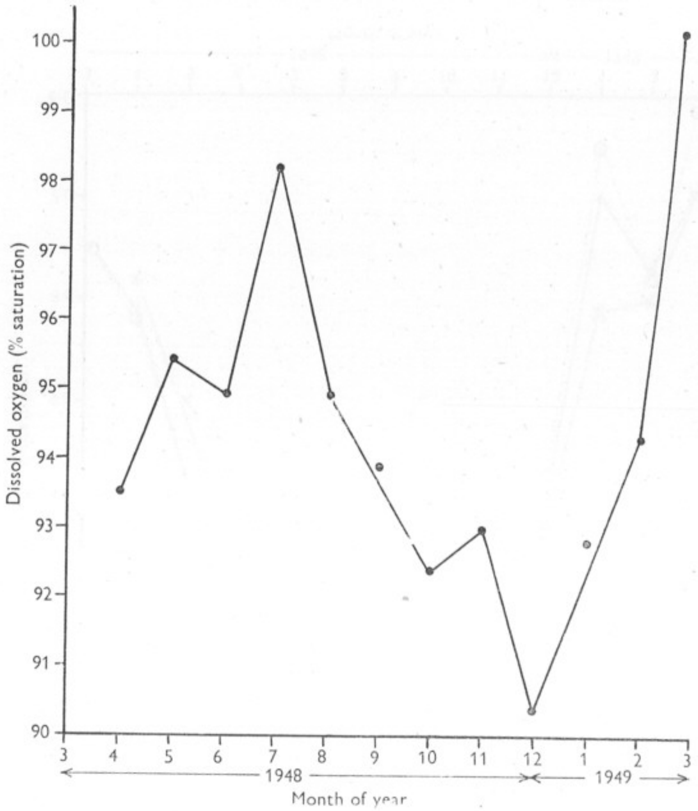


Fig. 3. Seasonal variation in dissolved oxygen. Shuna Island.

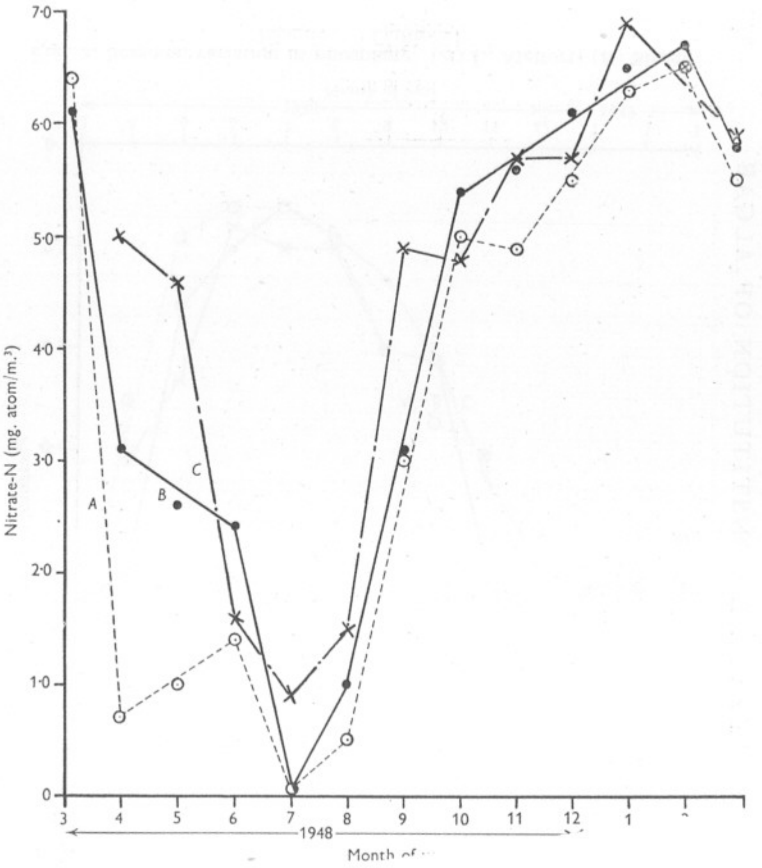


Fig. 4. Seasonal

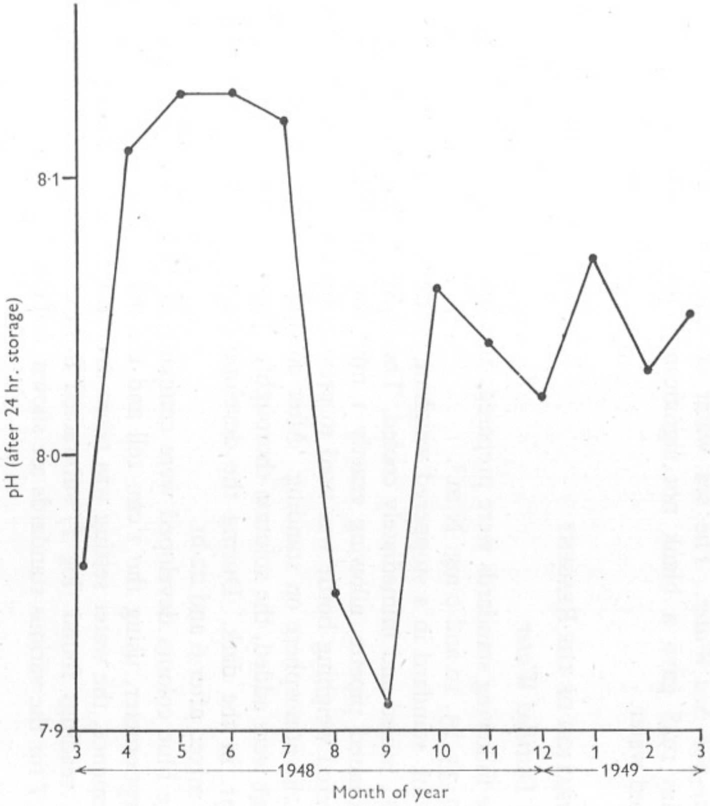


Fig. 5. Seasonal variation in pH. Shuna Island.

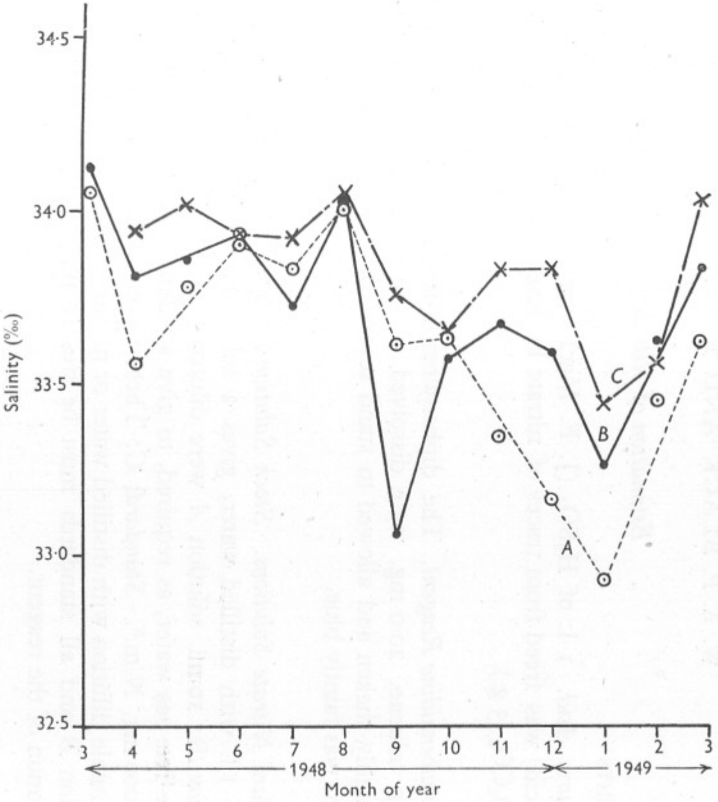


Fig. 6. Seasonal variation in salinity. (*A*) L. Melfort; (*B*) Shuna Island; (*C*) Cullipool.

### *Estimation of Nitrate*

REAGENTS

*Sulphuric Acid.* 1 l. of $H_2SO_4$ (J. F. MacFarlan and Co's special nitrate free acid) was freed from traces of nitrate by heating at 300° for 2 hr. with $(NH_4)_2CO_3$ (3 g.).

*Diphenylbenzidine Reagent.* The diphenylbenzidine was recrystallized from boiling toluene. 20·0 mg. were dissolved in 100 ml. $H_2SO_4$, the solution thoroughly shaken and allowed to stand several days before use. The final reagent was faintly blue.

*Standard Nitrate Solutions. Stock Solution A:* 0·7218 g. A.R. $KNO_3$, made up to 1 l. with distilled water, gives a solution containing 0·1 g. N/litre. *Solution B:* 10 ml. solution *A* were diluted to 1 l. with distilled water or nitrate-free sea water, as required, to give a solution containing 1 mg. N/l, i.e. 1000 mg. N/m.$^3$. *Standards C:* These were prepared from solution *B* by suitable dilution with distilled water or nitrate-free sea water as required. Solution *B* and all standards must be freshly prepared each day during calibration of the reagent.

*Nitrate-free Sea Water.* The sea water collected from Eilean Coltair on 11 May 1948 gave a blank not significantly greater than that given by distilled water.

CALIBRATION OF THE REAGENT

(1) *In Distilled Water*

The following standards were prepared: 100, 95, 90, 80, 75, 70, 60, 55, 50, 45, 40, 35, 25, 10 and 0 mg. N/m.$^3$.

2·5 ml. standard in a stoppered weighing bottle were treated with 6·0 ml. $H_2SO_4$, mixed and immediately cooled. The $H_2SO_4$ was added by means of a graduated pipette, allowing exactly 1 min. for delivery in each case. A stoppered weighing bottle was used to prevent the solution taking up water from the atmosphere on standing. After cooling, 1·5 ml. diphenylbenzidine reagent were added, the solution thoroughly mixed, and allowed to stand for 22·5 hr. in the dark. During the development period, the solutions were again mixed after 6 and 22 hr.

The blue colours developed were compared in the Spekker Photoelectric Absorptiometer, using the 1 cm. cell and the orange Ilford 607 filter. For convenience, the water setting was taken as 0·70 on the drum scale, and the drum readings found (log $I$) subtracted from 0·70 (log $I_0$). The values of log $I_0/I$ for the various standards are shown in Table III.

TABLE III

| Distilled water | | Distilled water | | Sea water | | 50% (v/v) sea water | |
|---|---|---|---|---|---|---|---|
| Standard | log $I_o/I$ | Standard | log $I_o/I$ | Standard | log $I_o/I$ | Standard | log $I_o/I$ |
| 100 | 0·523 | 50 | 0·203 | 100 | 0·331 | 100 | 0·468 |
| 95 | 0·485 | 45 | 0·177 | 75 | 0·211 | 75 | 0·295 |
| 90 | 0·456 | 40 | 0·162 | 50 | 0·136 | 50 | 0·161 |
| 80 | 0·413 | 35 | 0·141 | 25 | 0·080 | 25 | 0·088 |
| 75 | 0·329 | 25 | 0·080 | 10 | 0·050 | 10 | 0·048 |
| 70 | 0·324 | 10 | 0·042 | 0 | 0·035 | 0 | 0·032 |
| 60 | 0·238 | 0 | 0·030 | | | | |
| 55 | 0·239 | | | | | | |

There is not a linear relationship between colour intensity (log $I_0/I$) and nitrate concentration, but the graph gives a smooth curve.

(2) *In Sea Water*

In order to determine the salt error, a calibration curve was carried out using nitrate-free sea water in the preparation of the standards. The results, shown in Table III, indicate that the salts in sea water decrease the colour formation, when the colour is measured after 22·5 hr.

(3) *In* 50°/₀ *(v/v) Sea Water*

Solution *B* was made up in distilled water. The standards were prepared by taking the appropriate amount of *B*, adding 50 ml. nitrate-free sea water and making up to 100 ml. with distilled water. The results in Table III show that the colour intensities lie, for the most part, between the distilled water and sea-water values.

### ESTIMATION OF NITRATE IN SEA-WATER SAMPLES

2·5 ml. of the unknown sample were treated with $H_2SO_4$ and diphenylbenzidine exactly as described in the calibration of the reagent, and the value of log $I_0/I$ determined after 22·5 hr. The nitrate content of the sample in mg. nitrate-N/m.$^3$ was read off from the sea-water calibration curve.

### ACCURACY OF THE METHOD

It was found that the value of log $I_0/I$ for any given standard could, in general, be reproduced within ± 0·02. From the sea-water calibration curve, the accuracy at various concentrations has been estimated as follows:

| Nitrate concentration | Maximum error |
|---|---|
| 30 mg. N/m.$^3$ | ± 10 mg. N/m.$^3$ |
| 40 | ± 8·5 |
| 50 | ± 7·5 |
| 60 | ± 7·0 |
| 70 | ± 5·5 |
| 80 | ± 4·5 |
| 90 | ± 4·0 |

## *Estimation of Phosphate*

Phosphate was estimated by the Denigés method, as described by Wattenberg (1937).

## DISCUSSION OF RESULTS

### *Temperature*

In the spring, temperatures are at a minimum, 6–7° C. (Table I and Fig. 1). The loch water at Eilean Coltair gets warmer more rapidly than the open sea, reaching a temperature of over 12° C. by June. At Cullipool the surface waters take considerably longer to heat up, 12° C. only being reached in August. For Shuna Island, in general, the graph lies between the other two.

The opposite state of affairs prevails during the autumn and winter months. Cullipool maintains a temperature of 8° C. or more until February, while the loch water has dropped to 6·5° C. by January. One would expect loch water, because of its proximity to, and isolation by, land, to warm up and cool down more rapidly than the open sea. It is interesting to note that the maximum and minimum temperatures for the three positions do not vary appreciably, although the times required to reach these values do.

Marshall & Orr (1927) found the temperature of the surface waters (0–10 m.) at Clapochlar to be at a minimum (6° C.) in January/February, rising to a maximum of 14° C. in August.

### *pH*

The pH was measured 24 hr. after sampling. The effect of storage is to lower the pH for the following reasons: (1) On standing, the water warms up to that of its surroundings, and the pH falls with rising temperature. The pH *in situ*, however, can be calculated from the pH at temperature of observation by allowing for the temperature coefficient of sea water. In most cases, the decrease in pH per 1° C. rise can be taken as 0·01 pH unit. (2) Bacteria liberate carbon dioxide in respiration, and this lowers the pH. This effect cannot be corrected for, and may be appreciable during warm weather. Although care was taken to keep the temperature of the samples as low as possible during transport, the results may be slightly low.

In April a rapid increase in pH occurs, indicating that plant growth is beginning to utilize carbon dioxide at a greater rate. From April to July the pH values for all positions are 8·10 or greater, but in August and September figures of 7·86–7·96 indicate a slowing up in the rate of photosynthesis which coincides with a low nutrient content of the water. An increase in pH occurs in October, and from October to March fairly constant values of 8·00 ± 0·07 are obtained.

The pH of the surface water at Clapochlar (Marshall & Orr, 1927) was close to 8·0 during the early part of the year. This was followed by a sudden increase at the beginning of April following the spring diatom outburst, and figures of 8·3–8·4 are recorded during this period. Another peak in the pH graph was obtained in September due to the autumn phytoplankton growth.

*Transparency*

It was hoped, by means of a Secchi disk, to detect the phytoplankton outburst in the spring, but in practice very little variation was observed throughout the year. Maxima of 7–9 m. and minima of 5–6 m. are recorded, but these do not occur at any specific time and appear to have no significance.

*Salinity*

In ocean water away from the influence of land, variations in surface salinity are not great. Böhnecke (1938) has shown for an area of the North Atlantic Ocean, extending between latitudes 18° and 42° N., that the highest average surface salinity, 36·70 ‰, occurs in March and the lowest, 36·59 ‰, in November. The variations from one month to another are irregular, but on the whole the salinity is somewhat higher in spring than it is in autumn. In the open ocean variations in surface salinity depend mainly upon variations in the difference between evaporation and precipitation, in association also with currents. In inshore waters salinity values are complicated by the influence of land, which gives rise to coastal currents and dilution due to rivers and land drainage. For example, when heavy rain falls during the winter the increased volume of waters discharged by the rivers of the region will tend to decrease the salinities during the winter months. If, however, the precipitation is in the form of snow, the effect upon the salinity of the coastal waters may not be experienced until the summer.

The high salinity values obtained in this investigation, particularly for Cullipool, indicate that these waters have not been diluted by fresh water to any great extent, and the figures bear some relation to the rainfall for the 13 months. For all positions, highest values were obtained in March and August, and lowest values in January. In September an abnormally low figure, 33·06 ‰, was reported for Shuna Island. In general, the salinity of Cullipool water is higher than the loch water, and this is to be expected because land drainage after heavy rain will affect loch more than open sea water. Again, the graph for Shuna Island lies between the other two for most months of the year, although there are some exceptions.

Marshall & Orr (1927) found the salinity of the surface layer at Clapochlar lay between 33 and 34 ‰, although some values for the immediate surface layer were much lower, for example, some very low figures are recorded during March and October/November.

*Oxygen*

With the exception of March 1949, the samples were treated with the reagents, manganous chloride and sodium hydroxide-potassium iodide, about 24 hr. after sampling. In March 1949, the reagents were added immediately after sampling, and the iodine liberated and titrated the following day. This water was found to be slightly supersaturated (% saturation, 101·5). Thus it may be assumed that all the results, except the last, are low to the extent of 5–10%. Nevertheless, the relative values are of interest in detecting the period of photosynthesis in the spring. The explanation for these low results is twofold: (1) on standing, the water warms up to that of its surroundings, and a certain amount of oxygen tends to be expelled from solution at the higher temperature; and (2) when sea water is stored, bacteria rapidly consume oxygen in respiration, the amount utilized being quite appreciable even after 24 hr. Moreover, bacteria are particularly abundant in inshore water.

The highest saturations are obtained during the spring and summer months, the maximum (98·2%) being reached in July, which is further evidence of photosynthesis during these months. Saturations then decrease steadily to a minimum of 90·4% in December. Because of the uncertainty of these results, further discussion would be unwise, but it appears that this water is saturated, or very nearly saturated, for the greater part of the year, and probably slightly supersaturated during the period of photosynthesis.

Marshall & Orr (1927) found the dissolved oxygen saturations for the surface layers were close to 100% throughout the year, except during the diatom outbursts in the spring and autumn when values up to 138% were occasionally recorded.

### *Phosphate*

The phosphate estimations were carried out one day after sampling, the water being centrifuged before analysis if any turbidity was noticed. It is advisable, however, to estimate phosphate immediately after sampling, or to saturate the water with chloroform if estimations are to be carried out at a later date. On standing, the inorganic phosphate may increase slightly if much organic phosphorus is present, or it may decrease due to utilization by bacteria, but this error will not be great after only 24 hr., provided the temperature of the water is prevented from rising appreciably.

Fig. 2 indicates that the phosphate content begins to decrease after March, the decrease being most marked in the loch water, although the open sea at Cullipool has a phosphate content in April not much greater than the loch. Minimum values of 0·16–0·20 mg. atom phosphate-P/m.$^3$ are obtained in all localities by June, and remain at this low level until September, when there is an increase again to the winter maximum in December, January and February. Abnormally high values were obtained in December for Eilean Coltair (0·75 mg. atom P/m.$^3$) and Shuna Island (0·65 mg. atom P/m.$^3$), which can only be attributed to contamination by land drainage, as the value for Cullipool was normal.

The winter maximum for 1949 of 0·52 mg. atom P/m.$^3$ is in good agreement with the values quoted for the English Channel, although the summer minimum tends to be higher than that found in the Channel.

The seasonal variation in phosphate at a position in the English Channel has been followed at monthly intervals for a number of years. From winter maximum values varying between 0·69 and 0·47 mg. atom P/m.$^3$ it has fallen in some years to less than 0·02 in the surface layers, in other years 0·06 or 0·10 mg. atom remain (Atkins, 1923–30; Cooper, 1933*a*, *b*, 1938). The winter maximum values of phosphate in the water at the beginning of the year are not constant but fluctuate from year to year. Cooper (1938) has found lower winter maxima during the 1930's as compared with the 1920's, and these have been reflected in decreased plankton and fish populations (Russell, 1935, 1936*a*, *b*).

During February at Clapochlar (Marshall & Orr, 1927), phosphate in the surface layer was about 0·65 mg. atom P/m.$^3$. Within a few weeks, at the end of March and beginning of April, phosphate was reduced to 0·16 mg. atom P/m.$^3$, while by the end of May no trace of phosphate existed in the surface layer. Small quantities appeared in the waters at odd periods throughout the summer, but no full-scale regeneration of phosphate became apparent until the end of September. Maximum winter values were obtained by November.

### *Nitrate*

The estimations were carried out 1 day after sampling. The effect on the nitrate content of storing samples for 24 hr. is negligible, provided the samples are shielded from light. Fig. 4 shows that the seasonal variation of nitrate follows closely that of phosphate. After March nitrate begins to decrease, and again this decrease is most marked in the loch. Between March and April 1948 nitrate-N in Loch Melfort dropped from 6·4 mg. atoms/m.$^3$ to almost zero, and remained at this level until September. Complete exhaustion of nitrate was not observed at Shuna Island and Cullipool until July. Nitrate is almost certainly absent in all localities during July and August. As in the case of phosphate, nitrate is regenerated during September and increases gradually during the autumn and winter, reaching a maximum of about 6·8 mg. atoms N/m.$^3$ in January. Little or no evidence was obtained of the plankton outburst in the autumn, either from the phosphate or nitrate records.

The seasonal variation in nitrate has been followed during the course of several years in the English Channel (Harvey, 1926, 1928; Cooper, 1933*a*). Exhaustion of nitrate due to utilization by phytoplankton is frequently found in the surface water during the summer, while winter maxima may exceed 7 mg. atoms nitrate-N/m.$^3$. The absence of nitrate, however, does not necessarily mean that plant production in the sea is reduced to a low level, as nitrogen may still be available as ammonium, the concentration of which may reach 2 mg. atoms ammonium-N/m.$^3$ during the autumn and winter months. Harvey (1940) has shown that plankton diatoms utilize ammonium in preference to nitrate. This may explain why the autumn plankton outburst was not detected by following the seasonal variation in nitrate (Fig. 4), although the flattening of the graph from September to December might be taken as an indication of its utilization by plankton. In the spring, nearly all the available nitrogen is present as nitrate.

### *The Nitrogen/Phosphorus Ratio at the Winter Maximum*

If 0·52 mg. atom P/m.$^3$ and 6·8 mg. atoms N/m.$^3$ are taken as the winter maximum values for phosphate and nitrate respectively in 1949, the N/P ratio is 13·2.

The significance of these results on the growth of the adjacent seaweeds is discussed in Part II.

## SUMMARY

Monthly samples of sea water, taken from three localities on the Argyllshire coast, from March 1948 to March 1949, have been analysed for pH, dissolved oxygen, salinity, nitrate and phosphate, while temperatures and transparencies have been recorded.

Surface temperatures range from 6–7° C. in January/March to 13° in August. Transparencies remain fairly constant at 7–9 m. throughout the whole period, with occasional minimum values of 5–6 m.

pH values close to 8·0 are obtained from October to March, followed by an increase to 8·1 or over during the period of photosynthesis (April to July). Low pH values (7·86–7·96) are recorded during August and September.

Salinities vary over the narrow range, 33–34 $^0/_{00}$, with maxima in March and August and minima in January. These high salinities indicate that the inflow of fresh water from streams in the neighbourhood is negligible, even for Loch Melfort.

Dissolved oxygen saturations are highest in the spring and summer months and lowest in December.

Phosphate and nitrate begin to decrease after March, the reduction being most marked in the loch, and remain at a low level until September, when these nutrients are again regenerated. Winter maximum values of 0·52 mg. atom P/m.$^3$ and 6·8 mg. atoms nitrate-N/m.$^3$ are obtained by January.

Atkins's diphenylbenzidine method has been used to estimate nitrate, and a description of the method is given.

# PART II. CORRELATION OF THE COMPOSITION OF SEA WATER WITH THE CHEMICAL CONSTITUTION OF THE ALGAE

## INTRODUCTION

The larger algae, like most other forms of marine plant life are, apart from the influence of light, wholly dependent for their growth and development on the nutrient content of the surrounding sea water.

Although there is no experimental evidence to show that the growth rate of sea-weeds in the sea is ever brought to a standstill through lack of nutrients, Harvey's work (1926) indicated that lack of nitrate can limit plant growth. He also showed (1933) that a marked reduction in the rate of photosynthesis for the diatom *Nitzschia closterium* occurred with phosphate concentrations below 0·32 mg. atom P/m.$^3$, being most marked below 0·16 mg. atom P/m.$^3$. There appears to be no doubt that nitrate and phosphate are most important factors in the productivity of the sea, and plankton, at least, is richer where vertical currents aid in increasing their concentration. Whereas Harvey (1926, 1928) has recorded marked seasonal variations in the nitrate-content in the English Channel with non-detectable amounts in August, Dakin (1934) showed that at Sydney there was a much more uniform distribution throughout the year. It would appear, therefore, that marked seasonal variations in the nutrient content, with depletion of nitrate in the summer, occur mainly in inshore waters where a thermocline is set up during the summer preventing regeneration of the nutrients in the photosynthetic layer.

Marshall & Orr (1948), in carrying out experiments in Loch Craiglin on the effect of different plant nutrients on the phytoplankton, found that after adding a large excess of fertilizer a good increase in plankton was obtained, after an initial lag. At that time attached algae were abundant and these investigators believed that the needs of the algae had to be satisfied before any nutrients could be used by phytoplankton.

With marine diatoms, therefore, scientific investigations have established a direct correlation between their efflorescence and abundance, and the concentrations of nutrient salts, especially nitrates and phosphates, in sea water, and scientific literature pertaining to European, American, Antarctic and other waters furnishes numerous examples.

Parke (1948), in her studies on the British Laminariaceae, found for *Laminaria saccharina* that there were two periods of growth, a period of rapid growth between January and June/July with the most rapid growth between March and June, and a period of slow growth from July to December, but unfortunately no attempt was made to correlate this with the nutrient content of the water.

Tikhovskaya (1940) investigated the seasonal variations in the productivity and photosynthesis of *L. saccharina* in the Barents Sea. He reported maximum growth in April with a sharp drop in June and a slight increase in October, and stated, although no figures are given, that in summer the N and P content was the smallest for the whole year.

In view of the fact that in Norway, it has been possible to correlate the presence of herring with water of a particular temperature and salinity, it was thought that, since correlation appeared to exist between the chemical composition of the algae and the physico-chemical properties of the water, it might be possible from an analysis of the water to forecast the optimum annual harvesting periods. No previous investigator, however, appears even to have attempted to correlate the seasonal changes in the chemical composition of the fixed algae with changes in the composition of the sea water.

## PREPARATION AND ANALYSIS OF SAMPLES

Monthly samples comprising six plants of the following species of Laminariaceae were taken, two were used for dry weight determinations, and two were analysed by the methods previously employed (Black, 1948).

The inorganic nitrogen was obtained by difference, i.e. by subtracting the organic nitrogen from the total nitrogen. The total nitrogen was determined by modifying the standard Kjeldahl method using a reduction mixture containing sodium thiosulphate as a preliminary, to the ordinary digestion (Kelley, Hunter & Sterges, 1946). Any ammonium salts, however, present in the plant will be estimated as organic nitrogen (Kjeldahl).

(1) *L. saccharina* from 4 m. (low water) at Eilean Coltair, Loch Melfort.
(2) *L. saccharina* from 4 m. at Rudh-an-Aoil, Shuna Island.
(3) *L. cloustoni* from 4 m. at Cullipool, Luing Island.

The results for crude proteins, inorganic nitrogen, mannitol, laminarin, dry-weight content, fresh weight, total ash, and alginic acid are summarized in Figs. 7–14.

As the marked seasonal variations in composition occur in the fronds the results for the stipes, with the exception of the fresh weights for *L. saccharina*, have been omitted.

## DISCUSSION OF RESULTS

In comparing the variations in chemical constitution it should be borne in mind that *L. cloustoni* differs in many respects from *L. saccharina*, and it is unfortunate that the latter species was unobtainable at Cullipool.

On the west coast of Scotland, with *L. saccharina*, growth of the new frond begins much earlier than with *L. cloustoni*, and from August losses due to the shedding of the old frond of the current year may exceed the weight increment. In the autumn the rapid drop in laminarin may be due to this or it may be due to sporogenesis. On the other hand, *L. cloustoni* does not usually cast its old frond until April/May, although considerable wear has no doubt occurred

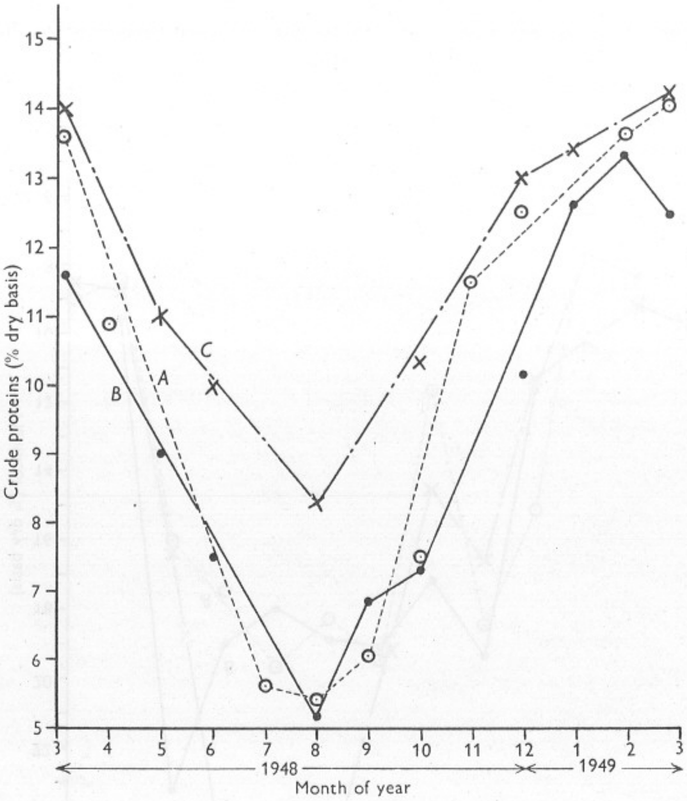


Fig. 7. Seasonal variation in crude proteins. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool.

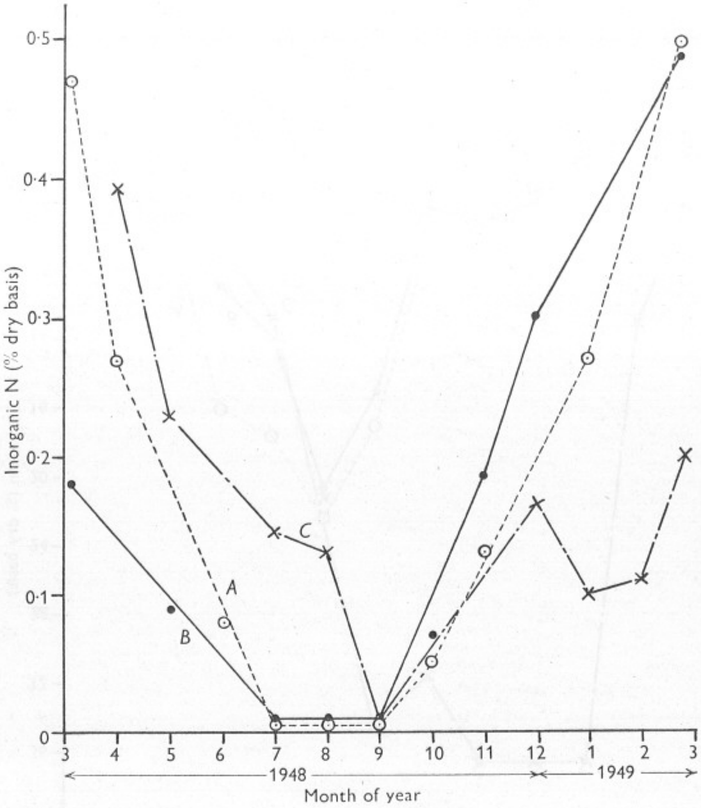


Fig. 8. Seasonal variation in inorganic nitrogen. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool.

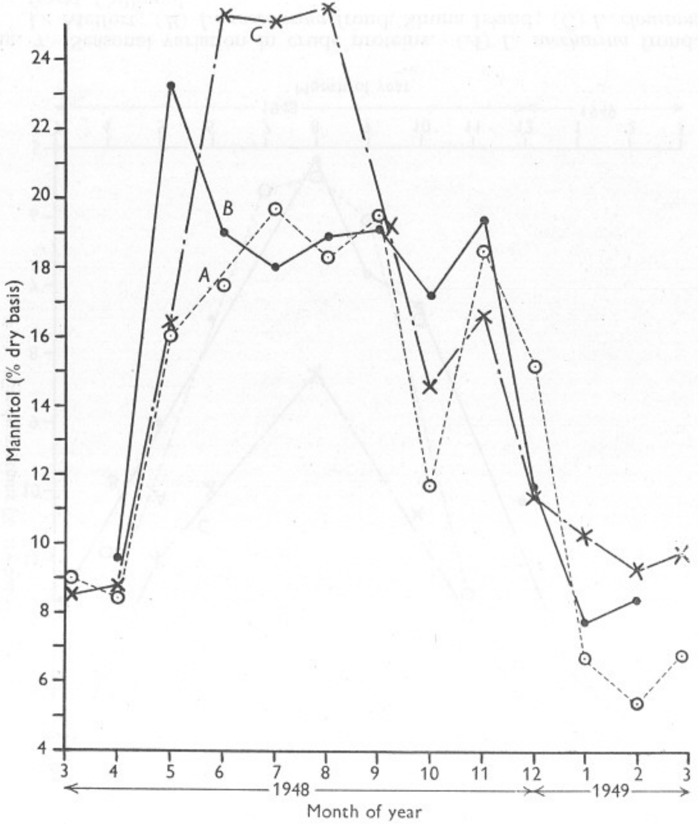


Fig. 9. Seasonal variation in mannitol. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool.

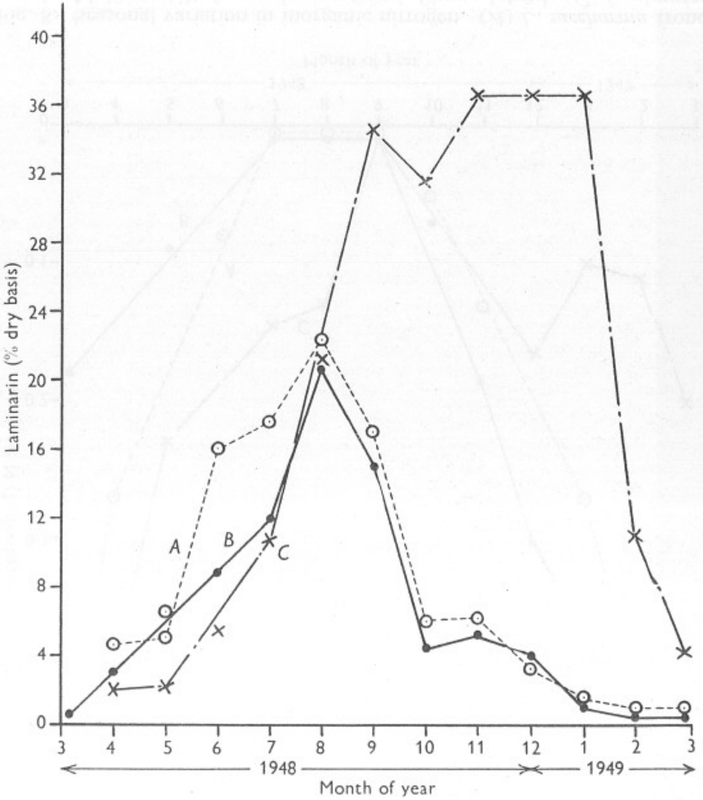


Fig. 10. Seasonal variation in laminarin. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina*, frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool.

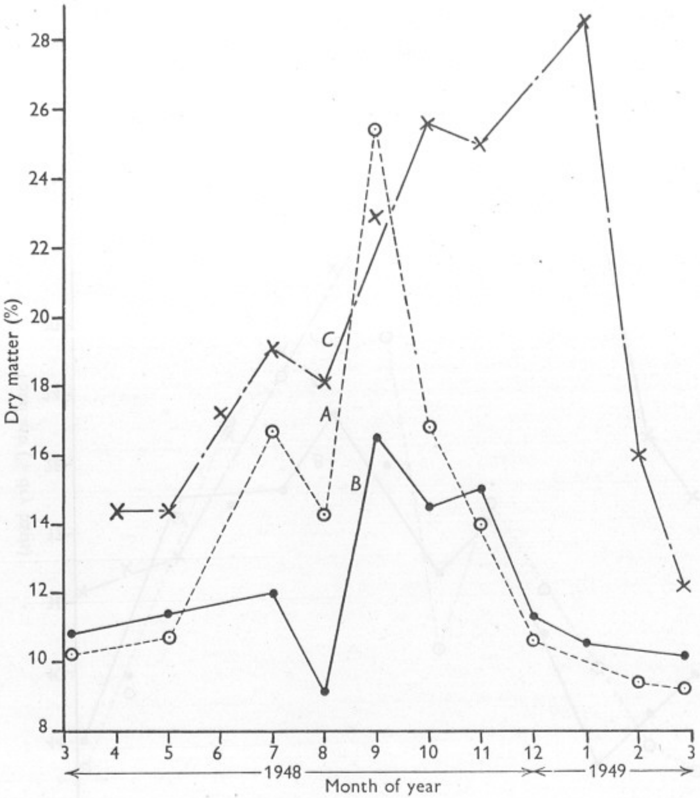


Fig. 11. Seasonal variation in dry matter. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool.

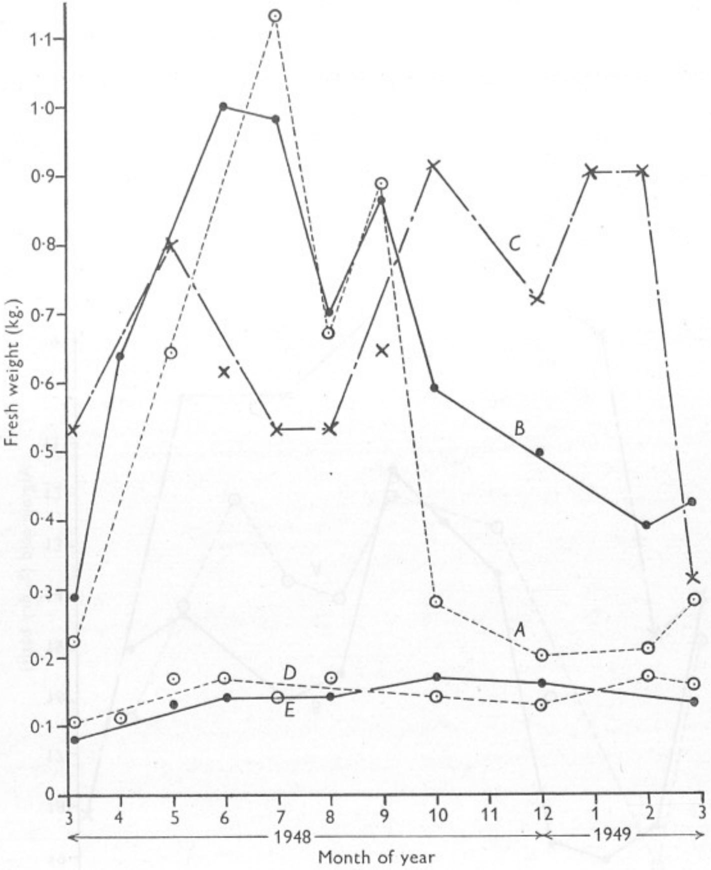
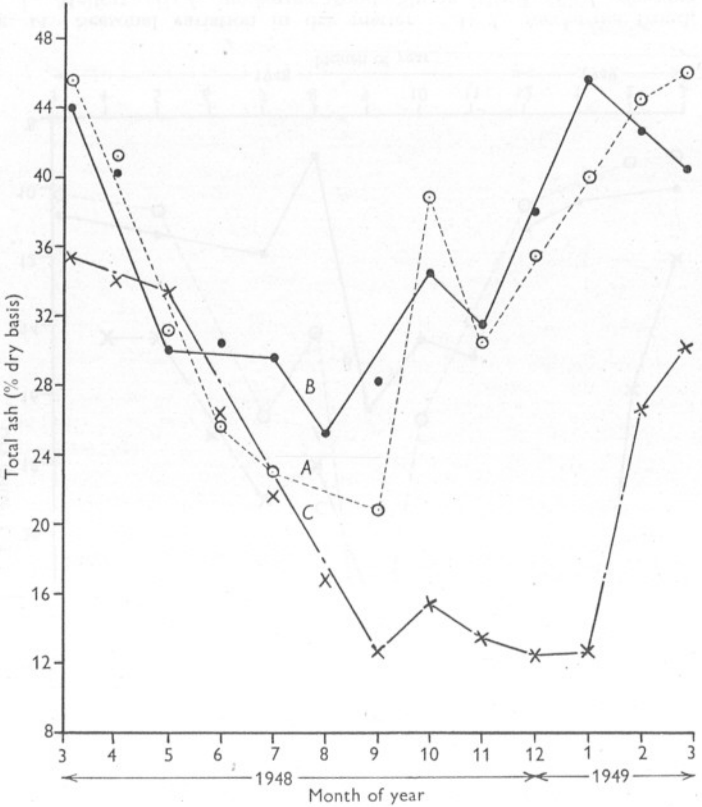


Fig. 12. Seasonal variation in fresh weight. (*A*) *L. saccharina* frond, L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. cloustoni* frond, Cullipool; (*D*) *L. saccharina* stipe, L. Melfort; (*E*) *L. saccharina* stipe, Shuna Island.



iation in total ash. (*A*) *L. saccharina* frond, L. Mel-
Shuna Island; (*C*) *L. cloustoni* frond,

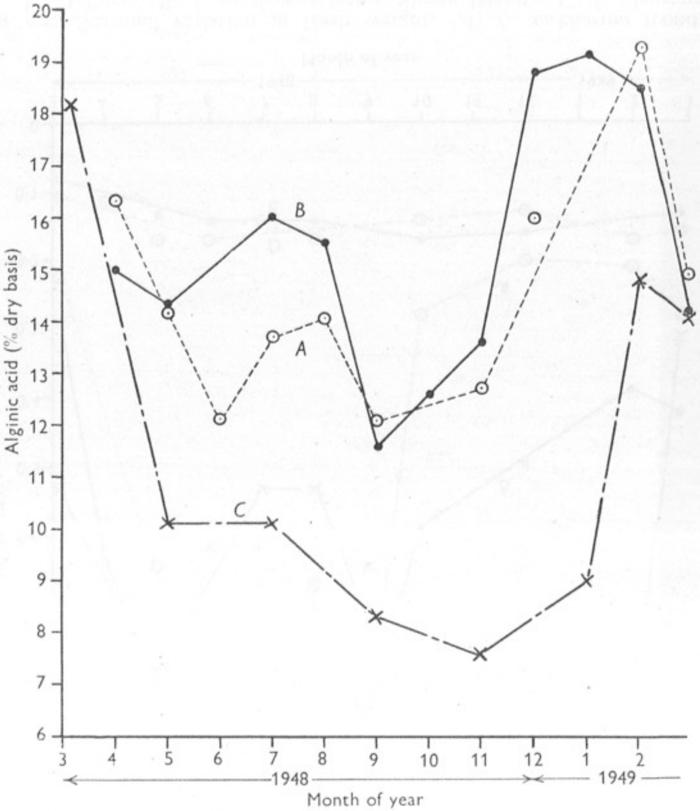


Fig. 14. Seasonal variation in alginic acid. (*A*) *L. saccharina* fr
L. Melfort; (*B*) *L. saccharina* frond, Shuna Island; (*C*) *L. clou*
frond, Cullipool.

before then. As distinct from *L. saccharina* laminarin is found at a high percentage in January when sporing of this species usually occurs. With *L. cloustoni*, therefore, the new frond may begin growth in water already depleted of nutrients, and this may account to some extent for the results obtained, and particularly the high laminarin content which the writers believe to be an indication of 'restricted growth'. It may be significant, however, that *L. saccharina* is often regarded as an annual, while *L. cloustoni* is a perennial.

In this investigation the plants have been weighed, but these weights cannot be taken as a measure of growth. First, differences may be due to variations in the weights of the individual plants; and secondly, the weight is determined by the rate of growth minus the rate of wear. Sporogenesis may also influence the weight, as a sporogenous frond has been found to be approximately twice as heavy as a sterile one (Report by State Oceanographical Institute, 1933).

It might be argued that the results expressed on the anhydrous basis do not give a true picture of the living plant and that a decrease in a particular constituent, for example, is due to growth and its redistribution in a larger plant. When the results are calculated on the wet basis, however, the graphs are, in general, parallel to those for the anhydrous basis.

The results, on the other hand, could be expressed per unit plant. If we consider the crude protein content, the maximum in the fronds, on the anhydrous basis, occurs in March 1948, when it is 50 g. per fresh frond. In August when it is at a minimum, on the anhydrous basis, it is 140 g. per fresh frond. In March the proteins will consist of reserve proteins and protoplasmic proteins. During rapid growth, however, the reserve proteins will no doubt be utilized to produce protoplasm; and synthesis of proteins, and consequently growth, will continue as long as inorganic nitrogen is present in the sea water or in the plant. By August the reserve proteins may all have been converted, and absence of inorganic nitrogen both in the water and the plant will consequently retard growth.

Although many of the changes in the composition of the sea water, such as the rapid utilization of nitrate in the spring, may in part be due to phytoplankton, during the summer, when the light is strong, plankton probably keep well below the surface and out of the sea-weed zone.

If carbohydrate assimilation with a corresponding decrease in crude proteins and ash can be taken as a measure of photosynthesis, the results indicate that a period of rapid photosynthesis occurs from March to June/July. During this period, with the exception of *L. cloustoni*, an increase in the fresh weight of the plants occurs indicating that this is also a period of rapid growth. A marked increase in the pH and oxygen saturation is further evidence of rapid photosynthesis. Growth and/or photosynthesis during this period utilizes all the nutrients in the water, so that by August nitrate is undetectable and phosphate is as low as 0·16–0·19 mg. atom/m.$^3$. The warming of the waters may have resulted in the setting up of a thermocline, thereby restricting vertical mixing so that regenerated nutrients do not reach the photosynthetic layer. In September cooling of the waters results in the autumn mixing and the replenishment of the photosynthetic layer with nutrients, so that in October/November a second burst of photosynthesis but on a reduced scale occurs, resulting again in increased carbohydrate assimilation. With light, no doubt, now the limiting factor, photosynthesis slows up and the nutrients accumulate again to reach their winter maxima in January/February.

In foreign waters such as the San Juan Channel, Washington, U.S.A., where *Nereocystis luetkeana* predominates, nitrate and phosphate have been determined for a period of 5 years (Phifer & Thompson, 1937). The great velocity of the tidal currents there creates very turbulent conditions and no thermocline is set up as in our inshore waters. At all times of the year the phosphate concentration was always sufficient for plant growth and could never be considered as a limiting factor. From a maximum of about 3 mg. atoms/m.$^3$ in December it decreased to 0·8 mg. atom/m.$^3$ in August, and this minimum value is considerably greater than our winter maximum. Nitrate, at a maximum of about 35 mg. atoms/m.$^3$ in December/January, dropped to 0·5 mg. atom/m.$^3$ in August, a minimum value of the order of magnitude of our winter maximum.

Although it appears that some correlation exists between the seasonal variation in the composition of the British Laminariaceae and variations in the sea water, it does not appear evident to the authors how, by taking and analysing a sample of sea water, it is possible to predict the appropriate time of harvesting, when a desired constituent will be at a maximum. A 4-year investigation (Black, 1948, and in the press) of the seasonal variation of some of the common British Laminariaceae has provided that information. To establish the correlations between the physico-chemical properties of the water and the fixed algae would require quite extensive work over a period of years, and once established it would still be necessary to keep sampling the sea water at intervals to ensure that the prognostication was being followed as expected.

In March the fronds of the Laminaria are low in mannitol and laminarin (Figs. 9 and 10) and high in proteins and inorganic nitrogen (Figs. 7 and 8), after the carbohydrates have been used up during the winter in respiration and probably in the synthesis of proteins, which are believed to be the product of a 'dark' synthesis. In March also, the alginic acid content is at a maximum (Fig. 14), but the frond is exceedingly small (Fig. 12) and high in water content (Fig. 11), while the cell sap contains much mineral matter (Fig. 13). During the winter months the rate of photosynthesis has been very low, if any photosynthesis occurs at all, and consequently the surrounding sea water is high in nitrates and phosphates.

In March/April a marked increase in photosynthesis occurs, accompanied by an increase in the fresh weight of the plant and an increase in the mannitol, while a decrease occurs in the crude proteins and inorganic nitrogen, all indicating that vigorous growth has commenced. Simultaneously, in the surrounding sea water a drop occurs in the nitrate and phosphate content as a result of their utilization by algae and other forms of marine life. At the same time an increase in the pH and oxygen saturation content occurs, which is further evidence of a marked increase in photosynthesis.

While a drop of only 0·03 mg. atom/m.$^3$ occurs in the phosphate content of the water at Shuna Island, the phosphate content at Loch Melfort falls 0·20 mg. atom/m.$^3$ during March/April. The change in the nitrate content is more marked during this period; at Shuna Island it falls from 6·1 to 3·1 mg. atoms/m.$^3$, while at Loch Melfort it decreases from 6·4 to 0·7 mg. atom/m.$^3$.

During May photosynthesis continues. *Laminaria saccharina* increases in weight, but a decrease in the weight of *L. cloustoni* occurs, no doubt due to the shedding of the old frond at this time. Mannitol shows an increase, and a decrease occurs in the crude proteins, inorganic nitrogen, alginic acid and ash. In the sea, the temperature of which is gradually increasing, the pH and oxygen saturation content show an increase, and a marked drop in the nitrate content at Cullipool and Shuna Island occurs, while phosphate decreases to 0·33, 0·26 and 0·19 mg. atom/m.$^3$ at Cullipool, Shuna Island and Loch Melfort respectively.

In June there is a suggestion of a 'falling off' in the rate of photosynthesis. The fronds of *L. saccharina* from Shuna Island show a decrease in mannitol, but an increase in fresh weight, however, occurs in both samples of *L. saccharina*, while a decrease in the weight of *L. cloustoni* is recorded. The crude proteins, inorganic nitrogen, ash and alginic acid contents show a further decrease with an appreciably higher protein figure for *L. cloustoni* at Cullipool. While the pH and oxygen saturation of the water remain constant, a further drop in the nitrate content occurs, while phosphate is between 0·16 and 0·20 mg. atom/m.$^3$.

In July/August there is evidence of a marked change in the rate of growth and/or the rate of photosynthesis. Laminarin shows an increase but this is characteristic of 'restricted' growth, mannitol remains relatively constant, but a drop occurs in the dry matter and fresh weight of *L. saccharina*. The water analysis shows the temperature rising to a maximum of 13° C. at the three localities. In July, nitrate and phosphate are at a minimum, the nitrate being 0·9 mg. atom/m.$^3$ at Cullipool, while at Shuna Island and Loch Melfort it is undetectable in the water, and phosphate is between 0·16 and 0·20 mg. atom/m.$^3$.

The pH and dissolved oxygen saturation, which reach maxima in July, fall rapidly in August, indicating reduced photosynthesis in the water. The ash content shows a slight decrease, but a marked increase occurs in the alginic acid content.

The months of July and August appear to be critical ones, and in all our work, and in the work of other investigators, comment has been passed on the change in composition and rate of growth which occurs at this time. There may be other influencing factors, but the water analysis shows that lack of nutrients must be a limiting factor. Although low concentrations of nitrate, for example, exist in the water at Loch Melfort in April the weed still contains a reserve of inorganic nitrogen, so that it is not until July, with the exception of *L. cloustoni* which always exhibits a lag, that nitrate is undetectable in the plant and the water.

Temperature may also be an influencing factor, as it reaches a maximum of 13° C. at this time of the year. The intensity of respiration and assimilation increases with temperature, but the effect on respiration is considerably greater than on assimilation. Consequently with increasing temperature, the surplus will eventually disappear and growth will cease.

In September/October a rise occurs in the protein content of all the plants, coinciding with an increase in the nitrate and phosphate contents of the water. This is the result of the autumn cooling of the water bringing about the breakdown of the thermocline, giving vertical mixing and regeneration of nutrients in the photosynthetic zone. A marked increase in the pH of the water signifies a second 'burst' of photosynthesis, less intense however, than the spring outburst. An increase in the fresh weight and dry-matter content occurs, but a considerable drop in the laminarin occurs which might be the result of further growth.

In November/December, although a drop in the dry matter and fresh weight of the plants occurs, there is a rise in the mannitol, laminarin and crude protein contents and a decrease in the ash, indicating that the rate of assimilation still exceeds the rate of respiration. The rapid increase since August in the nitrate concentration is checked, indicating its utilization.

From December to March photosynthesis proceeds at a low rate as light may now be the limiting factor. Little change occurs in the pH, while the carbohydrates are now utilized in growth and respiration at a greater rate than they are assimilated.

Nitrate and phosphate increase to a maximum in January/February and then begin to decrease again, the exception being the high phosphate figures for Shuna Island and Loch Melfort in December.

The large store of inorganic nitrogen present in the fronds during the winter and early spring is rather surprising and is worthy of further investigation.

These seasonal variations in composition appear to be characteristic of most forms of marine life. For example, Daniel (1922) investigated the seasonal variation in chemical composition of the mussel and found from May onwards a decrease in the proteins, on the dry ash free basis, reaching a minimum in September/October and then rising to a maximum the following March. The carbohydrates showed a steady increase from March, reaching a maximum in September/October, with a tendency to form a second maximum in December, and then a rapid decrease until March.

## ACKNOWLEDGEMENTS

The work described in this report forms part of the programme of research and development on seaweed undertaken by the Scottish Seaweed Research Association, to whom the authors are indebted for permission to publish. They also wish to thank the staffs at the Marine Stations at Aberdeen, Millport and Plymouth for their very valuable help, and for the loan of essential apparatus.

The assistance of Miss B. Graham and Mr W. Cornhill in the analytical work is also acknowledged.

## SUMMARY

Monthly samples of the Laminariaceae, *L. saccharina* and *L. cloustoni*, from three localities on the Argyllshire coast have been taken from March 1948 to March 1949, and analysed for dry matter, ash, mannitol, laminarin, crude proteins, inorganic nitrogen and alginic acid, and the seasonal variation in these constituents correlated with the changes in composition of the sea water.

The results show that a correlation does exist and that a period of rapid photosynthesis occurs from March to June/July, but is restricted in July/August when nitrate is undetectable in the water and phosphate is as low as 0·16–0·20 mg. atom/m.$^3$. The replenishment of the photosynthetic layer with nutrients is retarded in July/August, apparently due to the warming of the inshore waters, which may set up a thermocline restricting vertical mixing.

The autumn cooling of the uppermost waters facilitates vertical mixing, regenerating the nutrients in the photosynthetic region, and a second burst of photosynthesis at a reduced rate from the spring 'outburst' occurs in October/November.

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# A SOURCE OF ERROR IN THE ABSORPTIOMETRIC DETERMINATION OF INORGANIC AND TOTAL PHOSPHORUS IN SEA WATER

By F. A. J. Armstrong

From the Plymouth Laboratory

In the course of phosphate determinations by the Denigès method it has been noticed that use of stannous chloride solutions containing some stannic tin and a low concentration of hydrochloric acid may give misleadingly high values for the reagent blank in distilled water, when the extinctions[1] of the solutions are measured with a photoelectric absorptiometer in red light (Harvey, 1948). In daylight the solutions may show a perceptible yellow colour, or even, in extreme cases, a turbidity.

The magnitude of the effect has now been measured in reagent blank determinations with distilled water and in phosphate determinations with sea water. In sea water it is smaller or non-existent, so that the reagent blank value is inappropriate and causes over-correction of the measured phosphate content of the samples, leading to fictitiously low results.

The error may be from 1 to 2 mg./m.$^3$ of phosphate-phosphorus, or even higher when a turbidity is to be seen. It may be eliminated by ensuring that the stannous chloride solution contains about 5% by volume of concentrated hydrochloric acid.

The effect was first observed when an aged stock solution of stannous chloride was diluted with water to give a working solution which contained the required 0·3–0·45 mg. of stannous tin in three drops. When this was added to blank solutions these became faintly yellow in colour and the measured extinctions were greater than was expected. The stock solution had been prepared by dissolving 16 g. of Analar stannous chloride in 40 ml. of a solution containing equal volumes of concentrated hydrochloric acid and water. It had undergone aerial oxidation in the course of 11 months, and a test showed that only 53% of its tin content was in the stannous form. It seemed likely that the presence of stannic tin in this solution had caused the high extinction values found, by producing a colloidal suspension of basic stannic compounds which absorbed or scattered light. Since the production of these compounds is known to be hindered in presence of hydrochloric acid, the experiment of diluting this aged stock solution with 5% v/v hydrochloric acid

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[1] The term 'extinction' is here used to denote the function $\log_{10} I_0/I$, where $I_0$ and $I$ are the intensities of the light entering and leaving the coloured solution. In the concentrations used, the molybdenum blue colour obeys the Beer-Lambert law so that extinction is proportional to the amount of blue compound present. All measurements were made in a 15 cm. cell.

instead of water was tried. (When diluted with water only, the resulting solution contains about 0·8% by volume of concentrated hydrochloric acid.) When the more acid solution was used for reagent blank determinations the extinction measured was found to be about one-third of that given by the stock solution diluted with water, and no yellow colour was apparent.

Other concentrations of hydrochloric acid were tried with the results shown in Table I. The reagent blank solution contained 67 ml. of distilled water and 3 ml. of a reagent containing 18% by volume concentrated sulphuric acid and 10·7% ammonium molybdate. The dilute stannous chloride solutions were adjusted so that each contained 0·45 mg. stannous tin in the 3 drops used. The best concentration appears to be 5% by volume.

TABLE I. INCREASE IN EXTINCTION (MEASURED IN RED LIGHT) OF A REAGENT BLANK SOLUTION UPON ADDITION OF STANNOUS CHLORIDE

| Stock stannous chloride diluted with | Increase in extinction (in 15 cm. cell) | Calculated reagent blank (mg. phosphate-P/m.$^3$) |
|---|---|---|
| Water | 0·024 | 2·9 |
| | 0·024 | 2·9 |
| 1 % v/v HCl | 0·020 | 2·4 |
| | 0·022 | 2·6 |
| 2 % v/v HCl | 0·010 | 1·2 |
| | 0·009 | 1·1 |
| 5 % v/v HCl | 0·009 | 1·1 |
| | 0·009 | 1·1 |
| 10 % v/v HCl | 0·012 | 1·4 |
| | 0·012 | 1·4 |

To see how the reagent blank was affected by varying stannic tin content of the stannous chloride solution, three solutions were made as follows:

(1) By dissolving 16 g. of $SnCl_2.2H_2O$ in 40 ml. of 1:1 HCl, the salt being about 10 years old and badly oxidized. The solution was found to contain 68% of stannous and 32% of stannic tin.

(2) By preparing a similar solution from fresh stannous chloride of good appearance. This contained 93% of stannous and 7% of stannic tin.

(3) By dissolving 8·4 g. of tin in 32 ml. of conc. HCl and 8 ml. of water, adding two drops of 5% copper sulphate to assist solution. On test, this preparation was found to contain 100% stannous tin.

From each of these, diluted solutions of the same stannous tin content were made, in water and in 5% v/v HCl, and were used for reagent blank determinations. The results are shown in Table II.

From these it appears that in solutions diluted with water, high stannic tin content is accompanied by high reagent blank values. When hydrochloric acid is used the blanks appear to be independent of the stannic tin concentration. It is notable that even in the case of the reagent prepared by diluting the 100% stannous chloride with water there is an enhanced extinction, which may be due to the production of sufficient stannic tin in the diluted solution to cause some scattering of light.

After this demonstration that the reagent blank is increased in distilled water if the stannous chloride reagent has a low HCl content and high stannic tin concentration, the effect in sea water was measured. The experiments were carried out under the same conditions as are used when phosphate in sea water is determined, viz. to 67 ml. of sea water 3 ml. of a reagent containing 18% v/v $H_2SO_4$ and 10·7% ammonium molybdate were added. The extinction of the resulting solution was measured. Three drops of stannous chloride were added, and the extinction again measured when it had attained its maximum. To the solution 0·3 ml. of a standard phosphate solution was then added, increasing the phosphorus concentration by 20 mg. per m.$^3$, followed by a further two drops of stannous chloride. The extinction was measured again when it had reached its maximum. The difference between the first two readings was a measure of the phosphate-phosphorus content of the sea water, together with the blank contributed by the reagents. The difference between the second and third readings measured the extinction produced by unit quantity of phosphorus under the experimental conditions. A separate determination of the reagent blank allowed the phosphate-phosphorus content of the sea water to be calculated.

TABLE II. EFFECT OF VARYING STANNIC TIN CONTENT OF STANNOUS CHLORIDE REAGENT UPON REAGENT BLANK

| Fraction of total tin content of stock solution in | | Stock solution diluted with water | | Stock solution diluted with 5 % v/v HCl | |
|---|---|---|---|---|---|
| Stannous form (%) | Stannic form (%) | Extinction | Reagent blank (mg./m.$^3$) | Extinction | Reagent blank (mg./m.$^3$) |
| 68 | 32 | 0·023 | 2·7 | 0·009 | 1·1 |
| | | 0·029 | 3·4 | 0·008 | 1·0 |
| 93 | 7 | 0·024 | 2·8 | 0·007 | 0·8 |
| | | 0·022 | 2·6 | 0·008 | 1·0 |
| 100 | Nil | 0·018 | 2·1 | 0·009 | 1·1 |
| | | 0·019 | 2·3 | 0·008 | 1·0 |

Table III shows results obtained with a sample of sea water of low phosphate content which had been filtered to remove any particulate matter which might contain phosphate (Cooper, 1948, p. 298).

Although in absence of sufficient hydrochloric acid it is seen that the increase in extinction is enhanced by the presence of stannic tin, this enhancement is less in sea water than in distilled water; it has led in the extreme case to a negative value for the calculated phosphate-phosphorus. No significant alteration is seen in the extinction recorded after addition of phosphate subsequent to the first measurement.

The experiment was duplicated with the same sea water enriched with 8·9 mg./m.$^3$ of phosphate-phosphorus. The stannous chloride solutions in this experiment were different preparations. The results are shown in Table IV.

The difference in extinction values for the addition of 20 mg./m.$^3$ phosphate-phosphorus between Tables III and IV can be accounted for by the temperature difference.

TABLE III. ESTIMATION OF PHOSPHATE IN SEA WATER USING STANNOUS CHLORIDE REAGENTS CONTAINING EQUAL QUANTITIES OF STANNOUS, AND VARYING AMOUNTS OF STANNIC TIN. TEMPERATURE OF SOLUTIONS, 22° C.

| Stannic tin content of stock solution as fraction of total tin present (%) | Stock solution diluted with water | | | | Stock solution diluted with 5 % v/v HCl | | | |
|---|---|---|---|---|---|---|---|---|
| | Extinction in | | Further increase in extinction in sea water after subsequent addition of 20 mg./m.$^3$ phosphate-P | Calculated $PO_4$-P (mg./m.$^3$) | Extinction in | | Further increase in extinction in sea water after subsequent addition of 20 mg./m.$^3$ phosphate-P | Calculated $PO_4$-P mg./m.$^3$ |
| | Distilled water | Sea water | | | Distilled water | Sea water | | |
| 67 | 0·068, 0·069 | 0·037 | 0·168 | −3·8 | 0·011, 0·010 | 0·031 | 0·170 | 2·4 |
| | | 0·039 | 0·172 | −3·4 | | 0·033 | 0·168 | 2·6 |
| 32 | 0·030, 0·030 | 0·043 | 0·170 | 1·5 | 0·010, 0·009 | 0·030 | 0·171 | 2·4 |
| | | 0·040 | 0·172 | 1·2 | | 0·030 | 0·169 | 2·4 |
| Nil | 0·016, 0·015 | 0·031 | 0·167 | 1·9 | 0·010, 0·010 | 0·031 | 0·170 | 2·5 |
| | | 0·033 | 0·169 | 1·9 | | 0·033 | 0·168 | 2·6 |

TABLE IV. ESTIMATION OF PHOSPHATE IN SEA WATER ENRICHED WITH 8·9 MG. PHOSPHATE-P PER M.$^3$ USING STANNOUS CHLORIDE REAGENTS CONTAINING EQUAL QUANTITIES OF STANNOUS, AND VARYING AMOUNTS OF STANNIC TIN. TEMPERATURE OF SOLUTIONS, 20° C.

| Stannic tin content of stock solution as fraction of total tin present (%) | Stock solution diluted with water | | | | Stock solution diluted with 5 % v/v HCl | | | |
|---|---|---|---|---|---|---|---|---|
| | Extinction in | | Further increase in extinction in sea water after subsequent addition of 20 mg./m.$^3$ phosphate-P | Calculated $PO_4$-P mg./m.$^3$ | Extinction in | | Further increase in extinction in sea water after subsequent addition of 20 mg./m.$^3$ phosphate-P | Calculated $PO_4$-P mg./m.$^3$ |
| | Distilled water | Sea water | | | Distilled water | Sea water | | |
| 59 | 0·042, 0·032 | 0·107 | 0·166 | 8·4 | 0·010, 0·010 | 0·107 | 0·167 | 11·6 |
| | | 0·108 | 0·167 | 8·5 | | 0·107 | 0·168 | 11·6 |
| 32 | 0·030, 0·030 | 0·111 | 0·167 | 9·7 | 0·011, 0·011 | 0·109 | 0·167 | 11·7 |
| | | 0·116 | 0·168 | 10·2 | | 0·109 | 0·168 | 11·7 |
| Nil | 0·014, 0·013 | 0·108 | 0·167 | 11·2 | 0·009, 0·009 | 0·107 | 0·168 | 11·7 |
| | | 0·107 | 0·167 | 11·1 | | 0·107 | 0·168 | 11·7 |

The last columns of these tables, showing the calculated phosphorus in the sea water without and with the addition of 8·9 mg./m.$^3$, show a mean difference of 9·18 mg./m.$^3$ with a maximum difference of 9·3 and a minimum difference of 9·0. This estimated difference is considered to be in reasonable agreement with the known addition of phosphate, and indicates that the technique of 'subsequent addition' is valid (Harvey, 1948, p. 351).

It is therefore recommended that the stannous chloride used in this method should contain at least 5% by volume of concentrated hydrochloric acid.

This condition, it should be noted, is complied with in the original visual method of Atkins (1923, p. 144), in which the freshly prepared stannous chloride contains 10 to 20% by volume of acid. In any event the presence of stannic tin with a low acid concentration is less likely to upset the visual estimation of the reagent blank, as its effect is to discolour, not augment, any blue colour formed.

## SUMMARY

The results of phosphate determinations in sea water by the Denigès method, using red light, in an absorptiometer, may be in error if the stannous chloride reagent has low HCl concentration, and contains stannic tin.

The error is in the reagent blank determination, and seems to be caused by colloidal stannic compounds which increase the opacity of the solution. In sea water the effect may be smaller or immeasurable so that results are over-corrected.

When the stannous chloride solution contains about 5% hydrochloric acid, reagent blank figures are low, and independent of stannic tin concentration. This acidity is recommended.

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# THE SEASONAL ABUNDANCE OF YOUNG FISH

## X. THE YEAR 1948

By P. G. Corbin, B.A.
Zoologist at the Plymouth Laboratory

(Text-figs. 1–2)

Records of the young fish and plankton of Plymouth off-shore waters taken in $\frac{1}{2}$ hr. oblique hauls of the 2 m. stramin ring-trawl were continued in 1948. They show an even lower production of young fish than in 1947 and a continued poverty of plankton organisms other than young fish. The dates on which collections were made are given in Table I.

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1948

All 2 miles east of Eddystone, unless otherwise stated

| Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | 3 | 1 | 12* | 19 | 1 | 5 | 4 | 6 | 4* | 4 | 6 |
| 14 | 9 | 11† | 14 | 25 | 7 | 12 | 9 | 13 | 7 | 9 | 15 |
| 20 | 12* | 11* | | | 8* | 19 | 18 | 20 | 12 | 16 | 20 |
| 26 | 16 | 15 | | | 14 | 26 | 23 | 28 | 21 | 22 | |
| | | 23 | | | 21 | 29* | 30 | | 26 | 29 | |
| | | | | | | | 31* | | 27* | 30* | |

* Station E 1. † Station L 4.

TABLE II. FORTNIGHTLY AVERAGE CATCHES OF ALL YOUNG FISH EXCLUDING CLUPEIDS, 1930–34, 1947 AND 1948

| | | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1930–34* | 1st fortnight | 5 | 10 | 27 | 110 | 635 | 299 | 100 | 152 | 48 | 11 | 7 | 2 |
| (average) | 2nd fortnight | 8 | 15 | 89 | 374 | 573 | 78 | 85 | 48 | 9 | 6 | 3 | 2 |
| 1947 | 1st fortnight | n.r. | 5 | 6 | 5 | n.r. | 20 | 10 | 11 | 11 | 2 | 1 | + |
| | 2nd fortnight | 0 | 43 | 13 | 10 | 54 | 27 | 5 | 16 | 1 | 0 | + | + |
| 1948 | 1st fortnight | + | 3 | 15 | 12 | n.r. | 13 | 9 | 9 | + | 4 | 0 | 1 |
| | 2nd fortnight | 0 | 16 | 15 | n.r. | 65 | 32 | 17 | 5 | 0 | + | + | 0 |

* Data kindly supplied by Mr F. S. Russell.
n.r., no records. + average of less than 1.

The fortnightly averages of all young fish, excluding clupeids, are now too low to be graphed against the same averages for the period 1930–34 as in Fig. 1 of former reports: they are therefore given numerically in Table II below, with the 1947 averages for comparison. *Callionymus* spp. and *Solea variegata* contributed principally to the highest of these fortnightly averages in the second half of May; the next highest value in the second half of June was also mainly due to *Callionymus* spp.

Earlier parts of this series (Russell, 1930–47; Corbin, 1948) also give a table of the monthly average catches of young fish. These have now fallen to so low

TABLE III. MONTHLY TOTAL CATCHES OF POST-LARVAE PER HALF-HOUR OBLIQUE HAULS WITH 2 M. STRAMIN RING-TRAWL, 1948

The number of hauls per month is shown by the small figure against each month at the head of the column. A + is used in the 2nd, 4th and 6th lines to denote monthly average of less than 0·5.

| | Jan.$^{4}$ | Feb.$^{4}$ | Mar.$^{5}$ | Apr.$^{2}$ | May$^{2}$ | June$^{5}$ | July$^{5}$ | Aug.$^{6}$ | Sept.$^{4}$ | Oct.$^{6}$ | Nov.$^{6}$ | Dec.$^{3}$ | Total | Sum of monthly averages |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total young fish | 4 | 107 | 406 | 27 | 149 | 198 | 162 | 83 | 6 | 151 | 1 | 5 | 1299 | .. |
| Monthly average, T.Y.F. | 1 | 27 | 81 | 14 | 75 | 39 | 32 | 14 | 1 | 25 | + | 2 | .. | 331 |
| T.Y.F., less Clupeids | 1 | 26 | 74 | 23 | 130 | 83 | 70 | 39 | 2 | 14 | 1 | 3 | 466 | .. |
| Monthly average, ditto | + | 6 | 15 | 12 | 65 | 17 | 14 | 6 | + | 2 | + | 1 | .. | 138 |
| All Clupeid spp. | 3 | 81 | 332 | 4 | 19 | 115 | 92 | 44 | 4 | 137 | 0 | 2 | 833 | .. |
| Monthly average, ditto | 1 | 20 | 66 | 2 | 10 | 23 | 18 | 7 | 1 | 23 | 0 | 1 | .. | 172 |
| *Clupea harengus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Gadus pollachius* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Gadus merlangus* | .. | .. | 1 | 1 | 5 | 4 | 2 | .. | .. | .. | .. | .. | 13 | 4·4 |
| *Gadus minutus* | .. | .. | 7 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 8 | 1·9 |
| *Gadus luscus* | 1 | .. | 16 | .. | .. | .. | .. | .. | .. | .. | 1 | 1 | 19 | 3·45 |
| *Gadus callarias* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Onos* spp. | .. | .. | .. | 5 | 20 | 2 | .. | .. | .. | .. | .. | .. | 27 | 12·9 |
| *Phycis blennioides* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 0·3 |
| *Molva molva* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Merluccius merluccius* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Raniceps raninus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Capros aper* | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. | 1 | 0·17 |
| *Zeus faber* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Arnoglossus* spp. | .. | .. | .. | .. | .. | .. | 13 | 11 | .. | 7 | .. | .. | 31 | 5·57 |
| *Rhombus* spp. | .. | .. | .. | .. | .. | .. | 1 | 3 | .. | .. | .. | .. | 4 | 0·7 |
| *Scopthalmus norvegicus* | .. | .. | .. | .. | 6 | 6 | .. | .. | .. | .. | .. | .. | 12 | 4·2 |
| *Zeugopterus punctatus* | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | 1 | 0·2 |
| *Zeugopterus unimaculatus* | .. | .. | .. | .. | .. | 2 | .. | .. | .. | .. | .. | .. | 2 | 0·4 |
| *Pleuronectes platessa* | .. | .. | 13 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 13 | 2·6 |
| *Pleuronectes limanda* | .. | .. | .. | .. | 5 | 1 | .. | .. | .. | .. | .. | .. | 6 | 2·7 |
| *Pleuronectes flesus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Pleuronectes microcephalus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Solea vulgaris* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Solea variegata* | .. | .. | .. | .. | 33 | 2 | .. | .. | .. | .. | .. | .. | 35 | 16·9 |
| *Solea lascaris* | .. | .. | .. | .. | .. | .. | 1 | 2 | .. | 1 | .. | .. | 4 | 0·7 |
| *Solea lutea* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Serannus cabrilla* | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | 1 | 0·2 |
| *Caranx trachurus* | .. | .. | .. | .. | .. | .. | 9 | 4 | .. | 2 | .. | .. | 15 | 2·8 |
| *Mullus surmuletus* | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | .. | 1 | 0·2 |
| *Morone labrax* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Ammodytes lanceolatus* | .. | .. | .. | 5 | 1 | 2 | 4 | .. | .. | .. | .. | .. | 12 | 4·2 |
| *Ammodytes tobianus* | .. | .. | .. | 1 | .. | .. | 1 | .. | .. | .. | .. | .. | 2 | 0·7 |
| *Ammodytes marinus* | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 0·5 |
| *Ammodytes* sp. IV | .. | 12 | 13 | 2 | .. | .. | .. | .. | .. | .. | .. | .. | 27 | 6·6 |
| *Cepola rubescens* | .. | .. | .. | .. | .. | .. | .. | 1 | 1 | .. | .. | .. | 2 | 0·42 |
| *Callionymus* spp. | .. | .. | 2 | 7 | 60 | 27 | 8 | 4 | .. | 1 | .. | .. | 109 | 41·6 |
| *Labrus bergylta* | .. | .. | .. | .. | .. | 2 | 1 | .. | .. | .. | .. | .. | 3 | 0·6 |
| *Labrus mixtus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Ctenolabrus rupestris* | .. | .. | .. | .. | .. | 20 | 12 | 1 | .. | .. | .. | .. | 33 | 6·57 |
| *Crenilabrus exoletus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Trachinus vipera* | .. | .. | .. | .. | .. | .. | 1 | 3 | .. | .. | .. | .. | 4 | 0·7 |
| *Scomber scombrus* | .. | .. | .. | .. | .. | .. | 3 | 1 | .. | .. | .. | .. | 4 | 0·77 |
| *Gobius* spp. | .. | 1 | .. | .. | .. | 4 | 3 | 1 | 1 | .. | .. | .. | 10 | 2·07 |
| *Lebetus scorpioides* | .. | .. | .. | .. | .. | .. | 1 | 1 | .. | .. | .. | .. | 2 | 0·37 |
| *Blennius ocellaris* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Blennius pholis* | .. | .. | .. | .. | .. | .. | .. | 1 | .. | .. | .. | .. | 1 | 0·17 |
| *Blennius gattorugine* | .. | .. | .. | .. | .. | 9 | 6 | 5 | .. | .. | .. | .. | 20 | 3·8 |
| *Chirolophis galerita* | .. | 13 | 18 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 31 | 6·85 |
| *Mugil* spp. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 1 | 1 | 0·33 |
| *Agonus cataphractus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Trigla* spp. | .. | .. | 3 | .. | .. | 1 | .. | .. | .. | .. | .. | .. | 4 | 0·8 |
| *Cottus* spp. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Liparis montagui* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Lepadogaster bimaculatus* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| *Lophius piscatorius* | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Pipe fish | .. | .. | 1 | .. | .. | .. | 2 | 1 | .. | 2 | .. | .. | 6 | 1·1 |
| | | | | | | | | | | | | | 466 | 138 |

a level for almost all species that it is considered more informative to show the monthly total catches for species (Table III) rather than the monthly average catches, many of which are now considerably less than one. For comparison with previous records, the sums of the monthly averages for the year are given in the last column of this table, and the monthly averages of (i) total young fish, (ii) total young fish less clupeids, and (iii) total clupeids are also shown (2nd, 4th and 6th lines, in black). The number of hauls per month is included so that the monthly averages for the species are immediately derivable.

A few young plaice, *Pleuronectes platessa*, again occurred this year, in March. A single specimen of *Mugil* spp. was taken on 15 December: in 1947 another single specimen was caught at E 1, on 13 November (this haul was not included in the 1947 data).

A young specimen (33 mm.) of *Phycis* was also taken in the haul of 15 December this year. It very probably belongs to *P. blennioides* as this is the only *Phycis* species occurring in the area. No young stages of this genus have previously been recorded off Plymouth.

As already mentioned, plankton other than young fish was very scarce throughout the year. The maximum haul of *Calanus* (adult and stage V) contained 280 odd specimens (1 June 1948), and only four other catches during the year contained more than 100 *Calanus*. This, when compared with the rich catches of 1930 (Russell, 1933), gives some indication of the present poverty. In 1930, thirty-four of the forty-four hauls taken during the year contained more than 100 *Calanus* and seventeen out of the forty-four had catches of over 1000: the maximum haul contained the very large total of 318,450 specimens (7 May 1930).

*Sagitta setosa* was the dominant *Sagitta* species throughout the year (Figs. 1 and 2). It was, however, considerably less numerous than in 1947: on only two occasions were catches of more than 1000 taken (1 March, 31 August; 1200 odd). As in 1947, it was almost completely absent during the period April–July. The occurrence of *S. elegans* was very intermittent during the year and the numbers caught were extremely small (maximum, ten specimens).

A particularly noticeable feature of the *S. setosa* catches throughout the year was the preponderance of very small immature specimens (Stages I and II; Russell, 1932*a*). This departure from the normally expected proportions of development Stages (I–III) in the catches would appear to indicate an unusually low survival of individuals reaching maturity. Measurements and counts, comparable with those made by Russell (1932*b*), are required for verification of this trend. It is, however, felt that it should not remain unrecorded, since it may possibly represent a further aspect of the continued and progressive impoverishment of the macroplankton caught by the 2 m. ring-trawl in this area.

Except during April, *Muggiaea atlantica* was present during all months of

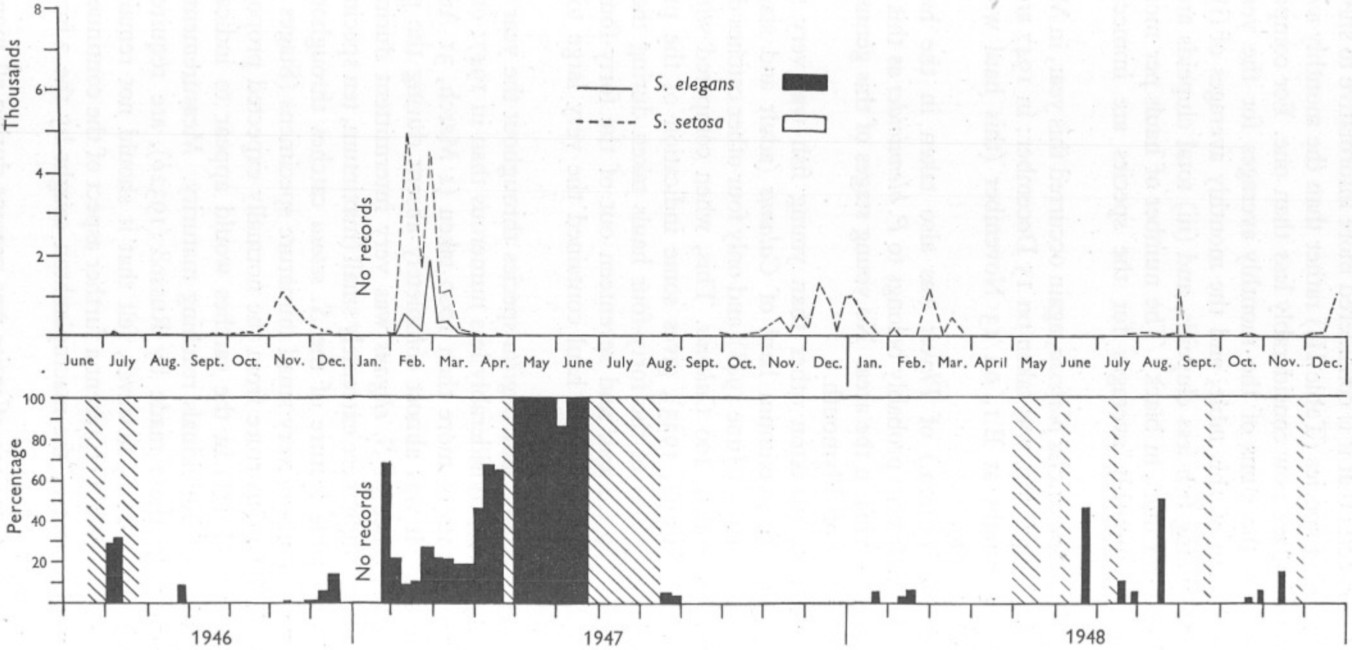

Fig. 1. Above, curves showing the actual abundance of *Sagitta elegans* (——) and *S. setosa* (-----) in half-hour oblique hauls with the 2 m. stramin ring-trawl during the period June 1946 to December 1948. Below, percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched. (Continued from Corbin, 1948, p. 720, fig. 2.)

the year: it was numerous from the end of July until the end of August and again from the end of September until the end of October.

*M. kochi*, which was present in very small numbers in 1946 (Russell, 1947) but did not occur in 1947 (Corbin, 1948), was also represented in the catches throughout the year except during February and April. It did not generally exceed one-third of the numbers of *M. atlantica*. In the earlier part (January–June) and at the end of the year (November and December), the catches of both *Muggiaea* species were small.

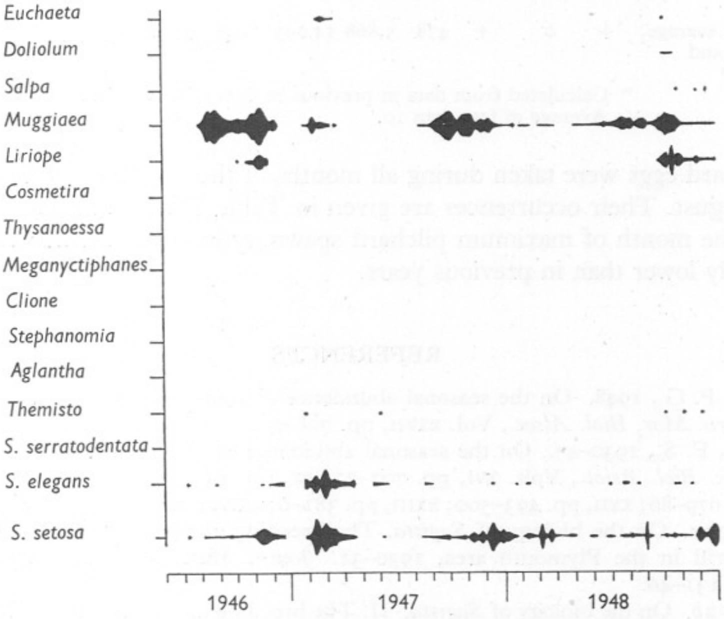

Fig. 2. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the period June 1946 to December 1948. (Continued from Corbin, 1948, p. 721, fig. 3.)

At the end of September (28th), *Liriope* appeared in considerable numbers. It continued until the end of the year in the catches, although only in small numbers in November and December.

Salps occurred on three occasions (27 October (35), 30 November (1), 15 December (69)), and doliolids were taken twice in October (4th (25), 21st (3)).

Three specimens of *Euchaeta hebes* also occurred in the catch of 4 October, and the hyperiid amphipod, *Themisto* was present in three hauls at the end of the year (4 October (1), 4 November (11), 6 December (1)).

*Beroe* was present during October, November and December, and *Aequorea pensilis* occurred in some numbers during November and December. Mr F. S. Russell kindly identified the *Aequorea* specimens.

Table IV. Pilchard Egg Catches, 1948

See Table I for dates of hauls.

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 0 | 0 | 17 | 3,160 | 1,860 | 1,300 | 0 | 0 | 57 | 1 | 0 |
| | 0 | 0 | 0 | 11 | 1,450 | 3,000 | 5 | 0 | 104 | 6 | 0 | 3 |
| | 1 | 0 | 2 | | | 7,980 | 103 | 0 | 14 | 7 | 4 | 1 |
| | 0 | 0 | 0 | | | 6,880 | 40 | 0 | 240 | 132 | 0 | |
| | | | 1 | | | 2,100 | 0 | 0 | | 10 | 0 | |
| | | | | | | | | 0 | | 0 | 4 | |
| Monthly average, 1948 | + | 0 | + | 14 | 2,305 | 4,364 | 290 | 0 | 89 | 35 | + | + |
| Monthly average, 1937–9 and 1946–7* | + | 0 | + | 478 | 5,868 | 14,093 | 6,196 | 385 | 415 | 305 | 398 | + |

* Calculated from data in previous reports of this series.

\+ Average of less than 10.

Pilchard eggs were taken during all months of the year except in February and August. Their occurrences are given in Table IV. The average catch in June, the month of maximum pilchard spawning in this area, was very considerably lower than in previous years.

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# A QUANTITATIVE METHOD FOR ESTIMATING THE PERIODICITY OF DIATOMS

By Anwar Abdel Aleem, M.Sc., Ph.D.
(Farouk University, Alexandria)
From Queen Mary College, University of London

(Plate I and Text-fig. 1)

## INTRODUCTION

The method described below was evolved as a substitute for counting, which is unsatisfactory for epiphytic marine diatoms. It depends upon the estimation of the amount of diatom-silica associated with unit dry weight of the substratum. The sea-weed samples are first freed from sand particles and are then treated with strong nitric acid in the usual way. In order to convert the insoluble silica of the diatoms into a soluble form suitable for chemical estimation, the material is fused in a platinum crucible with a mixture of $K_2CO_3$ and $Na_2CO_3$ and the fused mass is dissolved in (silica-free) distilled water and filtered. The amount of silica in the filtrate is determined colorimetrically according to the method of Dienért and Wandenbulcke (cf. Atkins, 1926). The method is simple in practice and saves considerable time and labour. The full procedure is illustrated by reference to a study of the periodicity of *Grammatophora marina* (Lyngb.) Kütz. at Swanage, Dorset.

This species (Pl. I) is found all the year round on *Cladophora rupestris* in a pit in one of the reefs at Peverel Point, Swanage. In summer it is the only epiphytic diatom on the *Cladophora*, while in spring and autumn small numbers of other epiphytes (*Cocconeis*, *Opephora*, *Rhoicosphenia*) are present. In order to obtain a fairly representative picture of the abundance of *Grammatophora* at different times, samples of the *Cladophora* were collected monthly from a definite area in the pit, each including 3–4 cm. of the apices of five to ten *Cladophora* tufts cut at random. The tufts are soaked in sea water to free them from sand particles and preserved in 4% formalin.

## METHOD OF ESTIMATION

After soaking in several changes of distilled water, the sample is transferred to a small crucible and dried in an electric oven at 100° C. for several hours; the crucible is then allowed to cool in a desiccator. When a constant weight has been attained, the contents of the crucible are boiled with concentrated nitric acid until all the organic matter is destroyed, as shown by the addition of a few crystals of potassium chromate. The remaining material is washed thoroughly with water, and subsequently repeatedly washed with alcohol or ether. After drying it is mixed with about twenty times its volume of $K_2CO_3$ and $Na_2CO_3$, in the proportions of 2:1, and the mixture is fused in a platinum crucible over a strong Bunsen flame for at least 20 min., care being taken to avoid a smoky flame. The melting-point is lowered by using the two carbonates.

After fusion is complete, water from a tap is allowed to play on the hot crucible in order to prevent the contents from adhering to the sides. The fused mass is then dissolved in warm distilled water and the solution filtered. If fusion has been carried out properly, no appreciable residue remains. The filtrate is diluted to 50 ml. with distilled water and shaken. According to the concentration of silica present, 1–5 ml. of this solution are pipetted into clean pyrex tubes, again diluted to 50 ml. and the amount of $SiO_2$ in the final solution determined colorimetrically. For each determination 2 ml. of a 10% solution of ammonium molybdate and four drops of 50% (by volume) sulphuric acid are required. After adequate stirring an intense yellow colour appears within 2–5 min. at 20–25° C. and this colour is matched with a standard colour produced by a known concentration of silica. For this purpose a set of B.D.H. 'V.H.B.' tinometer disks was used. The matching of the colour was carried out in daylight in front of a north window. The yellow colour is produced only within a certain range of pH (the resulting mixture should be close to pH 2), and one more drop of acid may suppress it altogether. Phosphates and arsenates give the yellow colour only when present in large amounts, but the diatom does not contain them. Errors in the chemical estimation of the silica owing to incomplete fusion or to incomplete production of colour during the colorimetric tests are easily avoided. The same interval of time was always allowed to elapse between adding the reagents and carrying out the tests which were always performed at approximately the same temperature.

For computing the amount of $SiO_2$ per gram dry weight of the *Cladophora* the following equation is used:

$$x = \frac{50e}{w},$$

where $x$ is the unknown quantity (in mg.) of silica found in 1 g. dry weight of *Cladophora*, $e$ the actual amount (in mg.) of silica present in 1 ml. of the filtrate as estimated with the tintometer, and $w$ is the actual dry weight of the sample in grams. $w$ includes the dry weight both of the substratum and of the epiphyte, but since that of the latter is negligible in comparison with that of the former a correction was deemed unnecessary. If sand is present, the cleaned diatom-material is well shaken in water, the liquid allowed to stand until the sand has settled and the supernatant liquid containing the diatoms poured off and centrifuged. The sandy sediment is dried and weighed, and the weight subtracted from the initial dry weight of the sample.

The results of a series of estimations are given in Table I.

TABLE I. ABUNDANCE OF *GRAMMATOPHORA MARINA* ON *CLADOPHORA* AT SWANAGE, EXPRESSED IN MG. OF $SiO_2$ PER GRAM OF DRY WEIGHT

| Date | $SiO_2$ |
|---|---|
| 1947 April | 80·0 |
| May | 58·8 |
| July | 17·6 |
| August | 12·7 |
| September | 26·6 |
| December | 21·7 |
| 1948 January | 37·8 |
| February | 88·1 |
| March | 34·5 |

### COMPARISON WITH THE COUNTING METHOD

The accuracy of the method was tested by counting the individuals of *Grammatophora* present in the samples (Table II). The cleaned diatom material was diluted with a definite volume of water, depending upon the density of the sample. After thorough shaking, a ml. at a time of the suspension was pipetted into a counting cell, ruled into 1 and $\frac{1}{16}$ mm. squares (corresponding to volumes of 1 mm.$^3$ and $\frac{1}{16}$ mm.$^3$ respectively), and holding just 1 ml. when covered with a cover-glass. According to the density of the sample, counts were made either, under low power, of the number of frustules in a square millimetre or, under high power, of the number within the field of the microscope. The squares or fields were chosen at random, the number counted ranging between 4 and 88. Half frustules were counted as such, although it was sometimes difficult, especially under low power to distinguish them from whole ones. After making the counts the contents of the cell were carefully washed back into the original suspension to be used for the fusion tests.

In computing the total number of frustules of *Grammatophora* per gram of dry weight of *Cladophora* in a sample the following formula was used

$$n = \frac{n_1 \times v \times 10^3}{w},$$

where $n$ is the total number per gram dry weight; $n_1$ is the average number of frustules in a cubic millimetre of the counting cell, $v$ the volume in ml. of the diluted diatom-material and $w$ the actual dry weight in grams of the original *Cladophora* material. This gives the number of individuals of *Grammatophora marina* per gram dry weight of *Cladophora* in April 1947 as

$$\frac{193{\cdot}6 \times 25 \times 10^3}{0{\cdot}5} = 9{\cdot}68 \times 10^6$$

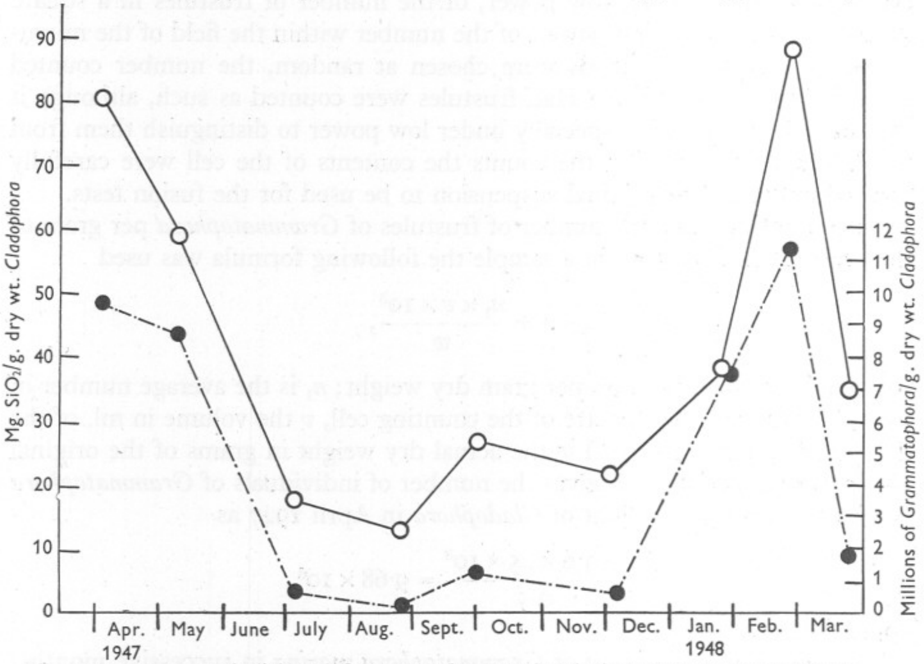
approximately.

The degree of abundance of *Grammatophora marina* in successive months, as determined by the two different methods, is shown graphically in Text-fig. 1.

The two graphs run almost exactly parallel and show clearly that *G. marina* has a pronounced maximum in early spring and a secondary one in autumn. Comparing the graphs and bearing in mind that they are drawn to different scales, that based on the silica content of the samples is relatively flat, the range of values being comparatively low. The amount of silica in the diatom material at the time of maximum abundance in February 1948 is only about seven times that found at the time of the minimum in August 1947, while the

TABLE II. COMPUTATION OF THE PERIODICITY OF *GRAMMATOPHORA* IN THE *GRAMMATOPHORA-CLADOPHORA* COMMUNITY AT SWANAGE BY THE COUNTING METHOD

| Date | Dry wt. of material (g.) | Volume of diluted material (ml.) | Average no. of individuals per 1 mm.$^2$ of the counting cell | No. of counts | $\sigma$ | $\sigma_{mean}$ | Total no. of individuals per g. dry wt. of material ($\times 10^6$) |
|---|---|---|---|---|---|---|---|
| 1947 April | 0·5000 | 25 | 193·6 | 14 | 57·41 | 15·34 | 9·68 |
| May | 0·5130 | 23 | 196·8 | 15 | 96·28 | 24·86 | 8·8 |
| July | 0·3922 | 28 | 10·0 | 4 | 3·7 | 1·85 | 0·7 |
| Aug. | 0·4374 | 23 | 1·5 | 16 | 1·07 | 0·27 | 0·08 |
| Sept. | 0·4360 | 30 | 18·0 | 13 | 1·86 | 0·52 | 1·2 |
| Dec. | 0·2303 | 46 | 3·2 | 15 | 2·18 | 0·56 | 0·64 |
| 1948 Jan. | 0·7940 | 46 | 128·0 | 35 | 53·52 | 9·04 | 7·4 |
| Feb. | 0·6810 | 50 | 152·0 | 76 | 29·67 | 3·4 | 11·2 |
| March | 0·7244 | 50 | 25·6 | 88 | 8·73 | 0·93 | 1·7 |



Text-fig. 1. Periodicity of *Grammatophora marina* during 1947–48, as computed by: (*a*) the silica-content method (——); (*b*) the counting method (—·—).

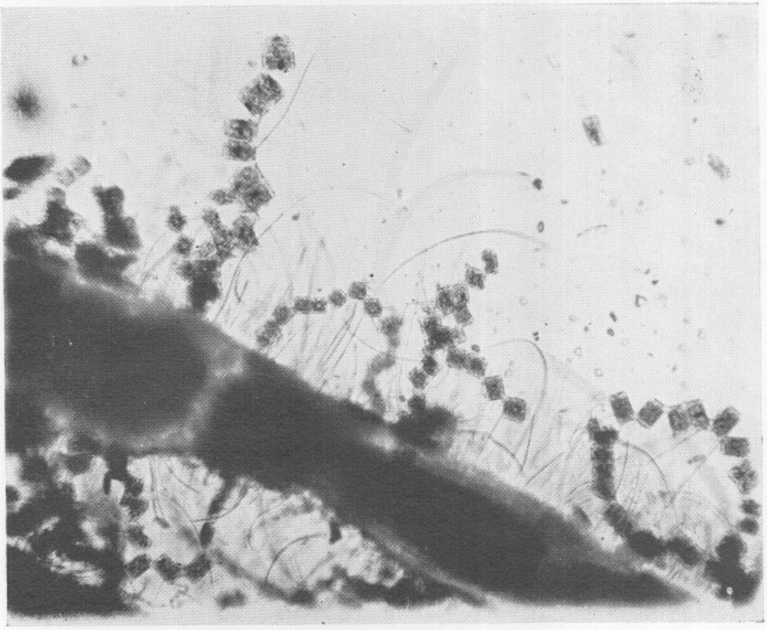


Fig. 1.

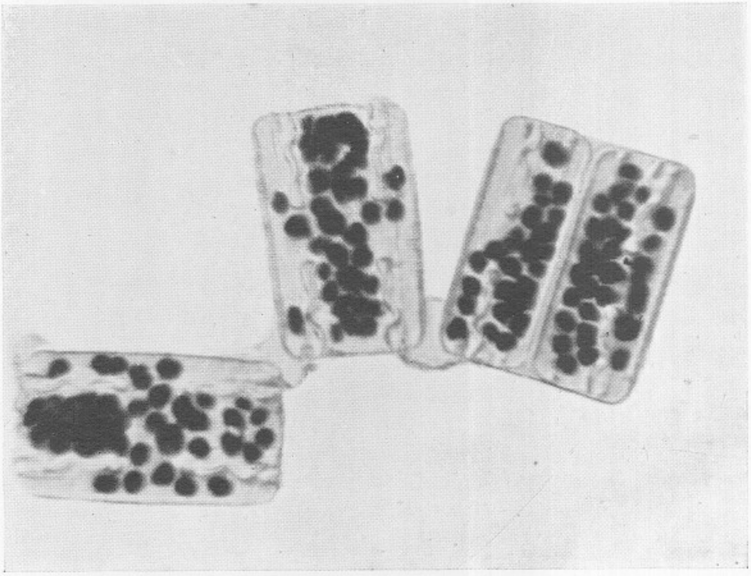


Fig. 2

counting method shows the ratio of the numbers of frustules on these two dates to be about 100:1. The discrepancy is due to the fact that the amount of silica is not actually proportional to the numbers of frustules, but to their total surface area.[1] At certain times, and especially when there is abundant multiplication, the individuals may be very small, a considerable number being only about one-quarter of the usual length. The occasional inclusion of a half as a whole frustule during counting is another cause for the discrepancy between the results of the two methods.

## Discussion

The ability of a diatom to assimilate silica from the medium and produce new frustules during multiplication affords a measure of its rate of growth. The total amount of growth at a given time will be represented by the quantity of silica present. The silica method is comparable to the pigment-extract method used by Harvey (1934), in which the amount of pigment extracted from a known volume of sea water is taken to indicate the quantity of phytoplankton present. The silica method, on the other hand, can be regarded as specific for diatoms.

The amount of silica in the diatom material can be expressed in terms of unit weight, unit area or unit volume of the medium or substratum. The method can therefore be used for determining the periodicity of planktonic, lithophytic (e.g. *Schizonema*) or epiphytic diatoms. The samples must not, however, contain other organisms having a siliceous envelope (e.g. Silicoflagellates).

The method is open to the criticism that the degree of silicifaction of the frustules of a given species of diatoms may not be the same at all times of the year or in individuals of different sizes. There is at present no accurate information on this matter, but it seems probable that the amount of silicification is constant in most species, judging from observations made at different times.

I am indebted to Prof. F. E. Fritsch, F.R.S., and to Dr W. R. G. Atkins, F.R.S., for valuable advice and criticism, and to Dr F. M. Haines for reading the manuscript.

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## EXPLANATION OF PLATE I

Fig. 1. Photomicrograph of the *Cladophora-Grammatophora* community.
Fig. 2. Part of the colony of *Grammatophora marina* shown above, enlarged.

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[1] It is assumed that the frustules are uniformly silicified and that the thickness of the valves is the same whatever the size.

# CASCADING OVER THE CONTINENTAL SLOPE OF WATER FROM THE CELTIC SEA[1]

By L. H. N. Cooper, D.Sc.
Chemist at the Plymouth Laboratory

and David Vaux, B.Sc.
Fisheries Laboratories, Lowestoft

(Text-figs. 1–14)

CONTENTS

This paper is an essay on the theme that water, cooled in winter, will sink and flow downhill over the sea floor. It will be shown that in some winters water in the Celtic Sea to the south of Ireland became heavy enough to flow to the edge of the continental shelf and there to sink to a depth of several hundred metres. It will be shown, further, that in one year it actually did so. A theory of this phenomenon, termed 'cascading', has been developed, and implications capable of test by observation are discussed.

## INTRODUCTION

A better understanding of the oceanography of the English Channel requires a fuller knowledge of the nature of the movements of water within the Celtic Sea, and of the water which enters or leaves the ocean over the Continental Slope. This need has been strengthened by the demand from the fishery naturalists for a statement of the physical and chemical conditions in the Celtic

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[1] For a definition of the name 'Celtic Sea', see Appendix, p. 750.

Sea during the mackerel investigations of 1937–39. In that area, and in the English Channel, attempts to correlate the distribution of plants, animals and chemical nutrients on the one hand with salinity and currents deduced from salinity and temperature diagrams on the other have been singularly barren. No correlation such as that between the winter maximum phosphate and the distribution of young fish has ever emerged.

This negative result has become so definite that it can have but one meaning; the presence of waters with similar salinities but very different physical and biological histories. Comparative study of the ocean water to the west and south-west seems essential. It would appear that there are three types of high-salinity water in the area: (*a*) North Atlantic Central water, with a well-defined temperature-salinity relation occupying the upper 600 m. well to the west and south-west; (*b*) the Mediterranean tongue between 800 and 1200 m. with a salinity in excess of 35·5 ‰ and 67–70 % saturated with oxygen, which may possibly, under certain conditions, be projected on to the continental shelf; and (*c*) 'cascade'[1] water formed by winter cooling of high-salinity waters on the banks to the west and south of Ireland with a salinity usually over 35·4 ‰ and an oxygen content over 90 % saturated. Since the problems are very complex, a complete and polished account must take many years to prepare. Here an attempt is to be made to dissect a single factor from the matrix of events; a final assessment of its importance relative to others must wait. The paper is an attempt to achieve a better understanding of exchanges between shelf and ocean for which Iselin (1940) so cogently argues.

It is widely recognized that the cold, dense abyssal waters of the ocean are formed in the Weddell Sea (Deacon, 1937), south-east of Greenland and to some extent in the Norwegian Sea (Nansen, 1912). In marked contrast the contribution to the intermediate layers of the oceans made by winter cooling of water over the extensive continental shelves in mid-latitudes has been neglected. None the less, the effect upon the oceans on the one hand and upon the productivity of fishing grounds on the other may well be profound. In this paper, therefore, the effect upon circulation in the Celtic Sea and the adjacent ocean of the increase in density of shelf water south of Ireland in winter is to be discussed.

## Present Views of Circulation in the Celtic Sea

The account given by Matthews (1914) remains unchallenged. In general, a current of salt warm water enters the English Channel from a south-westerly direction and in part turns northwards and north-westwards to escape into the Irish Channel. Part again follows the south coast of Ireland and, on occasion, there may be a centre to the cyclonic eddy in about 51° N., 6° 40′ W. It may be said at once that nothing here to be presented is in conflict with Matthews' account of a cyclonic circulation.

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[1] A very descriptive term due to Mr G. A. Steven.

## THEORY OF CASCADING[1]

In autumn and winter heat is lost from the surface of the sea mainly by radiation and evaporation. To a first approximation the extent to which this happens is directly dependent on the area of sea surface.

Let us consider two positions in winter, A and B (Fig. 1), having the same initial salinity, temperature and density, and exposed to similar meteorological conditions; at B the water is twice as deep as at A. If at B purely vertical mixing is sufficient to equalize the temperature there, the fall in temperature will be only half as great as at A. Although at both positions the loss of heat through the surface is much the same, at B, it would be distributed through twice the depth as at A. Since at A the water has become not only colder but heavier, it will tend to cascade or flow downhill along the bottom from A to B.

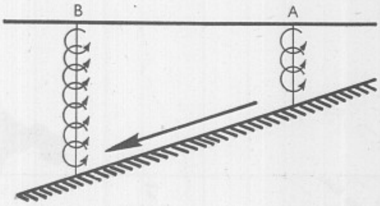

Fig. 1. The basis of cascading

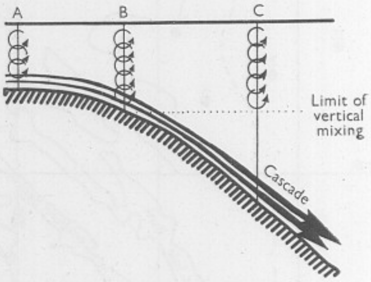

Fig. 2. Cascading over the Continental Slope.

Although in an enclosed tank the result would be an isothermal and completely uniform body of water in which it would be impossible to separate downhill movement from purely vertical mixing, in nature this need not be so.

Let us consider the edge of the continental shelf above the continental slope (Fig. 2). At the inshore and shallower station A the water should be cooled to a greater extent than at the deeper station B. In consequence a bottom or cascade current should become established from A to B. All the time straightforward vertical mixing due to wind and cooling *in situ* will be occurring down to the depth of maximum vertical mixing. The combined result should be a current setting from A through B with its greatest strength near the bottom. When the bottom current approaches the edge of the slope there should come a depth to which vertical mixing could no longer reach as indicated by the dotted line near station C. It would, however, continue to cascade as a heavy

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[1] After we had received proofs of the present paper, we saw, unfortunately, for the first time, a paper by Fridtjof Nansen (1913), describing the effect of winter cooling over the Rockall Bank and the descent of the resulting heavy water over the adjacent slope. Nansen has given a complete description of cascading there. Since the importance of his concept, as applied in temperate latitudes would seem not to have been widely recognized and accepted, a completely independent derivation and application in another area, accompanied by further deductions, may not prove unwelcome. Accordingly no alteration has been made in the present text.

relatively cold blanket of water until it should reach such a depth on the wall of the slope as would correspond to the density of the neighbouring ocean water. In a cold winter this depth would evidently lie deeper than in a mild one.

Since the cascaded water has to be replaced, somewhere or other compensation water must break in, most probably from the ocean. This theme will be more fully discussed on pp. 735–40.

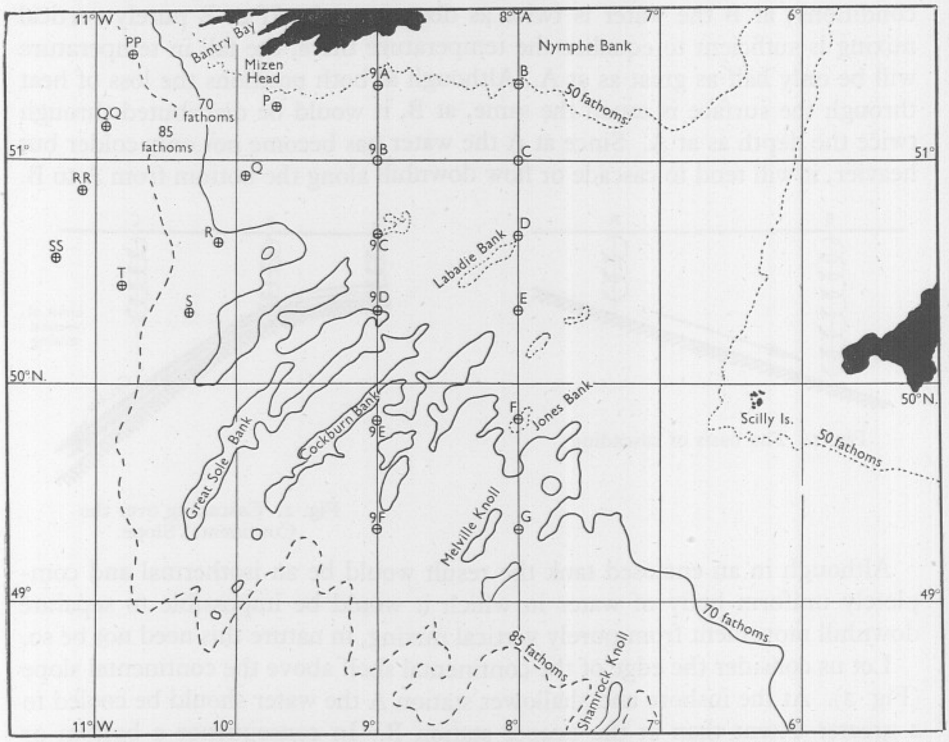


Fig. 3. Submerged 'river valleys' as revealed by the 70 and 85 fm. contours, and of banks as revealed by the 50 fm. contour; also positions of standard Irish Stations worked between 1921 and 1933.

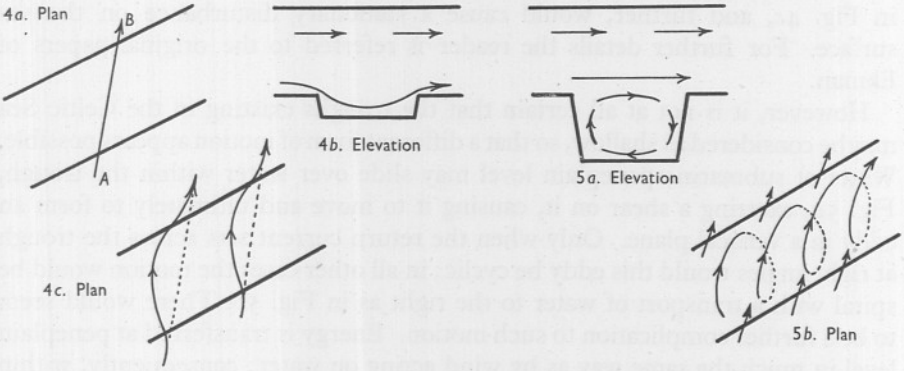
## The Influence of Banks and Submarine Valleys

It is necessary here to develop another concept needed later. Contouring the chart in the neighbourhood of the Great Sole and Cockburn Banks (49° 45′ N., 9° 30′ W.) reveals a very striking picture of a submarine peneplain[1] at 65 fm. (120 m.), dissected by troughs about 15–20 fm. deep like a series of submerged river valleys (Le Danois, 1938, fig. 10), the direction of which is south-west to north-east (see Fig. 3).

[1] A 'peneplain' is a gently rolling lowland produced after long-continued denudation of a land mass. The floor of the Celtic Sea conforms closely to this definition except that it is submarine. The term is graphic and more suitable than 'shelf' or 'terrace' for the arguments to be developed.

It may be remarked that the depth of 120 m. (400 ft. or 65 fm.) figures frequently in discussions of the maximum withdrawal of the sea during the Pleistocene Ice Ages (*inter alia*, Farrington, 1945; Flint, 1947).

The soundings on the charts, which are not dense enough to give any idea of the vertical sections across the troughs, do not require any gradient steeper than 1 in 100. However, it would seem that during the period of low sea-level when these troughs were probably cut, the climate was glacial and the rivers concerned drained the whole of northern France, southern and western England and Wales, eastern Ireland, and perhaps even the Clyde Basin. They should have been strongly seasonal with little flow in winter and very heavy erosive spates during the summer melting of the ice; such may well have led to deep entrenchment between steep banks when carved in consolidated rock. However, 60 miles to the south, Bullard & Gaskell (1941) have made two seismic soundings of the sea floor. They believe that unconsolidated sediments at 48° 54′ N., 9° 10′ W. extend to at least 1090 m., and at 48° 45′ N., 9° 48′ W. to 2470 m. below the sea floor. In such unconsolidated sediments glacial rivers would have cut down exceedingly quickly; with the return of the sea the banks would have been destroyed and the river beds filled in just as easily. Only an echo-sounding survey can show quickly whether any steep banks now remain. It may then be possible to say how far such submarine valleys may canalize bottom currents in this area in a south-westerly–north-easterly direction and impede currents whose direction is at right angles to the axis of the valleys.



Figs. 4 and 5. Diagrams illustrating possible water movements above valleys or troughs dissecting a submarine peneplain. Fig. 4*a*, *b* and *c*: motion above shallow troughs; Fig. 5*a*, *b*: over and in deep troughs.

We can investigate the situation theoretically by a simplification of the factors involved. Consider a parallel-sided trough in an otherwise level submarine peneplain, and let a current set across the trough at an angle to the longitudinal axis of the trough. In diagram Fig. 4*a*, *AB* represents the direction of the current at peneplain level. Such a current may be produced by tidal forces, density differences between adjacent masses of water, or wind. If the current be wind-produced, the direction of current at peneplain level would, according to Ekman's (1905) theory of wind drift, be different from that at the surface. However, if the current at peneplain level flows in a given direction *AB*, it is of no importance to the theory which follows whether the water above flows all in one direction or according to an Ekman spiral.

In order to continue the investigation, it appears necessary to differentiate between two possible forms of motion. If the water sinks into the trough and rises at the opposite side, as Fig. 4*b*, the theory developed by Ekman (1923, 1927, 1932), and summarized by Sverdrup (in Sverdrup, Johnson & Fleming, 1942, pp. 466–9), would seem to apply. In the Celtic Sea the influence of a shallow trough would be to cause a deviation in current direction, as shown in Fig. 4*c*, and further, would cause a stationary disturbance on the sea surface. For further details the reader is referred to the original papers of Ekman.

However, it is not at all certain that the troughs existing in the Celtic Sea may be considered as shallow, so that a different form of motion appears possible. Water at submarine peneplain level may slide over water within the trough, Fig. 5*a*, exerting a shear on it, causing it to move and ultimately to form an eddy in a vertical plane. Only when the return current sets across the trough at right angles would this eddy be cyclic; in all other cases the motion would be spiral with a transport of water to the right as in Fig. 5*b*. There would seem to be a further complication to such motion. Energy is transferred at peneplain level in much the same way as by wind acting on water; consequently, within the trough a form of Ekman spiral, much modified by turbulence, should be set up.

When conditions along the trough are not uniform, yet another possibility may arise. At a point where the current within the trough is weak, the water approaching its edge could turn back on itself at the same level, producing something akin to a 'rip current' (see Shepard, Emery & La Fond (1941) for a description of surface rip currents).

A theoretical solution at this stage seems impossible, but it appears from the survey outlined above that turbulence from bottom to surface should be great, and that energy is dissipated, causing diminution in the original currents. This turbulence may redistribute nutrients throughout the water column and, providing it is not excessive, favour their more efficient usage by plants.

Tentative inferences for the Great Sole-Cockburn Bank Area which can be substantiated only by fresh observations on the spot, are: (1) that currents, however caused, may tend to conform to the direction of the submarine valleys; (2) that in summer the thermocline should be more weakly developed than in neighbouring undissected regions of the shelf having the same depth and exposure to ocean swell; (3) that a useful stock of inorganic nutrients, including iron, may be maintained in the upper photosynthetic zone right through the summer; and (4) that the falling off in late spring in production of phytoplankton, so characteristic of the waters near Plymouth, where the thermocline may develop very strongly, may be much less marked.

### Cascading in the Winter of 1929–30

Within the 100 fm. contour of the Celtic Sea extensive salinity and temperature observations, collected mostly between 1921 and 1933 by the Irish Fisheries Service under the direction of the late Mr G. P. Farran, are available, but for the waters bathing the continental slope there are far fewer. All the observations have been taken from the 'Rapports Atlantiques' and the 'Bulletins Hydrographiques' published annually by the International Council for the Exploration of the Sea, Copenhagen. Satisfactory proof of cascading is difficult to adduce on the basis of salinity and temperature alone and to clinch the argument the measurements of oxygen and pH made on board *Armauer Hansen* in 1914 have been invaluable.

Other factors being similar, cascading should have developed most strongly in those winters in which air temperatures were low. To assess meteorological cooling of the sea, some way of integrating departures of temperature from the mean during the whole winter is needed; not an easy task. As a lead, air temperatures in February at Valencia (Cahirciveen), Scilly and Guernsey were examined. Of the years 1921–33, 1930 was the coldest at Valencia (below average by 2·7° C.) and at Scilly (by 2·3° C.); Guernsey was somewhat cold but only below average by 1·3° C. By contrast in 1929, whereas Valencia and Scilly were average, the Guernsey mean February temperature was 2·7° C. below average. This was reflected in the discrepancy in temperature difference between the Hurd Deep, north-east of Guernsey, and the waters south-west of Ireland (Cooper, in Steven, 1949, Appendix). In 1924, and again in 1932, the whole area was below average by 0·9–1·2° and 1·4° C. respectively. The year 1927 was average, whilst 1926 and 1928 were well above average, and consequently unattractive for our present purpose.

On this evidence the winter of 1930 appeared most likely to yield results. In mid-February of that year the density, $\sigma_t$, of bottom water in the northern Celtic Sea along the meridian of 8° W. was around 27·3 and along that of 9° W. 27·4. West of Co. Mayo, 200 miles to the north and 3 months earlier, H.M.S. *Ormonde* had found that water having $\sigma_t$ 27·3–27·4 lay between depths of 400 and 700 m. (Fig. 6). If one may correlate observations made so far apart, it would seem that the shelf water in the northern Celtic Sea was heavy enough to sink over the slope to between 400 and 700 m. Unfortunately, there is yet another consideration which makes it unwise to base the theory of cascading on events in 1930.

Wind must always be a force, often a very powerful force, able to initiate and maintain currents. If in any winter the distribution and power of winds were such as to set up a current system in the same sense as that demanded by cascading, then evidence from that winter ought not to be adduced in favour of cascading. For 21 out of the 28 days of February 1930, winds blew from the north-eastern quadrant and on 16 of those days the force exceeded three on the Beaufort scale. Such winds would, of themselves, provide a likely explanation of currents towards the west and south-west. This issue is discussed again later.

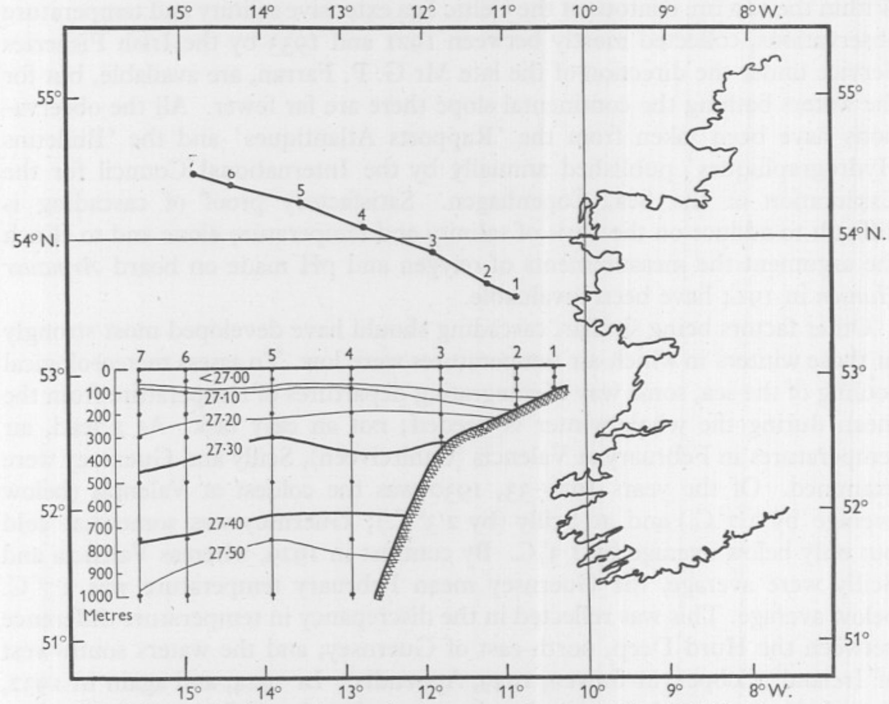


Fig. 6. Densities (shown in inset) along a section worked by H.M.S. *Ormonde* off the west coast of Ireland, 22–25 October 1929.

## Cascading in the Winter of 1926–27

Owing to the unsuitability of the winter of 1929–30, attention was switched to that of 1926–27. In this year the February air temperature at Valencia and Scilly equalled the average for the 13 years, 1921–33. With a very full network of Irish, English and French stations all worked between 15 and 20 February 1927, a simultaneous and revealing picture of the whole shelf is possible.

Temperatures were lowest ($<8^\circ$ C.) in the Irish Sea and the eastern end of the English Channel, and increased to the west and south-west. Within the Celtic Sea the coldest water ($<9^\circ$ C.) lay over the Nymphe Bank. The conditions are, however, best understood from the distribution of surface density. In the Irish Sea the low temperature was more than outweighed by the low salinity (34·3–34·4‰ on the Holyhead-Kingstown line). In consequence, density ($\sigma_t$) at the surface (Fig. 7) increased towards the south-west, exceeding

27·30 on the Nymphe Bank at the eighth meridian and reaching 27·40 at the ninth as in 1930.

The English Channel showed quite a different pattern, since a lane of high density (>27·30) stretched throughout its entire length from the Southern Bight of the North Sea to the Celtic Sea. North of 49° N. in the latter, the distribution of surface density well represents that of the deeper water as shown by the three vertical sections (Fig. 8) whose position is shown on Fig. 7; south of 49° N. the distribution of density was utterly different and has to be discussed later (pp. 737–9). Even so, to the north there was more than 10,000 square miles of sea with density exceeding $\sigma_t$ 27·30, potentially heavy enough to cascade and backed up by yet more heavy water in the English Channel.

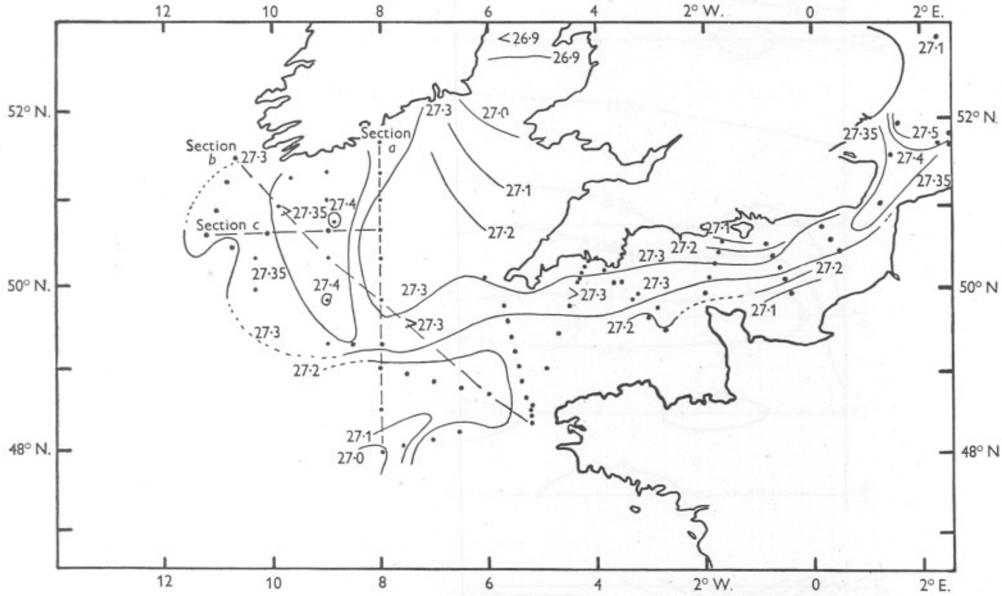


Fig. 7. Distribution of density of surface water between 15 and 20 February 1927. Also lines of three sections, vertical profiles along which are shown in Fig. 8. Profile *a* along section *a* (8° W. long.); profile *b* along section *b* (north-west to south-east); profile *c* along section *c* (approx. 50° 40′ N. lat.).

The only observations over the edge of the slope were at the Irish station SS (50° 34′ N., 11° 17′ W.) which was worked in August 1926 and February 1927. In August density increased downwards from $\sigma_t$ 27·01 at 60 m. to 27·32 at 400 m. and 27·40 at 600 m. The ocean there was prepared to receive water of density $\sigma_t$ 27·32 down to 400 m. By February such water ($\sigma_t$ 27·33, 10·52–10·67° C., 35·59–35·61 ‰ salinity) had arrived between the surface and 400 m. It is the thesis of this paper that it had arrived by cascading.

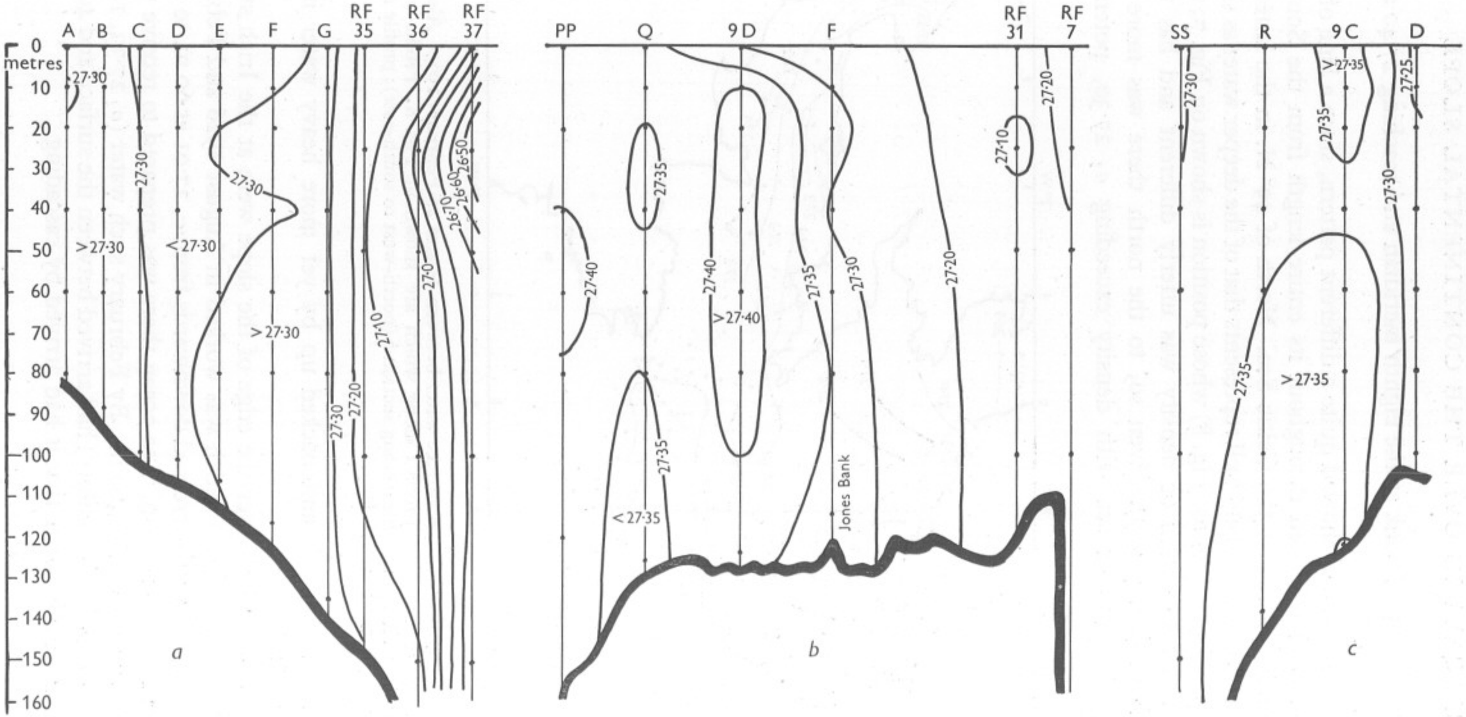


Fig. 8. Vertical profiles of density $\sigma_t$ along the three sections shown on Fig. 7.

This 1927 data will be used again (pp. 733–5) in an attempt to establish the course taken by cascade water.

## CASCADING IN THE WINTER OF 1913–14

The evidence considered so far has shown that cascading could have happened; it has not shown that it did. The observations beyond the slope have been scanty and, in any event, assurance can never be based on salinity, temperature and density alone. The most convincing evidence was obtained by the *Armauer Hansen* in June 1914, and to make best use of it requires knowledge of conditions in the preceding winter, 1913–14. The Irish observations were few; of the usual network only stations P and Q were worked, together with several stations in the Nymphe Bank area. Detailed examination of all the surface data, collected in February and March 1914, by merchant vessels in the eastern North Atlantic and Celtic Sea, has shown that some are under a heavy cloud of suspicion. The results of certain vessels, however, are consistent and appear sound, and these show that the distribution of temperature, salinity and density in the Celtic Sea in early 1914 was very similar to that in early 1927. At the Irish station P (51° 14′ 30″ N., 9° 43′ W.) and at Q (50° 56′ N., 9° 56′ W.) the temperature, salinity and density of the water at various depths have been compared with the means which had been calculated from all the observations ever taken there in February; at both stations the 1914 values agreed almost exactly with the mean. Moreover, in February 1914, air temperatures at Scilly, Valencia and Guernsey did not differ significantly from the respective means over the 13 years, 1921–33. Both of these statements have been shown to be similarly true for 1927. Since in 1927 (Fig. 8) surface values gave a sufficient picture of conditions on the shelf down to the bottom, it is highly probable that the same was true in 1914.

In February 1914, the surface observations showed that most of the Celtic Sea away from the coasts was occupied by water having $\sigma_t$ exceeding 27·30; a section of 120 miles along 49° 45′ N. latitude revealed no values of $\sigma_t$ less than 27·40. Such surface water was heavy enough to cascade, and evidently there was a great deal of it. Later two sets of observations were taken across the slope at the positions shown in Fig. 9 (sections *a* and *b*). There was an Irish line (*Bull. Hydr.*, 1913–14) at about 50° 30′ N. on 14 May, the densities along which are shown in Fig. 10, and a line by the *Armauer Hansen* (Helland-Hansen & Nansen, 1927) at about 48° N. on 5–6 June (Fig. 11*a*). No water heavier than $\sigma_t$ 27·30 was found along either at less than 550 m., while water having density between 27·30 and 27·40 occupied the next 250 m. interval. Thus the February shelf water with the same density limits, if it had cascaded, would by May-June have sunk to some depth between 600 and 850 m. at station 6 and between 700 and 1000 m. at station 7.

For a number of years we have shown that the water of the Celtic Sea

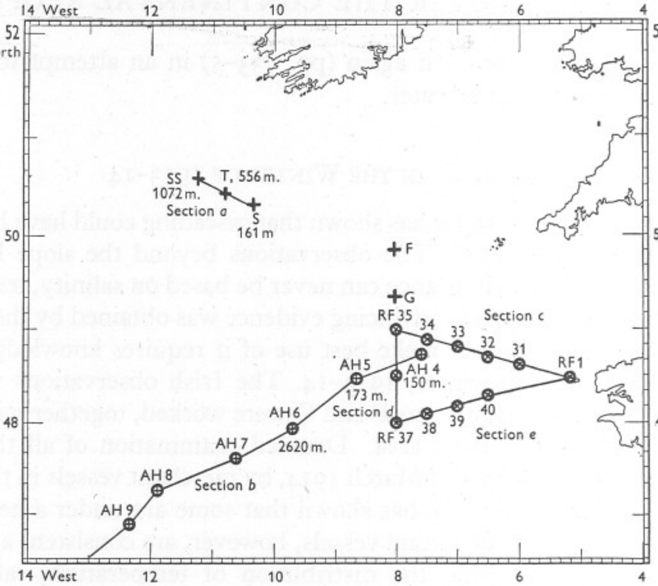


Fig 9. Chart of sections of which vertical profiles of density $\sigma_t$ are given in Figs. 10, 11 *a* and 13. **Section *a*.** Stations S–T–SS worked by the Irish Fisheries Service on 14 May 1914 (see Fig. 10). **Section *b*.** Stations 4–9 worked by the Norwegian research vessel *Armauer Hansen* on 5–6 June 1914 (see Fig. 11 *a*, *b* and *c*). **Sections *c*, *d* and *e*.** Stations RF 1 and RF 31–40 worked round a triangle by a French gunboat on 15–16 February 1927 (see Fig. 13 *c*, *d* and *e*).

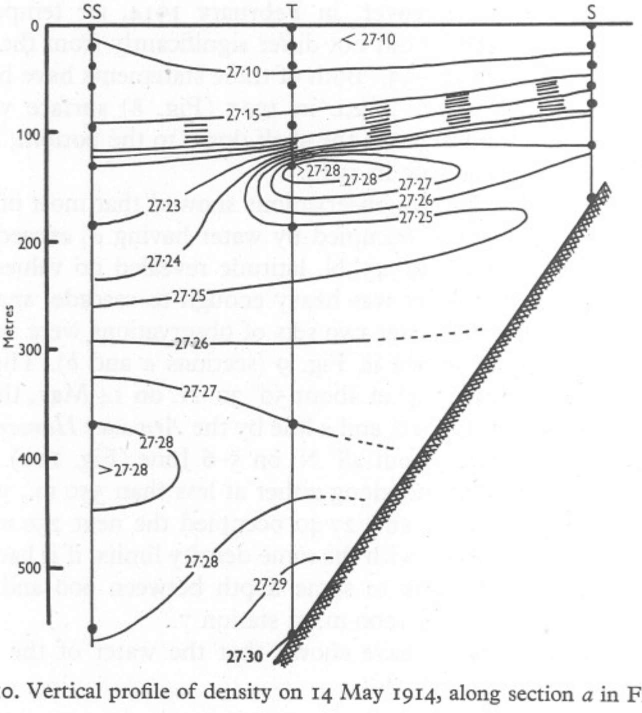


Fig. 10. Vertical profile of density on 14 May 1914, along section *a* in Fig. 9.

became heavy enough to cascade, but in only this one, 1914, can we show that it actually did. What is needed is some measurement to demonstrate beyond doubt that the deep water, having $\sigma_t$ 27·30–27·40, had been at the surface only shortly before. The oxygen determinations made by Gaarder (1927*a*) on board *Armauer Hansen* in the first week of June 1914 achieve this (Fig. 11*b*). His stations 8 and 9 represent conditions in the open Atlantic; since in the uppermost 40 m. of water recent production by photosynthesis had exceeded consumption by respiration and breakdown, oxygen was supersaturated with respect to atmospheric pressure. From 40 m. the oxygen content decreased steadily downwards to the minimum, 67–70 %, saturated, in the layers between 800 and 1000 m. depth. Still farther westward this happened in North Atlantic Central water but here it occurred in water with a strong, warm, highly saline Mediterranean component. Nearer the slope in water 2620 m. deep at station 6 (47° 57′ N., 9° 42′ W.), as shown in Fig. 9, a very different vertical distribution was present (Fig. 11*b*). At 400, 800 and 1200 m. there were three strata of oxygen-rich water sandwiched between oxygen-depleted layers. This odd result, standing unsupported, would carry considerable doubt as to the soundness of the single oxygen determinations; but they are supported. At 800 and 1200 m. the value of pH, 8·13, was the same as at 100 m. (Gaarder, 1927*b*). Much later Buch, Harvey, Wattenberg & Gripenberg (1932) and Buch (1933) evaluated the constants of the carbonic acid system in sea water so that it is now possible to evaluate partial pressures of carbon dioxide $p_{CO_2}$ from determinations of pH, salinity and temperature. It is necessary that pH should have been determined as described by Buch with due account of the several corrections needed. Consequently, it is unlikely that Gaarder's 1914 measurements could be suitable for accurate computations of partial pressure of carbon dioxide, $p_{CO_2}$, but none the less, they may be used for a rough and ready treatment sufficient for the present purpose. The results (Fig. 11*c*) are striking, since a partial pressure, $3{\cdot}4\text{–}3{\cdot}5 \times 10^{-4}$ atmospheres in water so deep as 800 and 1200 m. is very unlikely in water which had been unventilated for any considerable time. There seems no choice but to believe that all the water at 800 m. and most of that at 1200 m., bracketing the depleted Mediterranean tongue between, had cascaded from the shelf 3 months or so earlier. It should also be noted that the salinity at 50–200, at 800 and at 1200 m., 35·52–35·53 ‰, was constant; the waters agree in salinity, oxygen percentage saturation, pH and partial pressure of $CO_2$ and differ only in temperature and density. There can be little doubt that they represent successive stages in the cascading of essentially the same body of shelf water as the temperature fell and rose again. At 400 m., however, since the high oxygen content, 99 % saturated, was associated with pH 8·05, $p_{CO_2}$ $4{\cdot}4 \times 10^{-4}$ atmosphere and salinity 35·47 ‰, no firm conclusion may be drawn.

Water cascading down the slope should inevitably acquire considerable momentum; if, therefore, heavy shelf water should have sunk to a level of

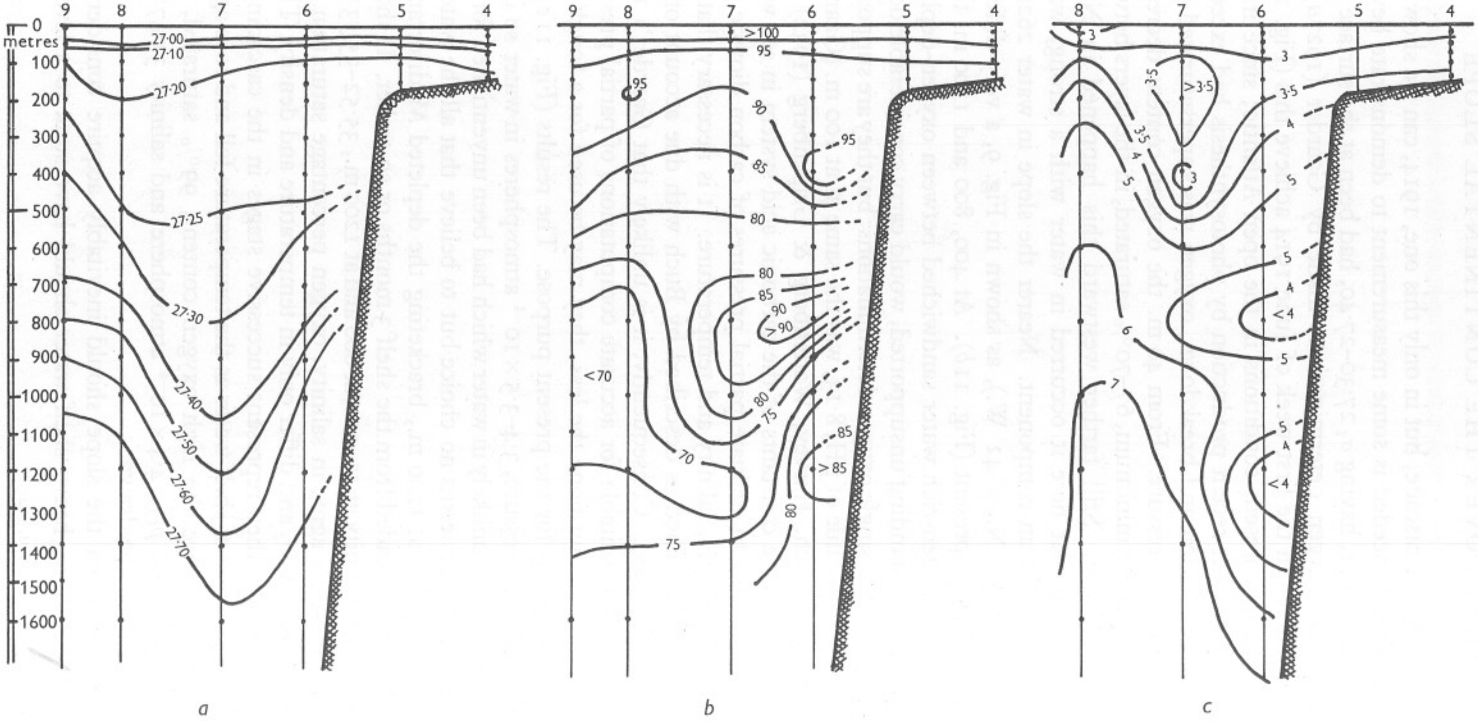


Fig. 11. Profiles drawn from *Armauer Hansen* observations on 4–6 June 1914 along section *b* of Fig. 9. *a*, density $\sigma_t$; *b*, oxygen as percentage saturation value under atmospheric pressure; *c*, partial pressure of carbon dioxide, $p_{CO_2}$, as atmospheres $\times 10^{-3}$, approximate only and computed without detailed corrections.

density equal to its own, it might perhaps spread out at that level giving rise to lateral mixing along surfaces of equal $\sigma_t$. Such mixing takes place with minimum change in potential energy, the momentum or kinetic energy being used to overcome internal friction or to displace other bodies of water. If the cascade on the slope should become canalized within a submarine canyon, it would become a core which might possibly penetrate at its appropriate $\sigma_t$ level many miles into the ocean. This may have been the origin of the oxygen-rich water, apparently a core, found on 7 June 1914, at *Armauer Hansen* station 10 (46° 26′ N., 13° 14′ W.) at 600 m. (94·5 % saturated) and at station 11 (46° 00′ N., 14° 03′ W.) at 800 m. (86 % saturated). These stations were respectively 190 and 220 miles from the nearest part of the slope. Moreover, their densities were no greater than 27·26 and 27·28, and the temperatures and salinities were typical of western Celtic Sea water in January or April.

## THE COURSE OF THE CASCADE

In general, the water near the slope has a higher salinity than that to the east at 9° W., at 8° W., and over the Nymphe Bank. When cascading happens it must necessarily draw colder but less saline water towards the west or south-west, so that during late winter and early spring, a decrease in salinity should mark the course of the water cascading from the Nymphe Bank.

In 1927, fortunately, the Irish records were unusually complete, not only in February, but also in May, so that in that year it is possible to assess the changes in salinity over a wide area and so to chart the most probable course of the northern part of the cascade current. The two cruises were run between 17 and 20 February and between 6 and 10 May; in Fig. 12 the stations worked on both are shown. It will be seen that the fall in salinity was especially marked on the eighth meridian between the coast and 51° 00′ N., at all stations worked on the ninth meridian, and at 51° 15′ N., 9° 43′ W. This is precisely the distribution that the theory of cascading demands. It would seem that water cascading from the region of the Nymphe Bank set west-south-west across the eighth meridian between the Labadie Bank and the coast of Co. Cork. Towards the ninth meridian it would seem to have divided; the northern branch hugged the coast and passed Mizen Head in a lane 20 miles wide, whilst the southern branch set south-west or south-south-west, with its axis crossing the ninth meridian at about 50° 20′ N. and heading towards the Great Sole Bank area. It is suspected that its further course was controlled by the bottom configuration of that much dissected region, but direct observations are lacking. A similar fall in salinity took place in other, but not in all, years.

In the 11 weeks elapsing between the two 1927 cruises, the isohalines had advanced about 50 miles to the west or south-west. This gives an average speed of the cascading water at 9° W. of about 0·6 miles per day.

A submarine bank in the way of the cascade should impede it, a submarine valley should encourage it; consequently, the fall in salinity between February and May 1927 should have been least over a bank and greatest over a valley. This was the case: on the ninth meridian at station 9C, on the edge of a bank, the fall in salinity was less by 0·03 $^{0}/_{00}$; and at station 9D, at the head of a valley, it was greater by 0·02 $^{0}/_{00}$ than a smoothed curve along the meridian would have suggested. A similar deficiency of about 0·04 $^{0}/_{00}$ shows up on the eighth meridian at station D at one end of the Labadie Bank. These results, slender though they are, combined with the considerations set out on pp. 722–4, have assisted in the extrapolation of Fig. 12 towards the Great Sole Bank.

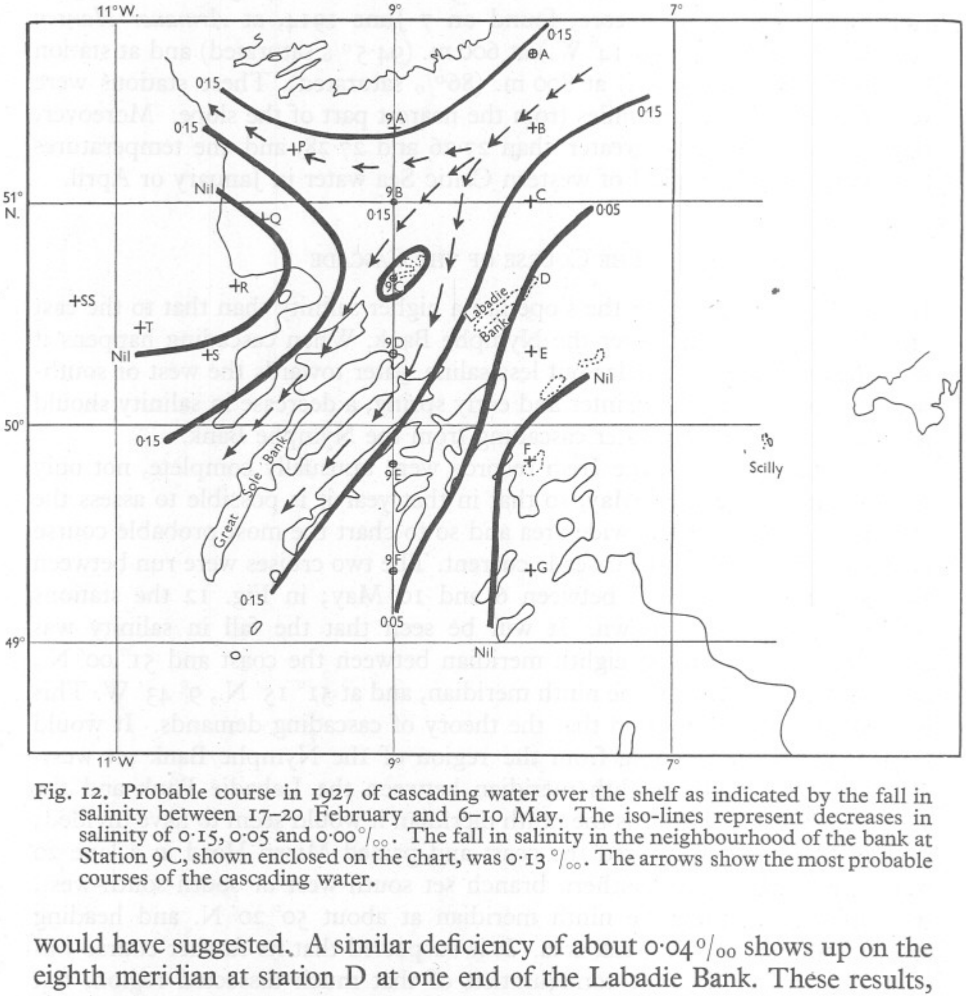


Fig. 12. Probable course in 1927 of cascading water over the shelf as indicated by the fall in salinity between 17–20 February and 6–10 May. The iso-lines represent decreases in salinity of 0·15, 0·05 and 0·00 $^{\circ}/_{\circ\circ}$. The fall in salinity in the neighbourhood of the bank at Station 9C, shown enclosed on the chart, was 0·13 $^{\circ}/_{\circ\circ}$. The arrows show the most probable courses of the cascading water.

It is not easy to assess the effect of the Corioli force, due to the earth's rotation, upon the cascade. It operates not on residuals, but on the currents which actually flow and include relatively large alternating tidal components. One can say only that the effect of the earth's rotation should be to encourage the cascade to hug the Irish coast and this the northern branch seemed to do.

Water from south-east of the Labadie Bank may also have contributed materially to the cascade. Since it was warmer but more saline, its course cannot be followed by these devices.

### Compensation Water

The theory of cascading requires that loss of heavy water over the slope shall be made good by an inflow somewhere or other. Five sources of such compensation water may be considered:

(*a*) From the north-eastern Atlantic via the North Channel and the Irish Sea.
(*b*) From the North Sea via the Straits of Dover.
(*c*) By upwelling at a restricted part of the slope of the Celtic Sea.
(*d*) By an influx of saline but relatively warm and light Atlantic oceanic surface water.
(*e*) By an influx of coastal water from the French Biscayan shores.

(*a*) According to Proudman (1946, p. 591) the mean current through the Irish Sea is from south to north, entering through the St George's Channel and leaving through the North Channel. In February 1927, water having density ($\sigma_t$) 26·7 lay right across the Irish Sea from Holyhead to Kingstown, so that then the Irish Sea could have made no contribution to the cascade. It is unlikely that it ever does.

(*b*) The flow of water through the Straits of Dover has been very fully investigated at the Varne Lightvessel by Carruthers (1935). The mean flow of water in the nine Februaries of 1927–35 was 1·9 sea miles per lunar day towards N. 1° W. true. In all other months the flow was directed to between N. 14° E. and N. 33° E., whilst the strength ranged from 2·6 to 4·1 miles per lunar day. In February there is evidently strong westing and diminution of the 'normal' flow. Although this is precisely the effect which one would expect cascading from the Celtic Sea to have on the Straits of Dover current at the Varne, little confidence can be placed in the correlation. Following winds play a large part in impelling water towards the north-east through the Straits of Dover, and it so happens that February has been the month with least favourable winds. Again, March, which should be a month of strong cascading in the Celtic Sea, shows a set of average strength (3·0 miles per lunar day). Possibly more revealing is the average direction of the current, arranged in Table I, according to direction, by months for the 8 years, June 1926–May 1934.

Apart from September, which is irregular, the months with a set between N. 9° W. and N. 18° E. were those when some measure of cascading might have been expected, those with a set between N. 22° E. and N. 35° E. were months when cascading should not have occurred.

TABLE 1

AVERAGE DIRECTION OF CURRENT AT THE VARNE LIGHTVESSEL, STRAITS OF DOVER, ARRANGED BY MONTHS, FOR THE 8 YEARS, JUNE 1926 TO MAY 1934

| | | | | | |
|---|---|---|---|---|---|
| February | N. 9° W. | July | N. 22° E. | October | N. 26° E. |
| May | N. 11° E. | August | N. 22° E. | December | N. 26° E. |
| September | N. 13° E. | | | January | N. 34° E. |
| April | N. 15° E. | | | November | N. 35° E. |
| June | N. 17° E. | | | | |
| March | N. 18° E. | | | | |

One is entitled to ask whether the backing of the current by 43° between January at the end of the Table and February at the beginning is brought about in some measure by initiation of cascading from the Celtic Sea.

This possibility is supported by the distribution of density between 14 and 20 February 1927 (Fig. 7); for then a continuous line of water heavy enough to cascade ($\sigma_t > 27\cdot30$) connected the Southern Bight through the English Channel with the Celtic Sea. Some compensation water for the Celtic Sea cascade could have been recruited along this lane.

A coincidence which may not have been due to chance should be noted. In his first report on current measurements at the Varne Lightvessel, Carruthers (1928) discussed at length the strongest set of the current towards the French coast, as assessed between 24 June 1926 and 8 January 1928. This set of 6·1 miles per day towards S. 81° E. occurred between 16 and 19 February 1927 during light local winds. Although not a reversal of the current it was a marked departure from normal. It would seem to reflect the pulse of the Celtic Sea cascade, transmitted along the Channel and revealed at the Varne in the absence of the currents, due to prevailing winds, which often completely obscure it.

Again, the strongest south-westerly set, 12·9 miles per day towards S. 51° W., reported in Carruthers's second paper (1935), occurred in the cold winter of 1930—on 7–10 February—when we have reason to believe that the Celtic Sea cascade was very strongly developed (pp. 743–4).

It is, therefore, possible that cascading from the Celtic Sea in February and March may provide one, but only one, of the forces which control currents in the Straits of Dover. Its effect may be to oppose, but seldom to cancel, the forces which tend most often to drive water from the Channel into the Southern Bight. The amount of compensation water from this source is probably small.

(*c*) Strong persistent easterly or north-easterly winds, blowing surface water from the shelf over the ocean, should here create the situation recognized the world over as favourable to upwelling of deeper nutrient-rich ocean water from several hundred metres. In winter such winds are cold winds which also favour cascading. Much of the slope west of the Celtic Sea should then be blanketed with a poorly stratified water which has recently cascaded. Upwelling of this, even if it should happen, would merely restore the *status quo*.

It is suspected but not proved (Cooper, 1947) that internal waves in stratified deep oceanic water approaching the slope may run up it like a surface wave up a beach, so introducing nutrient-rich waters to higher levels. If a weakly stratified blanket of cascaded water lies between the stratified ocean water and the slope, the energy of the waves should be absorbed by the blanket and fail to reach the slope. Upwelling due to internal waves should therefore occur, never in winter and early spring, but perhaps in summer and autumn. Simultaneous cascading and upwelling seem to be incompatible. Unless very definite evidence can be found, it would seem that compensation, by upwelling, of water lost by cascading is very unlikely.

(*d* and *e*) It would seem, therefore, that the main compensation for water lost by cascading should be provided by surface oceanic or Biscayan water entering the Celtic Sea from the south-west. Such intrusion of oceanic water frequently occurs and has been called by Le Danois (1938, p. 150) in French a 'transgression' and in English an 'expansion'. He defines a transgression as '*un mouvement périodique, d'amplitude variée, des eaux atlantiques d'origine tropicale, déterminant un empiètement momentané de ces eaux sur les eaux d'origine polaire et sur les eaux continentales. Les eaux de la masse transgressive ont toujours une salinité supérieure à* 35 °/₀₀'. This concept has been strongly attacked by von Schubert (1935), although it may apply on occasion. None the less, on the theory here presented, in February and March cascading provides the primary driving force in the circulation of the Celtic Sea and the intrusion of Biscayan or oceanic water is the necessary consequence.

The inflow of very warm and saline (14° C., 35·43 °/₀₀ salinity) water in mid-February 1927 at about 48° N., 8° W. has already been described by Le Danois (1929), who hailed it as '*un phénomène de transgression très net et d'une grande intensité*'. He figured the distribution of salinity and temperature but not that of density. Unfortunately, the French observations of temperature reported in the 'Bulletin Atlantique' for 1927 scarcely meet modern requirements, since they were printed either as whole numbers, e.g. 10°, or to one decimal place which was never a cypher. Statistical examination suggests that they may not be accurate to better than ± 0·3° C. equivalent to an uncertainty in $\sigma_t$ of about ± 0·05. This numerical uncertainty, combined with the apparently fantastic distribution of density which they revealed, has led to their being regarded with reserve. Now they dovetail with the other data here considered to give a credible but still remarkable account. It is unfortunate that the cliff-like break in density occurred in the narrow zone between the Irish and the French observations and could have been produced by a systematic error in either. The Irish records through the years include some evident misprints, but otherwise very extensive work on them has left little doubt as to their essential accuracy. The French records, as has been said, have not inspired confidence. It is of importance, therefore, that surface densities at three positions near Ushant worked by three different ships within five days are concordant. Consequently, it is not unreasonable to accept the whole of the French observations of temperature in 1927 within the limits of accuracy suggested above.

| Date | Vessel | Position | Temperature (° C.) | Salinity $(^\circ/_{\circ\circ})$ | Density ($\sigma_t$) |
|---|---|---|---|---|---|
| 16. ii. 27 | *Salpa* (M.B.A., Plymouth) | E3 48° 34′ N., 5° 13′ W. | 10·05 | 35·39 | 27·27 |
| 16. ii. 27 | French gunboat | RF1 48° 30′ N., 5° 13′ W. | 9·5 | 35·28 | 27·27 |
| 11. ii. 27 | Liverpool-Charente steamer | 48° 27′ N., 5° 13′ W. | 10·1 | 35·37 | 27·24 |

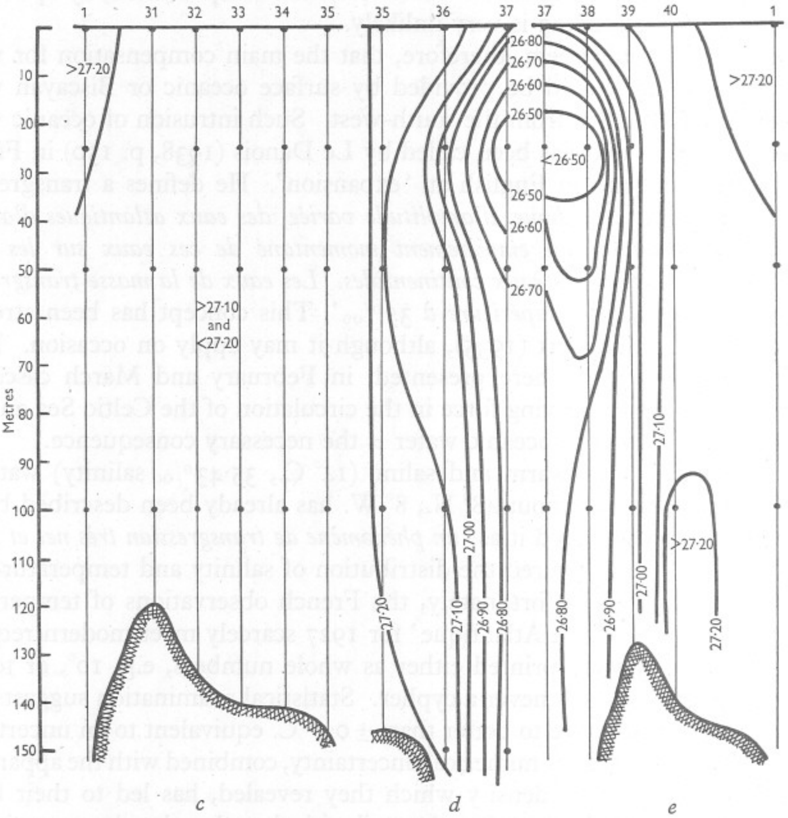


Fig. 13. Three vertical sections of density, *c*, *d*, and *e*, forming a triangle west of Ushant worked by a French gunboat on 15–16 February 1927. Positions are given in Fig. 9. Section *d*, Stations 35–37 also forms part of Fig. 8*a*.

Three vertical sections (Fig. 13), one along the eighth meridian between 48 and 49° N. and the other two completing a triangle to a point near Ushant (as shown on Fig. 9), illustrate the nature of the intrusion: an invaginated core or current about 30 miles wide and about 50 metres thick, sheathed on all sides by denser water. The most spectacular feature was the overlay or apron of surface water 0·5 $\sigma_t$-unit heavier than the water at 25 m. Considered as a problem in statics, such a distribution was impossible, for it should have been destroyed by vertical mixing in a very short time. It could have persisted only in a strongly dynamic system; the core of water of density ($\sigma_t$) 26·5, driving east-north-east through the position 48° N., 7° 45′ W. must have been moving very fast towards the 30-mile-wide gap between the Shamrock Knoll and Parson's Bank. This seems to be another example of how bottom configuration may control currents.

At first sight the overlay of colder water having density 27·0 might seem to have arrived on the scene as a rapid surface drift driven over the main current by northerly or north-easterly winds. This could not have happened since the Daily Weather Reports show that no such winds blew. Alternatively, one may ask whether surface cooling of the warm intrusion could have been brought about quicker than the cooled water could be carried downwards. The air temperature over the northern Celtic Sea, taken as the mean of all observations between 6 February (0100 hr.) and 14 February (1800 hr.) at Valencia, Roches Point (Cork Harbour), St Ann's Head (Pembroke) and Scilly was 6·3° C. To the southward, air temperatures are in general higher, but on that occasion they were unlikely to have been so; although temperatures over inland Britain were much lower than over the Celtic Sea, those over the whole of France were lower still, being continuously below freezing-point from 8 to 13 February (Synoptic Charts to Daily Weather Reports). Winds blowing from the south-east over France should have been even colder than those from the north-east over Great Britain.

The entering oceanic water, warmer than 14° C., was therefore exposed to air at least 8° C. colder, a situation inevitably leading to warming of the air and surface cooling of the water. The warming of the cold continental air as it passed over the Celtic Sea shows up very clearly on the synoptic charts. The open question is: could isohaline water 2·5° C. colder, due to rapid atmospheric surface cooling, and more than 0·5$\sigma_t$-unit heavier than the water beneath have persisted long enough to be observed? Even when wide allowance is made for the nature of the observations, there remains little doubt that it did. If this is accepted, then the core of warm light water at 25–50 m., to have remained recognizable, would need to have moved very fast indeed. So far, there has been no opportunity to clothe this qualitative model in quantitative dress.

It is suggested that the invaginated current or core of warm water had been sucked in at a point of weakness over the slope, as into a void, to compensate water lost from the shelf by cascading. Such a compensation current may be expected on occasion to be narrow, fast and well defined. By contrast, a 'transgression' due to forces at work in the open ocean, and pressing warm water into the Celtic Sea against the inertia of the water already there would seem likely to create not such a core but rather a phalanx of water advancing slowly and relentlessly on a wide front.

On this occasion the balance of evidence is considered to lie heavily against a 'transgression' due to oceanic causes and in favour of a compensation current, called into existence and demanded by earlier and simultaneous cascading south-west of Ireland.

Productivity of the Celtic Sea and English Channel will be much affected by whether this oceanic or Biscayan water, entering to compensate the cascaded shelf water, has a greater, similar, or less content of nutrients. There are no nutrient analyses of Atlantic surface water at midwinter when the total stock may be assessed. At mid-January 1947 in the English Channel north of Brittany an extensive patch of warm (11·5°C), saline (35·39–35·46‰) water was found, which had evidently entered recently either from Biscayan coastal regions or from the Atlantic to the south-west. Its phosphate content was very low, 0·38–0·40 mg.-atom/m.$^3$, less than two-thirds of that in the Celtic Sea at the same time. Although this may not have been compensation water in the sense considered here, none the less, it may indicate the nature of the change in nutrient balance which cascading brings about. The result suggests one line which future investigation should take.

## CASCADING ELSEWHERE

The principle of cascading, i.e. winter cooling over relatively shallow banks or shelves in temperate latitudes to form water heavier than that in the neighbouring ocean at a greater depth, may apply widely. The Celtic Sea faces the Atlantic Ocean to the south and west, and is bordered by land and the shallowing Irish Sea to the north, and by the Bristol and English Channels to the east; its exposure to the continental slope and the ocean has a strong southerly component. In the northern and north-easterly parts of the Sea, water in winter will be most strongly cooled because it is shallower and always it will tend to be colder because it is farther from the equator than the water to the south. The two effects reinforce one another, so that cascading is favoured. In general, it is in border seas facing the equator that cascading is most likely to develop strongly.

In a sea, such as the North Sea, which faces towards the Pole, the two effects oppose one another so that cascading is much less likely to develop. Off the Atlantic Coast of North America the cold, low-salinity Labrador current introduces a complicating factor of great magnitude. In the neighbourhood of the Falkland Islands results obtained by the *Meteor* (Wattenberg, 1933, and other relevant *Meteor* reports), in no way conflict with extensive cascading occurring there, but no definite conclusions can be drawn. At first view, the shelf around the Cape of Good Hope seemed a likely place for cascading, in spite of its poleward exposure, but examination of the Meteor and Discovery Station Lists shows that cascading does not take place; the inflow of the warm water in the Agulhas and Benguela currents far more than compensates winter cooling. The writers know of no other data for seas bordering the Atlantic where cascading might occur. In the eastern basin of the Mediterranean, Nielsen (1912, p. 142) recognized that the temperature of the deep water is determined by the inflow of colder masses of water from the Aegean Sea, and the Adriatic. This is nothing but a statement of cascading from two seas which face the equator.

### A Possible Apron of Surface Water beyond the Slope Rich in Zooplankton

Let us reconsider Fig. 2. As the water moves from A to B it should carry with it its content of plankton. Furthermore, when at C it cascades over the slope those plankton organisms, lacking the power to swim, should be carried down. Neritic species should be found in the cascade water, perhaps at a considerable distance from the slope. It should be possible from amongst them to establish biological indicators by means of which cascade water may be recognized.

Plankton animals able to swim, especially those which undertake diurnal vertical migrations towards the surface, would swim up from the cascade into the overlying apron of warmer more oceanic water. In general, this apron would not be moving in the direction of the cascade away from the shelf, so that the cascade may be considered as flowing under it. Animals and plants unable to leave the cascade will be carried on and down; vertical migrants, whilst in the apron above, will not. Vertical migration should therefore tend to concentrate the more vigorous zooplankton from the cascade into a narrow stationary zone in the more oceanic water which would not normally provide their habitat and in which they might not be expected.

A characteristic of this zooplankton community should be the high proportion of vigorous shelf species known to undertake vertical migrations, and the scarcity amounting, perhaps, to complete absence, of shelf zooplankton with only weak powers of swimming and of shelf phytoplankton which should remain in the cascaded water.

In the absence of cascading, plant food will be available in quantity only in the illuminated layers; in contrast, cascading over the slope should each day carry down below the illuminated zone a supply of plants and of the herbivores which have recently fed. This supply may be replenished each day. The vertical range within which vertical migrants can find relatively rich food supplies should therefore be extended during cascading into the region between, say, the 100 and 200 fm. contours. Such conditions may favour the production of zooplankton of the kind which the 2 m. stramin ring net catches. Moreover, these concentrations of zooplankton are likely to be sought out by pelagic fish.

The above picture should apply where the cascade flows over a smooth slope. If, however, the slope should be dissected by strongly developed submarine valleys or canyons, an even more strongly differentiated distribution might result. If such a valley should cut back into the shelf, it would seem that it could act as a gutter into which the heavy cooled water might tend to collect. Sample models should show whether this conception is, in fact, physically sound. If the gradient of the floor of the valleys should be steeper than that of the shelf, the rate of descent of the cascade should be accelerated, resulting in a concentration of vigorous zooplankton in a restricted zone above the valley at the expense of neighbouring undissected sections of the slope. The richest regions of all in winter may therefore lie above submarine valleys or 'canyons' in the slope where such exist.

The economic conclusion from this line of reasoning is that in the apron of more oceanic water overlying the cascade above the edge of the continental slope, pelagic fish are likely to find concentrations of food organisms greater than anything to be found on the continental shelf. They may provide a rich drift net fishery for vessels able to stand up to the weather.

The whole of this picture applies only when cascading is proceeding strongly, say in February and March, and not then in every year. It is suspected that in those months cascading provides one of the dominant driving forces of the water circulation in the whole of the Celtic Sea, and may have a powerful effect on the life patterns and rhythms of all animals living there. With the cessation of cascading, this concentration of planktonic food organisms and pelagic fish should tend to break up.

## THE TRANSPORT OF IRON

Other investigations (Cooper, 1948) have shown that the stock of iron in the sea water of the Celtic Sea tends to become concentrated in particles suspended in the bottom-most layers. A cascading bottom current of the type described here should have a powerful tendency to strip the stock of iron from the Celtic Sea, and to carry it over the slope into the ocean abyss from which much of it may never return. Although soluble nutrients may be made good by upwelling somewhere at some season or other, it is not easy to see how the stock of iron, mostly particulate, can be replaced in this way. Indeed, there may be no cycle of iron unless a geological time scale is used; plants and animals over the shelf may have to rest content with a supply of iron on slow but steady one-way passage from rivers to the ocean bed.

## REDISTRIBUTION OF NUTRIENTS

Nutrients carried over the slope in cascading water would be lost from the shelf. Lack of balance between loss and replenishment may underlie the large variations in the nutrient resources in the English Channel in different years.

It may be profitable to discuss the likely fate of nutrients in the Celtic Sea at the end of this cascading period. As the surface waters warm up in spring they will become too light to cascade, although the underlying unheated water would continue able to do so. A marked redistribution of the waters would then start, and should have a number of consequences.

One result of the vernal phytoplankton outburst is an increase in the amount of faeces and detrital matter containing nutrient elements. These particles tend to sink into deeper water, leading to an enrichment of this with nutrients at the expense of the upper illuminated layers, a cumulative process. When this happens in an enclosed area, the autumn overturn restores the original situation and, in the course of the year, there is no loss. But when this deeper, enriched water is moving towards the west or south-west under the influence of the cascade while the warmed surface water is relatively stationary, a redistribution of nutrients should come about. The deeper water would be carrying away a rich store of nutrients of which some would spill over the slope whilst some, at the end of cascading, should come to rest as a rich reservoir towards the edge of the shelf.

The surface water in the eastern and north-eastern area of the Celtic Sea would have been depleted. If, in that area, the water which compensates the lost deep water has an equal nutrient content, by the autumn the position will become restored. If, however, as the slender evidence would suggest, the compensation water is poorer in nutrients, an overall impoverishment in the eastern area will result. Whatever the effect may prove to be, it should be most marked in those years in which cascading of bottom water persists particularly late, say, into May. Near the slope a high concentration of nutrients would naturally always be attributed to upwelling; however, at the season when cascading is coming to an end, a high nutrient content there might equally well have resulted from redistribution on the shelf beneath the discontinuity layer. The two situations should be distinguishable by the distribution of density along sections from the shelf over the slope to the deep ocean. Upwelling should not occur when the distribution of density strongly favours cascading.

### Some Applications

In 1927, the stage was set for cascading to occur, but only in 1914 has it been possible to show beyond question that it did. This was due to the measurements of oxygen content and of pH made by Gaarder on board *Armauer Hansen*. In future studies of slope oceanography in this area, determinations of oxygen will be essential, for with their help bodies of water with similar salinities but very different histories may be distinguished.

Although in 1930 conditions were very favourable for cascading, owing to the north-easterly and easterly winds, the evidence was not presented on behalf of the theory of cascading. Now that that theory has been tested in other years, a debating point must be made. The strong cooling in the winter of 1930, reinforced by favourable winds, should have driven an abnormally large amount of water off the shelf. This water would have had to have been replaced somewhere within the Celtic Sea by an abnormally large influx of some other water. About 9 months later in the English Channel near Plymouth the change-over occurred in the nature of the sea water which has had such far-reaching consequences. All we can now do is to note the coincidence; whether they were cause and effect we cannot yet say.

How often cascading occurs we do not know. The winter of 1948–49 has been exceptionally mild, the mildest since 1921. Fortunately, it was possible to work two stations on the eighth meridian on 9–10 March 1949, which have given a good idea of cascading potential then (Table II). The cascading potential of Celtic Sea water having density ($\sigma_t$) around 27·15 is probably slight; there have been years in which it has been even less. It is clear that the tendency of Celtic Sea water to cascade, and for consequent incursion of Atlantic surface water in compensation, will vary greatly from year to year. Although it provides a theme fraught with possibilities in studies of the biological productivity of the whole area, its further examination has had to be deferred. So far, stress has been placed on cascading of shelf water to considerable depths over the slope, but it should be clear that at the beginning and end of the cascade the water of intermediate density will flow off only as a shallow subsurface flood. Consequently, when cascading has occurred, water which has acquired 'neritic' or coastal characteristics whilst on the shelf should stretch out into the Atlantic beyond the slope for many miles, with consequent effects on the character of the plankton living there.

TABLE II

| Position | Temperature (° C.) | Salinity ($^\circ/_{\circ\circ}$) | Density ($\sigma_t$) |
|---|---|---|---|
| 50° 36′ N., 8° 04′ W. Near Station D on Labadie Bank | 9·97–10·00 | 35·23–35·24 | 27·15–27·17 |
| 49° 50′ N., 8° 00′ W. Station F | 10·28 | 35·22–35·23 | 27·09–27·10 |
| 50° 03′ N., 5° 43′ W. Longships bearing 3·5 miles 355° | 9·58–9·65 | 35·21–35·23 | 27·19–27·22 |

Since an ultimate aim is to correlate the physical oceanography of the Celtic Sea with the distribution of plants and animals, attention should be drawn—for what it is worth, which may prove to be little—to a notable resemblance of the diagrams showing the probable course of the cascade in 1927 as deduced from the fall in salinity (Fig. 12) to Steven's diagram (1948, p. 525, fig. 5) illustrating the migrations of the mackerel at this season. In both diagrams there are bifurcating arrows south of the Irish coast about 8°–8° 30′ W., the one suggesting cold relatively brackish water drawn towards the cascades over the slope, the other mackerel migration routes.

### The Effect upon Fisheries in Shallow Waters of Autumn Cooling over Banks

As a rider to the general thesis of this paper let us now consider a shallow flat-topped submarine bank rising from a considerable depth on all sides (Fig. 14). From the basic argument (p. 721), in cold weather a shallow bank of limited extent would seem always to be the site of convergence and descent, never of divergence and ascent.

The local divergences and convergences studied by Woodcock (1944) and others, were not the result of bottom topography and are quite different from the phenomenon here to be described.

On such a declivity plant cells are likely to be carried below the photosynthetic zone before they can have had time to divide and multiply. Phytoplankton should be sparse. None the less plankton, plant and animal, should be sucked into the convergence from a distance and then carried down the slope of the bank.

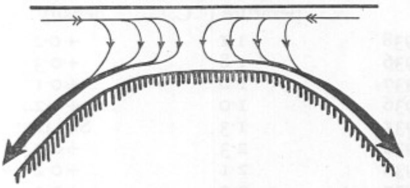


Fig. 14. Local cascading over a bank on a shelf

On such a declivity, demersal fish and filter-feeding sessile organisms should continuously be presented with a fresh supply of food. Such animals may tend to congregate on declivities in cold weather rather more than they do in warm. Again, there are animals which undertake the arduous process of reproduction in autumn and winter when the supply of food in the sea is sparse; is there any evidence that such animals seek declivities where they are exposed to cascading water?

This local form of cascading may arise during cold weather at any season of the year, but it should develop most strongly during the autumn when the rate of cooling of the water is at its greatest. Only then is it likely to occur on a scale sufficient to compete with the forces opposing its development, viz. wind drift, waves and tides.

One of the declivities where mackerel congregate in November and December is the Voyageur Bank in the Straits of Dover (Steven, 1949). Nearby lies the Varne Lightvessel from which very large numbers of surface hydrographical observations have been made. Those for the autumns of the 4 years, 1935–38, have been examined. During October and November the average rate of cooling was about 0·07° C. per day rising during December to 0·10° C. per day; after Christmas, further cooling took place much more slowly and sporadically.

Since the higher the temperature the greater the effect of a fall of 1°C. upon increase in density (Atkins, 1925) the rates of increase in density in November and in December were about the same. Moreover, local cascading should have developed just as strongly in October. If, therefore, local cascading is the magnet which draws mackerel to the declivity in November and December, it ought to do so during October also.

Falls in temperature of the water at the Varne of more than 1°C. in 4 days, accompanied by increases in density ($\sigma_t$) of more than 0·15 are as set out in Table III.

TABLE III. OCCASIONS AT THE VARNE LIGHTVESSEL IN THE FOUR SEASONS (OCTOBER–MARCH) OF 1935–36 TO 1938–39, WHEN TEMPERATURE FELL BY MORE THAN 1°C. IN 4 DAYS AND DENSITY INCREASED BY MORE THAN 0·15 $\sigma_t$ UNIT.

| Date | Fall in temperature (° C.) | Increase in density ($\sigma_t$) | Fall in air temperature at 01.00 hr. at Lympne (° C.) |
|---|---|---|---|
| 5–9 Nov. 1938 | 1·1 | +0·21 | See text |
| 13–17 Nov. 1936 | 1·8 | +0·33 | 7·9 |
| 13–17 Nov. 1937 | 1·0 | +0·17 | 5 |
| 1–5 Dec. 1936 | 1·0 | +0·24 | 6·5 |
| 9–13 Dec. 1935 | 1·3 | See text | See text |
| 17–21 Dec. 1938 | 2·3 | +0·44 | 15·5 |
| 21–25 Dec. 1938 | 2·1 | +0·25 | |
| 25–29 Dec. 1937 | 2·3 | +0·20 | 8·3 |

The air temperatures at the near-by meteorological station at Lympne at 01·00 hr. for each period have been extracted from the Daily Weather Report. In early November 1938, it is clear that local air temperatures had little to do with the fall in sea temperature which must have been associated with horizontal currents. The period 9–13 December 1935, has to be considered as part of the longer period, 1–13 December, during which the air temperature at Lympne at 01.00 hr. was 6–11°C., colder than that of the sea at the Varne which was falling rapidly. Density increased by 0·33 $\sigma_t$-unit over the whole period, but air and sea temperatures and density do not correspond in detail. On the other occasions a sharp fall in the temperature of the air accompanied that of the sea, and leaves no doubt that the one was the cause of the other. Local cascading should have been much favoured on these occasions. Most favourable of all should have been 14 and 15 November 1936; 13, 14 and 15 November 1937; 1 and 2 December 1936; 2–13 December 1935; 18–26 December 1938; and 25 and 26 December 1937. If records are extant to show that landings of mackerel from the Voyageur Bank area were well above average on these occasions, the general thesis would be very strongly supported. Unfortunately, a negative result would not finally dispose of it since, if no mackerel were present in the area, they could not be caught either on declivities or anywhere else.

The autumn of 1938 differed from the other three. The rate of cooling was greatest in October and December, and slight in November. On the present hypothesis, therefore, any mackerel present in the Straits of Dover should have congregated on the Voyageur and similar Banks in October, scattered in November and reassembled in December. Since this issue is evidently of direct importance to the fisherman it merits further direct observation.

## SUMMARY

In the Celtic Sea, to the south of Ireland, water in some winters becomes sufficiently cooled and heavy to flow to the edge of the continental shelf and to run down the continental slope to a depth of several hundred metres. A theory of the phenomenon, termed 'cascading', has been developed. Three winters have been examined in detail.

In February 1927 much water, heavy enough to cascade, was present in the Celtic Sea and also in the English Channel. A probable course and speed of the cascading water over the shelf has been established. Since there were few observations of salinity and temperature over or beyond the slope, and none of oxygen anywhere, the theory cannot be completely established on the basis of the 1927 observations, full though they were.

What is needed is some measurement to demonstrate beyond doubt that water, having density $\sigma_t$ 27·30–27·40, had been ventilated at the surface only shortly before. The measurements of oxygen content and pH made by Gaarder on board the *Armauer Hansen* in June 1914 achieve this. The distribution of density on the shelf in the previous winter has been pieced together. There remains little doubt that water off the slope at 800 and 1200 m. depth had cascaded shortly before. Direct observations, designed for the purpose, are now needed to clinch the argument.

Loss of water from the Celtic Sea by cascading requires that somewhere or other compensation water must enter. The Irish Sea appears to contribute neither to the cascade nor to the compensation water. The cascade may reduce the strength of the current through the Straits of Dover towards the North Sea, but seems seldom able to annul it. Little compensation water would seem to come that way. Since simultaneous cascading and upwelling over the slope seem incompatible, the only considerable sources of compensation water would seem to be the surface waters of the Atlantic Ocean and Bay of Biscay. A very strong inflow from the Atlantic into the southern Celtic Sea in February 1927, previously considered to be a 'transgression', is here regarded as compensation water, the necessary consequence of cascading.

The inflow consisted of an invaginated core of warm, saline water sheathed on all sides by heavier water. The surface water was heavier by 0·5 $\sigma_t$-unit than the water at 25 m. The meteorological and dynamic meaning of this odd, very unstable distribution has been discussed.

Although the tendency to cascade was strong in February 1930, events in that year have not been adduced as evidence for cascading. Strong north-easterly and easterly winds could have driven water off the shelf without help from cascading. Winds and tendency to cascade, together, should none the less have brought about great loss of water from the northern Celtic Sea, and made necessary a large inflow of compensation water somewhere or other. Attention is drawn to the coincidence of this with changes in the nutrient salt regime in the western English Channel a few months later.

It is considered that the submarine banks and valleys of the Celtic Sea are likely to exert considerable control over the direction taken by currents initiated by cascading or by winds. A final conclusion demands more knowledge of bottom configuration and of the currents which actually flow, particularly in winter.

Theoretical argument suggests that during strong cascading an unusually high concentration of large vigorous carnivores may develop in the apron of more oceanic water overlying the cascade over and beyond the slope. This apron might possibly be the site of a rich pelagic fishery.

It is suggested that the stock of iron in the Celtic Sea may be on slow but steady one-way passage from rivers to the ocean bed.

Marked redistribution of nutrients may result, particularly from cascading of cold bottom water underlying surface water which has warmed up and been the site of production of plants and animals.

As a rider to the general thesis, local cascading over shallow flat-topped banks on the continental shelf during autumn cooling has been considered. Circumstances may then favour the concentration of fish over declivities.

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## APPENDIX

### THE NAME 'CELTIC SEA'

This paper has been concerned with the 'sea area to the south of Ireland and off the western entrance to the English Channel', a cumbrous description which defies repetition. The accounts of previous biological and hydrographical investigations in the area have suffered from the lack of any concise name, while reference to different parts of the whole has been even more difficult. The name 'Western Approaches' is incomplete, and 'Chops of the Channel' too colloquial. The area is geographically, oceanographically and biologically a unity, and it is for this reason that a new name should be justified. The need was first recognized and met by E. W. L. Holt who, at a meeting of Irish, Scottish, English and French fishery experts held at Dublin in 1921, proposed the name 'Celtic Sea', after the Celtic lands of Brittany, Cornwall, Wales and Ireland, which border it. Holt seems never to have used the name in his publications, neither is there any record of its formal adoption or of a definition. Even so, his ideas were well formulated and known, as Le Danois (1938, p. 84) testifies. The term had attained currency in French writing, as in Le Danois' book, but none in English, until Corbin (1942) used it. Since 'Celtic Sea' is so concise and self-explanatory it has been used here but is felt to need definition as follows:

The Celtic Sea covers that part of the continental shelf of the Eastern North Atlantic Ocean bounded:

(*a*) On the east by the shortest line between the western point of the Island of Ushant (Ile d'Ouessant) and Lands End (Cornwall) and by the shortest line between Lands End and Ramsey Island, off St David's Head, Pembrokeshire.

(*b*) On the north by the shortest line from Ramsey Island to Carnsore Point, Co. Wexford, by the south coast of Ireland from Carnsore Point to Dursey Head, Co. Kerry, and by the shortest line from Dursey Head to the 200 m. (or alternatively the 100 fm.) contour.

(*c*) On the west and south-west by the 200 m. (or 100 fm.) contour.

(*d*) On the south by the shortest line from the western point of Ushant to the 200 m. (or 100 fm.) line.

# A BALANCE-BY-DEPTH METHOD FOR THE PHOTOELECTRIC MEASUREMENT OF THE VERTICAL EXTINCTION COEFFICIENT OF WATER

By W. R. G. Atkins, Sc.D., F.Inst.P., F.R.S., H. H. Poole, Sc.D.,
and F. J. Warren, A.I.P.R.E.
From the Plymouth Laboratory

(Text-fig. 1)

When discussing the programme of work with Mr F. S. Russell, F.R.S., he stressed the importance of being able to make routine measurements of the clearness of the water quickly and with relatively inexpensive apparatus—something more accurate than measurements of the visibility depth of the Secchi disc. The following method is offered as a solution of this; it has several advantages; but it is naturally limited in its range as compared with the standard potentiometer method used here since 1924.

## OUTLINE OF THE METHOD

It is now possible to obtain selenium rectifier cells of high sensitivity which with low-resistance galvanometers give curves relating current and light intensity that are almost straight lines up to about one milliampere. Thus if two cells give the same current in fairly bright light, in half, a quarter, or one-tenth of the intensity they will also agree. This will hold even if there is some curvature in the above relation, provided that the characteristic curves of the two cells are similar. Accordingly, connecting two such cells, positive to negative in a circuit (Fig. 1), and reducing the illumination on the more sensitive by an iris diaphragm or an opaque varnish on one of the diffusing opals mounted over each, one can use a cheap 0–50 microammeter to indicate balance. Ordinary sensitive galvanometers cannot be used at sea, and the specially balanced type developed for work at sea is expensive. The microammeter, resistance 925 ohms, is mounted as a bridge between the two circuits—as in the Campbell-Freeth method—and, since when balanced no current flows through it, its resistance is immaterial. A current does flow, however, in the cell circuit, and were there large temperature differences between the two cells some error might be occasioned. The cells are connected positive to negative, since in the reverse position, at balance, no current flows in the cell circuit and the arrangement is in effect equivalent to open circuit on a potentiometer. This would be the best method for balance with thermopiles, but it is not so with rectifier cells, because the internal leakage then becomes relatively very important, and the cell voltages tend towards saturation in bright light.

Selenium rectifier cells are not stable, and undergo a diminution in internal resistance with age, very slow under good conditions, quite rapid when exposed to damp and high temperature. The photometer cases should contain well-dried silica gel to absorb included moisture.

It is convenient to use the more sensitive of the pair of cells for use in the sea, mounted as usual in a water-tight gun-metal or brass box, the other being mounted in a case suitable for exposure on deck. Each cell case has over its plain glass a green glass transmitting no red, and an opal-flashed diffusing glass. The uppermost should be flush with the rim so as not to cut off low-angle light. As usual the sea cell is suspended by a bridle with two wires, to which the twin-cored rubber cable is attached by a wide loop, so as not to cast much shadow. It was possible to bring the pair of cells, as mounted, to exact equality by applying a little opaque varnish to the under side of the deck-cell opal. The deck cell was the more sensitive when mounted. Placing similar pairs of opal discs over each reduced the illumination equally, and balance was maintained right down to 6% of the initial current.

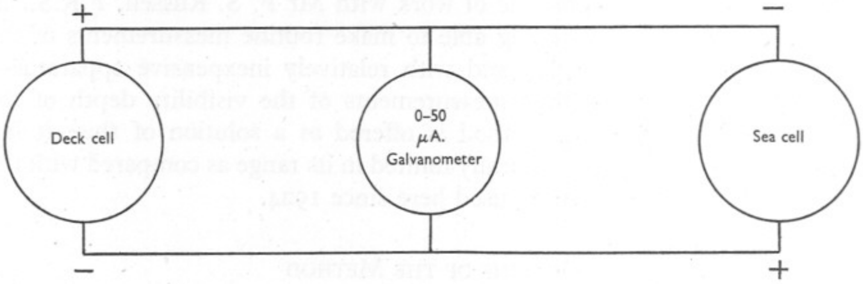

Fig. 1.

For use at sea the deck cell should be placed in gimbals.

Having equalized the cells in air an additional surface-flashed opal can be placed on the deck cell and the sea cell lowered till balance is again obtained. This depth is noted on a metre wheel. The percentage illumination at that depth then equals the percentage transmission of the opal. We cannot, however, use this reading to find the vertical extinction coefficient of the water unless we apply an uncertain correction for surface loss and reflexion error, so we must make a second balance at a greater depth with a more opaque disc on the deck photometer. The latter disc is opalized throughout.

It is, however, better to eliminate surface effects by using an opaque varnish, applied to the under-surface of the deck-cell opal, to reduce the sensitivity so that without any extra opal on the deck cell a balance can be found by lowering the sea cell to about one metre below the surface. The ship should be stern to sun so as to cause as little shading as possible.

The sequence of operations with our apparatus is then as follows. The cells are balanced with the sea cell at say 0·9 m. below the surface. The illumination is then called 100 %. A flashed opal, *A*, transmitting 61·8 %, is placed on the opal of the deck cell; the sea cell is lowered to balance and depth noted. *A* is replaced by *C*, a thick solid opal transmitting (when over the deck-cell opal) 32·3 %, and the depth for balance is observed. *A* is now placed over *C*, forming a combination which, when over the deck-cell opal, transmits 21·1 %. Another solid opal *B* is then added; the combination $A+B+C$ transmits 11·0 %.

We thus have observations of the depths at which the light intensities are 61·8, 32·3, 21·1 and 11·0 %, of that 0·9 m. below the surface.

The vertical extinction coefficient $\mu_v$ is obtained from

$$\mu_v = \frac{2{\cdot}303}{d} (\log_{10} p_1 - \log_{10} p_2),$$

where *d* is the difference in depth, in metres, between the two points at which the percentage values of the balance depth illumination are found. This method has the advantage that instead of measuring air and under-water illuminations in quick succession and obtaining an average on which to base the ratio, the latter is obtained immediately, since changes in illumination affect both cells equally. The use of the green filter restricts the measurement to a fairly narrow band. This was used since $\mu_v$ is dependent upon wave-length and green has the greatest transmission in coastal waters. Were the filter not used there would be a fictitious alteration in $\mu_v$ with depth, as the red—and later the blue—are cut off.

Since in the above formula the values of *p* are constants for the opals and their combinations, one can obtain a factor for each, which has only to be divided by the corresponding value for *d*. Table I shows the transmissions of the opals and their combinations. These are not multiplicative, but must be determined for each. This was done using a Weston rectifier cell which gave a rectilinear relation between current and illumination up to over 4 mA. when tested with a 10 Ω galvanometer on photometer bench and by the use of opals in full daylight on the roof, using a 2 mm. red-free Schott VG9 or a Chance's very similar green glass beneath the permanent opal disc. The opals and combinations selected as most appropriate for use at sea are marked with an asterisk, also the factors which have to be used for the most suitable ranges of transmission as shown in the table, which may serve as a guide for the choice of the combinations with opals of different transmission.

With a homogeneous liquid and approximately monochromatic light the relative reduction in illumination for equal increments in depth would be equal. It would be an advantage to approximate this by the use of opals; it is also obviously best to have a good interval between the observations. The series selected for use, namely opals $A$, $C$, $A+C$, $A+C+B$ gives reductions in illumination as follows (each calculated taking the previous illumination as 100%), $A$ 61·8, $C$ 52·3% (namely $C$ transmits 32·3% or 52·3% of 61·8); similarly, for $A+C$, 65·4 and for $A+C+B$ 52·2%. The intervals are thus well spaced.

TABLE I. RELATIVE TRANSMISSIONS AND FACTORS OF DIFFERENT FILTERS AND COMBINATIONS OF FILTERS

| Light filter | Transmission (%) | Interval | Factor $f$ |
|---|---|---|---|
| Flashed opal $A$* | 61·8 | Datum level to $A$ level* | 0·481* |
| Thick solid opal $C$* | 32·3 | Datum level to $C$ level | 1·130 |
| Thin solid opal $B$ | 31·2 | Datum level to $B$ level | 1·165 |
| $(A+C)$* | 21·1 | Datum level to $(A+C)$ level | 1·554 |
| $(A+B)$ | 20·6 | Datum level to $(A+B)$ level | 1·580 |
| $(B+C)$ | 16·1 | Datum level to $(B+C)$ level | 1·826 |
| $(A+B+C)$* | 11·0 | Datum level to $(A+B+C)$ level | 2·208 |
| | | $A$ level to $C$ level* | 0·649* |
| | | $A$ level to $B$ level | 0·684 |
| | | $C$ level to $(A+C)$ level* | 0·426* |
| | | $C$ level to $(A+B)$ level | 0·450 |
| | | $C$ level to $(B+C)$ level | 0·696 |
| | | $(A+C)$ level to $(A+B+C)$ level* | 0·652* |
| | | $(A+B)$ level to $(A+B+C)$ level | 0·628 |
| | | $(B+C)$ level to $(A+B+C)$ level | 0·381 |

*Notes:* The vertical extinction coefficient per metre for a depth interval between two levels at which the illuminations are $p_1$ and $p_2$% of that at datum level, respectively, is $f/d$, where the factor $f = 2{\cdot}303\,(\log_{10} p_1 - \log_{10} p_2)$.

The filters and combinations marked with asterisks give convenient intervals which would not differ very greatly in thickness in uniform water. These intervals are also marked with asterisks.

## WORK AT SEA

A comparison was made between this method and our standard potentiometer method using the top cell of our cube photometer, mounted beneath similar green glass and opal. It was found necessary to reduce the sensitivity of the deck cell so that in the position of balance, without extra opal in air, the sea cell remained under water always, whether the sun were shining or not. On account of shading from the ship, the under-surface balance position is necessarily higher when the sun is obscured.

To reduce the error due to drift, final measurements were made by a quick drop to an approximately ascertained position. For the same reason a 7 lb. weight was slung below the cell, as the latter was far lighter than the cube photometer.

The method is quick, the depths of balance for the four standard opals and combinations were done twice in 10 min., and with the added weight the preliminary run and the quick drop agreed very closely.

The comparison was made at station L 4, between Plymouth and the Eddystone, in 55 m. of water. The light was very variable, which made accurate work with the standard method rather difficult. The agreement was as close as could be expected. The standard method gave $\mu_v = 0{\cdot}111$ over the depth range 5–20 m.; no balance could be obtained above 5 m. With the balance-by-depth method the range 0·5–21·0 m. gave $\mu_v = 0{\cdot}108$ for the quick drop. At L 3, near Rame Head, over the same range of illumination, namely down to 11·0% of the subsurface balance point, $\mu_v = 0{\cdot}123$, and near the Breakwater Light in Plymouth Sound $\mu_v = 0{\cdot}310$.

We desire to express our thanks to Captain Hoodless and the crew of the R.V. *Sabella* for assistance in handling the gear at sea.

## SUMMARY

Vertical extinction coefficients can be determined in water using selenium rectifier cells and colour filters. The cells are connected positive to negative with a simple 0–50 microammeter across the circuit, as in the Campbell-Freeth method. There is no deflexion when the two points of contact are brought to the same potential. This is done by lowering one cell into the sea to balance the rather less sensitive deck cell. The light reaching the latter is then reduced by the successive addition of opalized plates, to approximately 60, 30, 20 and 10%, and the sea cell is lowered further to balance at each stage. The extinctions can then be calculated by the usual formula from the known percentage transmissions and the observed depths of balance. For each plate or combination a factor may thus be obtained which when divided by the appropriate depth gives the extinction. The method is rapid in operation and the drift error can be rendered negligible. The results agree with those found by the standard potentiometer method, but the applications of the new method are necessarily more limited.

# MEASUREMENTS TO DETERMINE EXTINCTION COEFFICIENTS AND TEMPERATURE GRADIENTS IN THE NORTH SEA AND ENGLISH CHANNEL

By M. H. W. Gall
Pembroke College, Cambridge

(Text-figs. 1–13)

CONTENTS

This is an account of work undertaken in the yacht *Colleen* during July-September 1948, to measure extinction coefficients of the sea and to collect plankton and sea-water samples in the southern part of the North Sea and English Channel.

The results of observations at twenty-five stations in the North Sea and English Channel are recorded, with descriptions of the apparatus used. Some laboratory experiments with the apparatus are described, and some of the difficulties encountered are discussed.

## ACKNOWLEDGEMENTS

The encouragement I received from the Director of the Marine Biological Association really accounted for the expedition yielding these results.

I am deeply indebted to Dr W. R. G. Atkins, F.R.S. and to Dr H. H. Poole for their help in the writing of the paper, and for many suggestions concerning the interpretation of the results.

I am also grateful to many of the staff of the Marine Biological Association for their help and interest before and after the expedition took place.

I would like to express sincere thanks to the fifteen yachtsmen from Cambridge, Oxford and London who came to sea with me at various times

throughout the summer of 1948, and whose seamanship and patience, often under distressing conditions in spite of regular doses of Hyoscine, made the measurements possible.

All the apparatus was made by Messrs H. Tinsley & Co. Ltd. and I am grateful for their co-operation in all my requests.

## Description and Use of Apparatus

The apparatus for measuring opacity consisted of two matched selenium photocells of the barrier layer type, each in a sealed box with a perspex aperture (Fig. 1). Each aperture was covered with a cellulose nitrate blue-green filter, the transmission curve of which is given in Fig. 11, p. 768. Immediately above each cell was an opal-flashed glass screen to diffuse the light. Bi-cored rubber-covered electric cable was sealed into each box. The sea cell was suspended in a cradle (Fig. 2) to which the cable was suitably fastened for lowering. The deck cell was fixed to a wooden wedge (Fig. 2), which brought the surface of the cell horizontal when placed on the deck-house roof. The sea cell had about 30 m. of marked electric cable attached to it, and could be lowered into the sea over a pulley at the end of a 14 ft. spar which kept it clear of shadows round the ship (Fig. 2 shows a model set up).

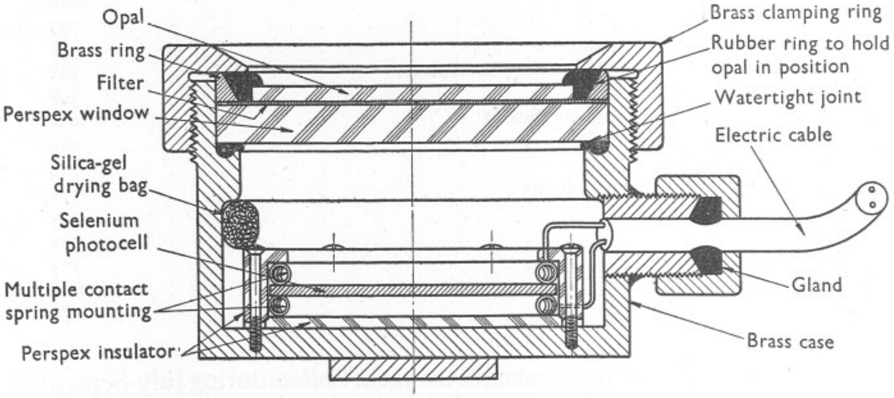

Fig. 1. Submarine photometer, in section.

The inboard ends of the cables from both photocells were connected to a ratiometer (Figs. 3 and 4) consisting of a 200 Ω resistance across each cell, the positive sides of each resistance were made common and a null point was found between the negative side of the sea-cell resistance and a point along the deck-cell resistance by means of a specially constructed galvanometer.[1] This null point determined the ratio of the cell currents, and hence the ratio of the cell illuminations, provided the cells had linear response curves.

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[1] Full details will be published elsewhere.

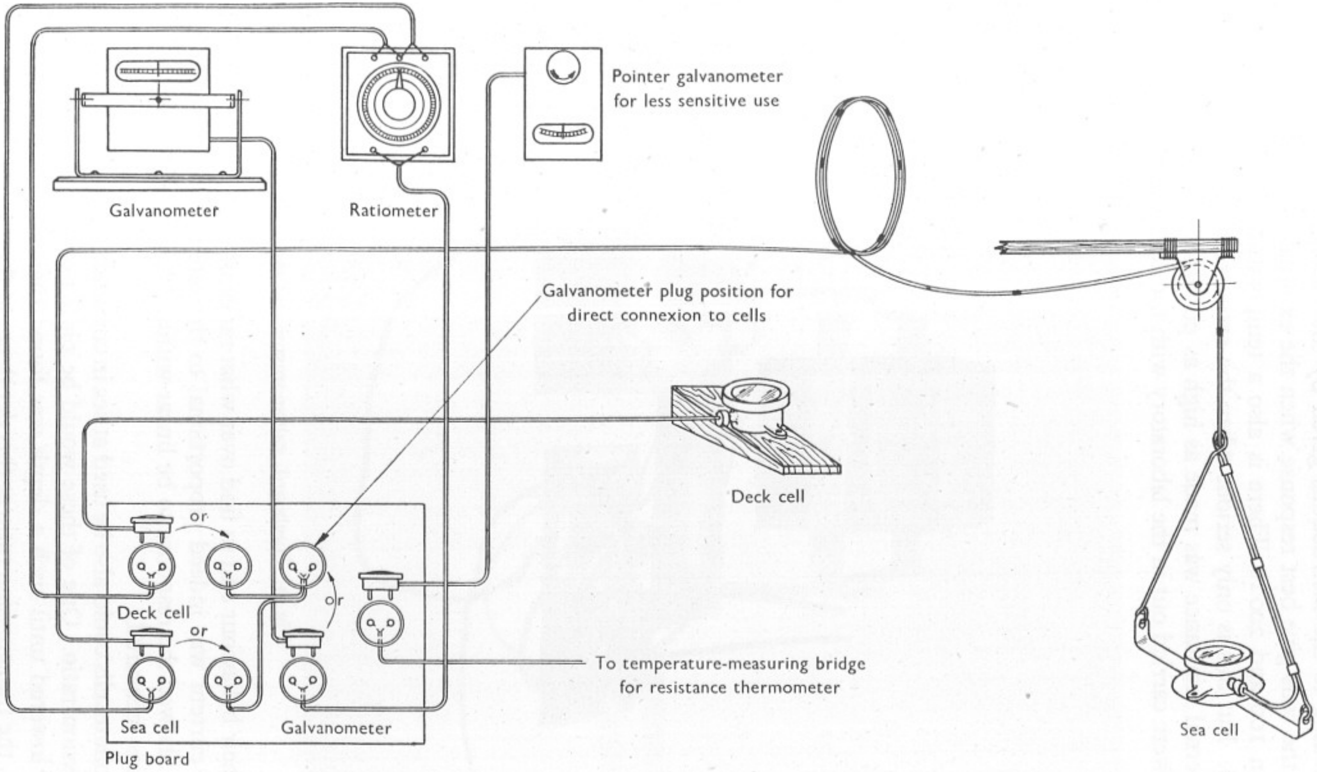

Fig. 2. Diagram of the photoelectric opacity apparatus.

According to the instructions given by the makers (the Magnetron Company), the cells give best response when the external resistance across each is between 100 and 200 Ω. There is also a temperature coefficient to be considered. But this is only serious when the external resistance is very low, so the external resistance was made as high as possible, namely 200 Ω. Experiments were carried out in the laboratory with the cells actually used at sea, to study their behaviour and to find over what range of light intensity the photoelectric current was indeed proportional to the intensity of the illumination. Results showed the response to be linear within 1 %, from 100 to 5 % of light intensities measured.

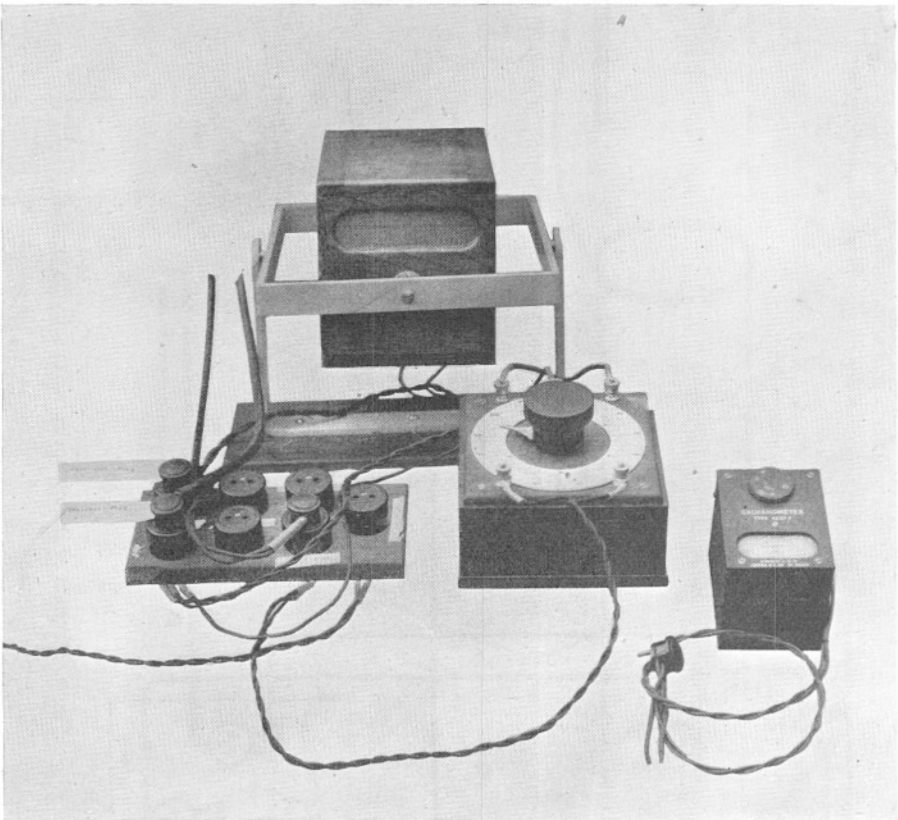

Fig. 3. Plugboard, galvanometer and radiometer.

The photocells could also be used at sea in conjunction with filters of a known transmission ratio. One of these would be placed over the deck cell, and the sea cell lowered until such a depth was found that both cells gave the same current, the transmission ratio at this depth could then be considered the same as that of the filter placed over the deck cell. This method was used only as a check on the ratiometer method. The apparatus consisted simply of a galvanometer placed across the cells connected in parallel. The galvanometer in this case offers the same external resistance to each cell and was 200 Ω. Fig. 5 shows a circuit diagram.

The method of using the photoelectric apparatus was first to set up both the deck cell and sea cell side by side on deck in such a position that they were both free from shadows and received light from all directions. An initial reading made in this way always showed the sea cell to be slightly more sensitive than the deck cell. The sea cell was next rigged over a large pulley at the outboard end of a 14 ft. spar placed over the ship's side in the manner shown in Fig. 2. This was always put out in a direction towards the sun, so that it was clear of any shadows under the ship.

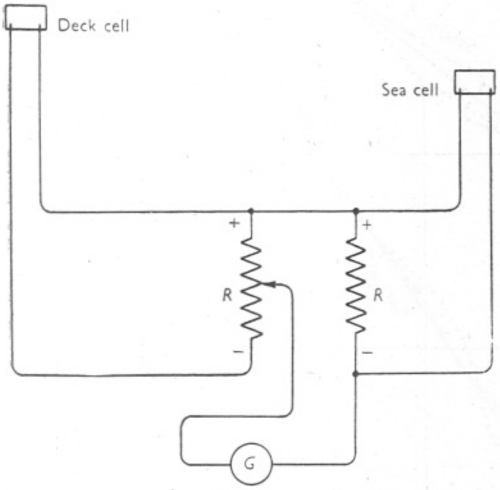

Fig. 4. Ratiometer circuit.

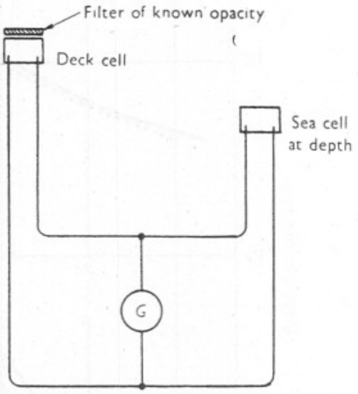

Fig. 5. Comparator circuit.

The ratio of sea-cell current to deck-cell current was then measured, with the sea cell hanging clear of the surface and was always less than the 'on deck' ratio due to the lowering cradle being above the sea cell, thereby shielding some light off it. Finally the sea-cell was submerged to suitable depths and a series of ratiometer readings made.

The deck cell was not built on gimbals, but swung with the ship. As long as the sun was not shining, or was high enough not to cast a serious shadow from the rim of the cell across the deck cell, readings were fairly easy to make. Even when the ship was rolling considerably, the setting of the ratiometer which made the galvanometer deflexion zero could be satisfactorily determined. Violent jumping of the galvanometer spot at once told the observer down below that something was wrong with the deck cell, and that either the helmsman had let the ship's head full off so that the sun was causing shadows

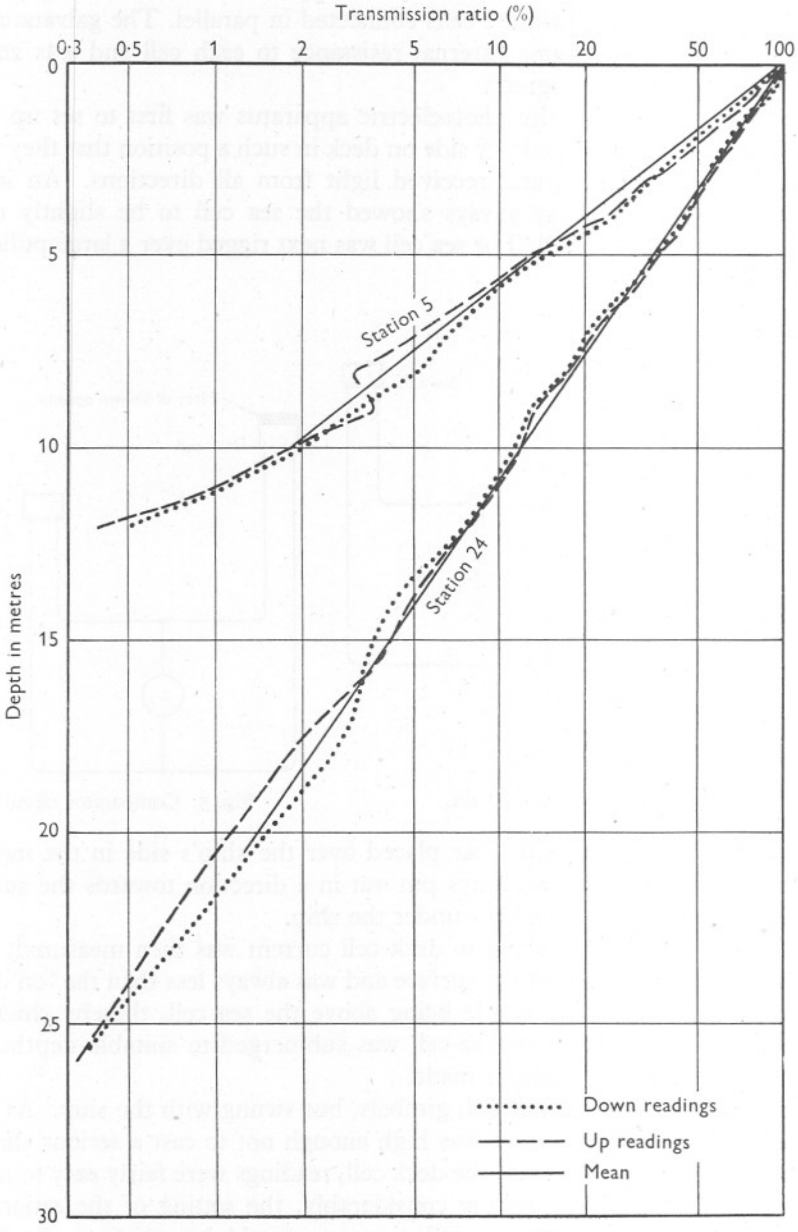

Fig. 6. Transmission ratio curves for stations 5 and 24.

from the rigging to dart across the deck cell, or that someone had carelessly walked too near the deck cell.

Even under unfavourable conditions, namely low sun and much rolling, once the sea cell was below about 10 m., the measurements became fairly easy.

In each reading the ratiometer was adjusted to make the mean deflexion of the galvanometer zero. It can be argued that more accurate results would have been obtained if the adjustment had been made so that the maximum deflexion of the galvanometer had been made zero, corresponding to the maximum illumination of the deck cell as the ship rolled. The very special nature of the galvanometer used for these measurements, which had a sensitivity of 6 mm. per microampere and a periodic time of about $\frac{1}{20}$ sec., and suspended so as to operate independently of its orientation, caused it to follow these variations like an oscillograph. In practice, the results were more consistent by taking the mean position.

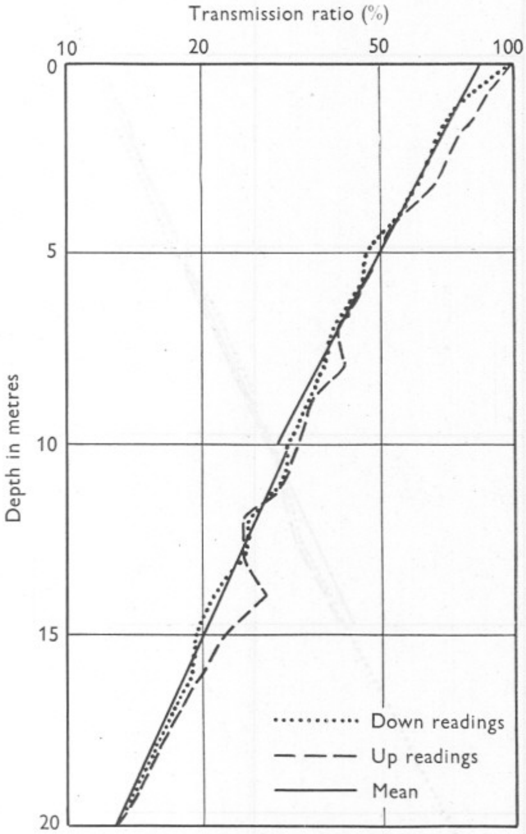

Fig. 7. Transmission ratio curve for station 7.

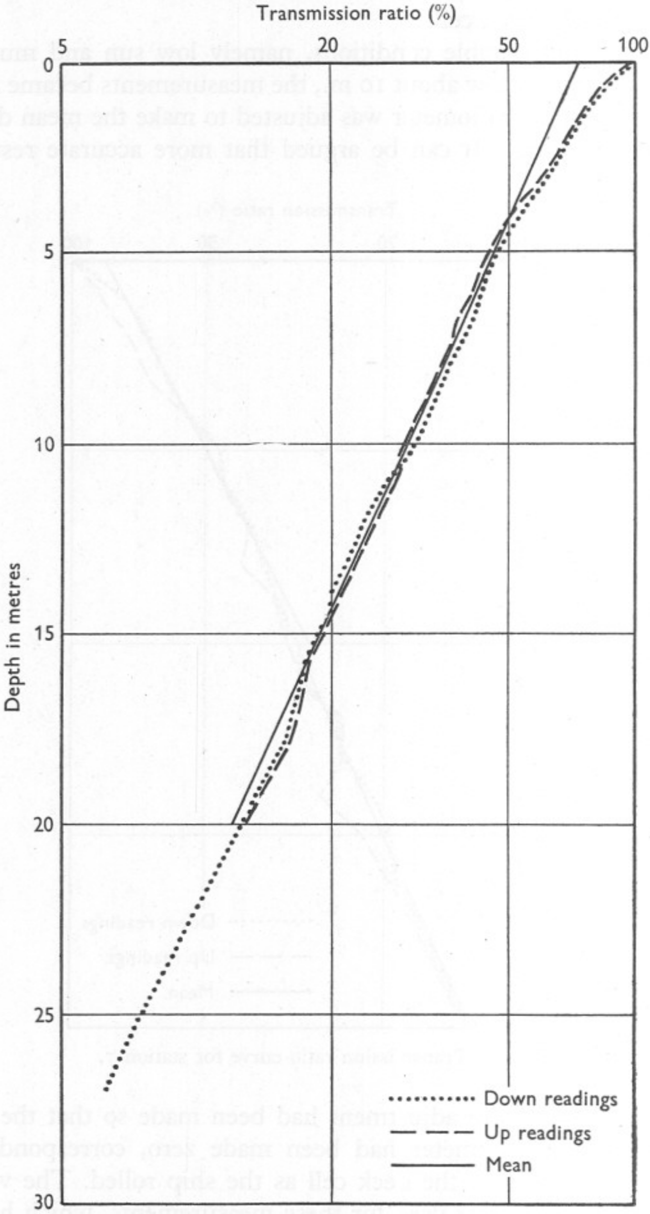

Fig. 8. Transmission ratio curve for station 8.

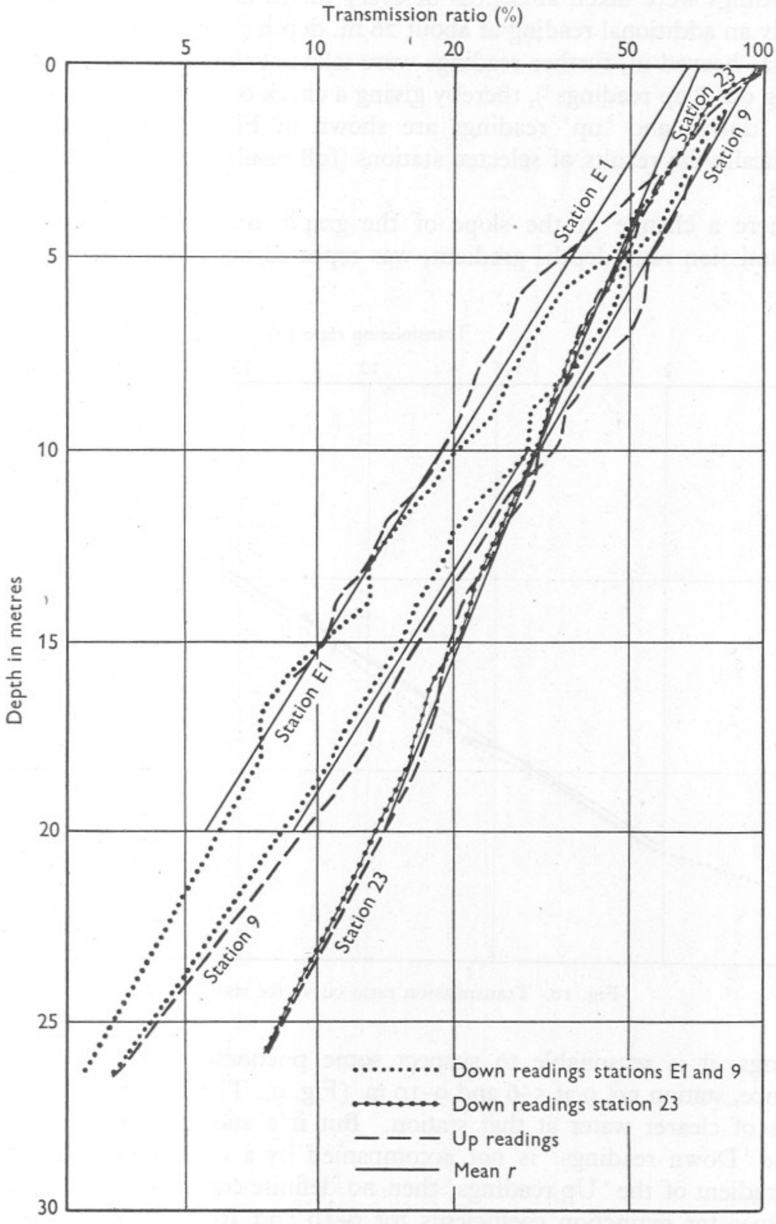

Fig. 9. Transmission ratio curves at stations E1, 9, and 23.

Readings were taken at depths of every metre down to about 18 m., and usually an additional reading at about 26 m. depth ('down readings'). As the cell was heaved in, further readings were taken at the same depths as during paying out ('up readings'), thereby giving a check on the value at each depth. Both 'down' and 'up' readings are shown in Figs. 6–10, which express graphically the results of selected stations (full results are given in Table II, p. 773).

Where a change in the slope of the graph, or, more explicitly, of the 'transmission ratio/depth' gradient, was repeated on upward and downward readings, it is reasonable to suspect some phenomena at that depth; for instance, station no. 9 at 5–6 and 9–10 m. (Fig. 9). There appear to have been layers of clearer water at that station. But if a sudden change in gradient in the 'Down readings' is not accompanied by a corresponding change in the gradient of the 'Up readings' then no definite conclusions can be drawn.

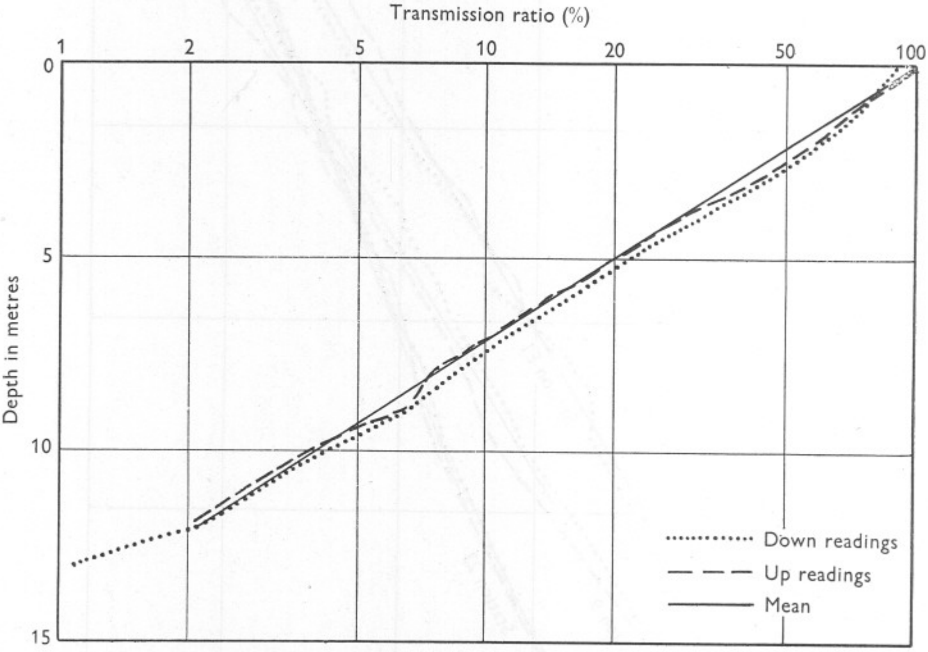

Fig. 10. Transmission ratio curve for station 12.

Values for extinction coefficients for 0–10 and 10–20 m. depth, given in Table II on p. 773, were derived from the mean slope of the 'up' and 'down' readings for those ranges of depth—plotted as straight lines in Figs. 6–10, in addition to the curves for the 'down' and 'up' readings. The formula used for deriving the extinction coefficient is given on p. 769.

Inconsistencies in the graphs are believed to be caused either by bad weather, when the depth of the sea cell was not always very certain, or by turbulent layers of subsurface currents which made the sea cell ride up so that its real depth was considerably less than the amount of cable paid out. The curve for station no. 7 (Fig. 7) is an example of this, particularly at 8 and 14 m. depth.

At station no. 5 (Fig. 6) there were patches of visibly opaque water drifting about, and these caused big changes in both Secchi disk readings and transmission ratio when the ship passed through one. The graph is made up of results obtained in clear patches.

Station no. E 1 (Fig. 9) is an example of bad weather results. Station no. 12 (Fig. 10) is a straightforward example of rather high opacity. Station no. 8 (Fig. 8) is an example showing possible underwater currents at 7 and 14 m. and apparently a layer of rather opaque water at the surface down to 4 m., but this may be due to the shading of the ship giving false readings near the surface. Station no. 23 (Fig. 9) is a straightforward example of low opacity but apparently showing a surface layer of high opacity, this may be due to the shading of the ship. Station no. 24 (Fig. 6) shows a good agreement between readings taken when lowering and when raising the sea cell, in spite of the water being very turbulent.

The details of other stations are left out of the text, but all the results are brought together in Table II (p. 773).

## TRANSMISSION OF FILTER USED IN BOTH PHOTOMETERS

An experiment was carried out to determine the wave-length transmission curve of the filters used in the photometers. The apparatus used consisted of a spectrometer in which the field was split in two. In one half the light passed through the filter, in the other half through a sheet of polaroid. Light reached the spectrometer from a 'Pointolite' source through a collimator and a mounted Nicol's prism.

A spectrum was produced in the eyepiece by means of a diffraction grating. The intensity of the part of the field that passed through the polaroid could be controlled by the orientation of the Nicol, the intensity obeying a sine-squared law, the total extinction position being taken as zero angle.

The image seen in the eyepiece consisted of two spectra, one above the other. The bottom one being the light transmitted by the filter, the top one light transmitted by the polaroid. Having determined the extinction position of the Nicol, the cross-wires were set to different parts of the spectrum, the angle of deviation being read and the Nicol adjusted so that at the vertical cross-wire both halves of the field matched in intensity. If $\theta$ is the angle of deviation of light through the grating, then

$$\lambda = d \sin \theta,$$

where $d$ is the line spacing of the grating and $\lambda$ is the wave-length, and plotting

$d \sin \theta$ against $\sin^2 \phi$ (where $\phi$ is the angle of orientation of the Nicol) gives a transmission/wave-length graph.

Experimental values are given in Table I, and a smoothed curve plotted from them in Fig. 11. The position of the first sodium line was also determined, giving a check on the wave-length values.

TABLE I

| Wave-length (A.) | Transmission (%) | Wave-length (A.) | Transmission (%) |
|---|---|---|---|
| 4341 | 5·64 | 5199 | 46·89 |
| 4440 | 15·29 | 5273 | 32·30 |
| 4494 | 21·04 | 5360 | 32·35 |
| 4525 | 29·08 | 5428 | 16·13 |
| 4587 | 39·55 | 5539 | 7·54 |
| 4612 | 45·29 | 5588 | 4·18 |
| 4710 | 57·76 | 5636 | 2·37 |
| 4735 | 58·34 | 5684 | 1·28 |
| 4857 | 60·34 | 5747 | 0·58 |
| 4872 | 67·32 | 5805 | 0·20 |

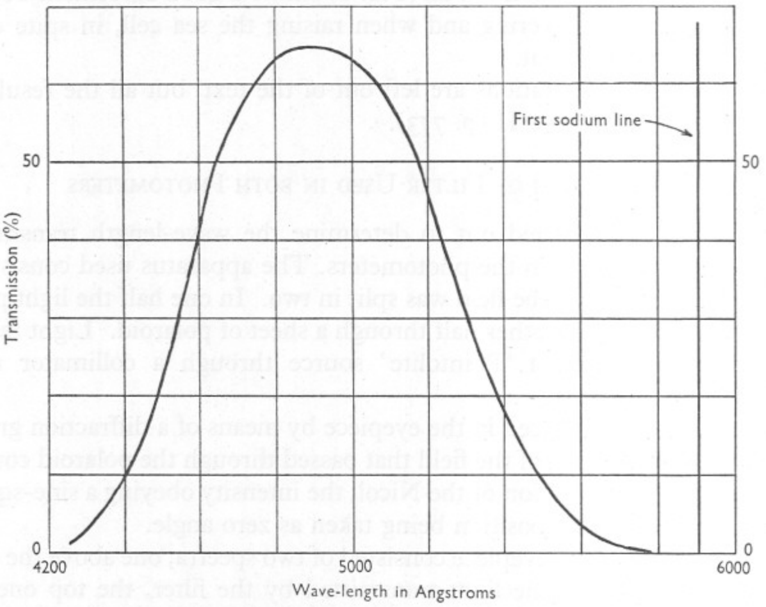

Fig. 11. Transmission ratio curve for the photometer filters.

### ERRORS

The quantity measured by the ratiometer has been called 'transmission ratio'. The ratiometer does not measure a true ratio of light-at-depth to light-at-surface, owing to three types of error: (i) the internal and external reflexion factor (see Atkins & Poole, 1933), (ii) errors due to difference in sensitivity of the two cells, and (iii) error due to shading of low-angle sky by the rim of the photometer. These errors are consistent, and after suitable calibration a measurement of a real ratio could be made. There are, however, two random errors for which corrections cannot easily be made: they are (i) error in estimating the depth of the sea cell, and (ii) error due to surface reflexion at the sea surface. The first of these random errors lay in not knowing the exact depth of the instrument, due to drag on its supporting cable, caused by the ship making leeway. This was only serious where the wind was force 3 or more. An efficient depth-recording instrument fitted to the submarine instrument would permit measurements to be made in winds up to force 5. The second correction is a matter of experience. The photoelectric current ratios for Secchi disk readings shown in Table III are subject to the same errors.

## DETERMINATION OF EXTINCTION COEFFICIENT

Since no absolute measurements of light were made but only light ratios ascertained, there is no point in determining more than the extinction coefficient at each station, and this has been done by taking the mean gradient between 0–10 and 10–20 m. depth of the 'log transmission ratio/depth' curves for each station and using the following formula:

$$P_5 = \frac{2 \cdot 3\,(\log r_0 - \log r_{10})}{10}, \quad P_{15} = \frac{2 \cdot 3\,(\log r_{10} - \log r_{20})}{10},$$

where $P_5$ = extinction coefficient at 5 m. depth, $P_{15}$ = that at 15 m. depth, $r_0$ = transmission ratio at surface, $r_{10}$ = that at 10 m. and $r_{20}$ = that at 20 m. depth.

## SEA-TEMPERATURE MEASUREMENT

A resistance thermometer was used to measure the temperature of the sea at different depths. It consisted of fine platinum wire on a threaded former about 1 in. long; $\frac{1}{4}$ in. diameter enclosed in a tube. The resistance was about 100 Ω at 0° C. The tube was fixed to the end of 3-cored rubber-covered copper cable.

Compensation for the resistance of the copper cable is effected by using the 3-cored cable, and thus having an equal amount of copper resistance in opposite arms of the bridge. The third core of the cable is connected to the end of the platinum thermometer and goes to the galvanometer. By this arrangement, the copper cable is equally divided between the two arms of the bridge so that variations in its resistance with temperature are compensated. The two cores of the cable having the most equal resistance are chosen for this purpose.

The thermometer has been calibrated directly experimentally, and a table drawn up for interpolating measurements made at sea. Fig. 12 shows a diagram of the thermometer bridge. At sea the calibration was checked at each set of readings by making a temperature measurement at the surface with a mercury thermometer.

Temperature measurements were usually made at the same time as the opacity measurements, and the nature of the temperature gradient determined down to 20 m. depth. These results are tabulated, together with the extinction coefficients. The temperature gradients were in no cases large (usually of the order of 0·02 degrees per metre) they are indicated in the last column of Table II (p. 773), a plus sign means the temperature falls with depth, a negative sign means it increases with depth and a zero sign means no appreciable change.

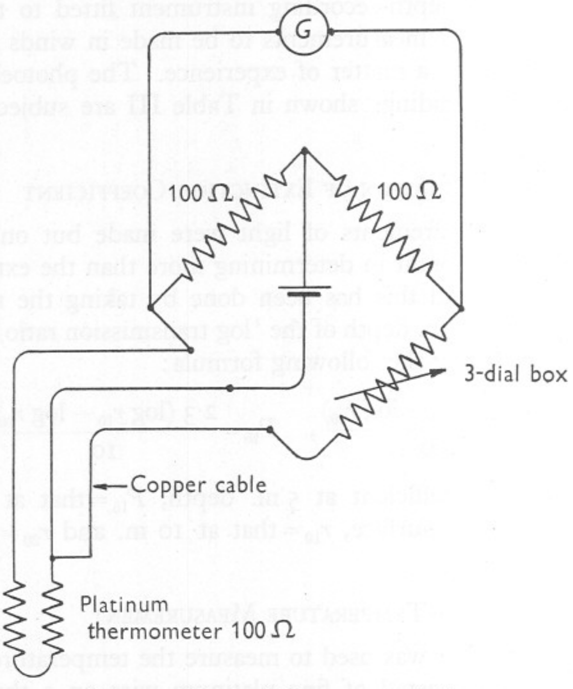

Fig. 12. Circuit of thermometer bridge.

### SECCHI DISK READINGS

Readings were taken with a 12 in. Secchi disk at each station, even when weather conditions were too bad for photoelectric measurements to be made, and there are a sufficient number of contemporary Secchi disk and photoelectric readings to interpret any Secchi disk reading taken when no photoelectric reading was taken as an extinction coefficient to within certain limits of accuracy (see Table III, p. 774).

It is interesting to notice the relationship between Secchi disk readings and the transmission ratio at the depth at which the Secchi disk disappeared as measured photoelectrically.

Very roughly, the Secchi disk disappears from view at a depth where transmission ratio is approximately 20%, but from the data available (see Table III) it varies from 16·1 to 25·0%. The mean of all the values is 20·7 with a standard deviation of 3·0. By placing the readings in columns, for conditions of bright sun, no sun, rough sea and calm sea, etc., we should expect to get a smaller error for each set of conditions. Unfortunately there are not enough readings available to draw satisfactory conclusions (see Appendix II, p. 780), but the indications are as follows:

(i) In a rough sea, whether there is no sun or intermittent sun, the transmission ratio at which the Secchi disk fades out is of the order of 24·1%. (There are insufficient readings to show whether sun or no sun really makes a difference, still less to show the degree of error.)

(ii) In a calm sea, the transmission ratio at which the Secchi disk fades out is about 19·5%, possibly a little higher in bright sun than when overcast (20·4 and 18·6% are values for bright sun and no sun, but the difference is scarcely significant). The lower value for a *calm sea* as opposed to a *rough sea* is suggestive.

(iii) The standard deviation ($\sigma$) for all 'calm sea' readings is estimated as 2·7. For calm sea 'with bright sun' (seven readings) it is 2·8, and for calm sea 'with no sun' (five readings) it is 1·9. The latter conditions would be expected to be ideal, and do in fact produce more consistent readings than those in bright sun (as far as significance can be attached to the relatively low value of $\sigma = 1{\cdot}9$). But the increase in consistency cannot be called very great.

## A Discussion of Opacity Results

The positions of the stations and the main results from them are given in Table II, and further details from some stations respecting Secchi disk measurements are given in Table III. The course taken by the yacht can be seen on the accompanying map (Fig. 13), on which are also marked station numbers and grades of opacity of the water.

The particulars in Table II include extinction coefficients, which have been determined from measurements of the light transmission with depth and from Secchi disk readings,[1] and temperature measurements at the middle of the two depth ranges for which extinction coefficients were calculated.

From Table II it will be noticed that in the southern North Sea extinction coefficients of between 0·40 and 0·092 were obtained (except for one station

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[1] A sufficient number of contemporary Secchi disk readings and photoelectric readings were made for independent Secchi disk readings, to be interpreted as extinction coefficients within sufficient accuracy for many purposes. See also above, p. 770.

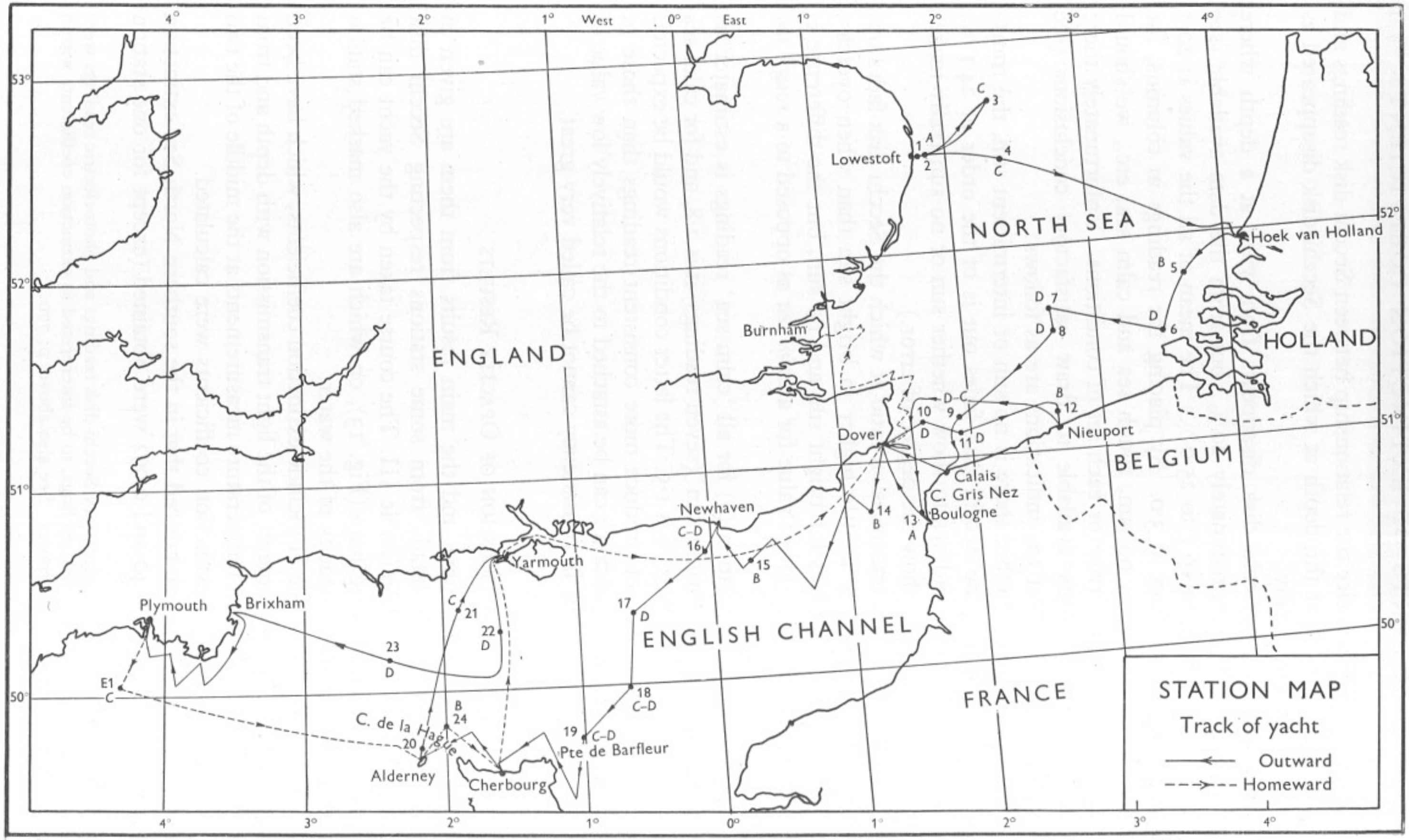

Fig. 13. Map showing the course of the yacht and the position of stations at which readings were taken.

## TABLE II. POSITIONS OF STATIONS WORKED AND MAIN RESULTS OF THE LIGHT AND TEMPERATURE MEASUREMENTS

| Station no. | Position | Date | Extinction coefficient |  | Secchi disk (m.) | Opacity | Salinity (°/₀₀) | Temperature (° C.) |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | 0–10 m. | 10–20 m. |  |  |  | 5 m. | 15 m. | Gradient |
| 1 | 52° 28·8′ N., 01° 47·5′ E. | 15. vii. 48 | 1·24 | — | 1¼ | *A* | 33·81 | 14·1 | — | – |
| 2 | 52° 29·4′ N., 01° 52·0′ E. | 15. vii. 48 | — | — | 3 | *A* | — | 13·0 | 12·9 | + |
| 3 | 52° 43·8′ N., 02° 18·2′ E. | 16. vii. 48 | 0·143 | 0·139 | 12¼ | *C* | 34·31 | 13·1 | 13·1 | 0 |
| 4 | 52° 26·8′ N., 02° 24·5′ E. | 19. vii. 48 | — | — | 11 | *C* | — | — | — | – |
| 5 | 51° 51·0′ N., 03° 38·0′ E. | 23. vii. 48 | 0·396 | — | 10½, 3¼ | *B, A* | 32·73 | 13·5 | 13·3 | + |
| 6 | 51° 35·0′ N., 03° 29·0′ E. | 23. vii. 48 | — | — | 15¼–16¾ | *D* | 35·07 | 15·0 | 15·0 | 0 |
| 7 | 51° 48·5′ N., 02° 38·5′ E. | 24. vii. 48 | 0·104 | 0·092 | 13 | *D* | 35·25 | 14·5 | 14·6 | – |
| 8 | 51° 36·1′ N., 02° 41·2′ E. | 24. vii. 48 | 0·088 | 0·092 | 13½ | *D* | — | 15·4 | 15·3 | + |
| 9 | 51° 12·0′ N., 01° 54·0′ E. | 25. vii. 48 | 0·101 | 0·124 | 11½ | *D–C* | — | 16·1 | 16·1 | 0 |
| 10 | 51° 11·8′ N., 01° 39·0′ E. | 29. vii. 48 | 0·097 | 0·097 | 14½ | *D* | 35·23 | 15·4 | 15·1 | + |
| 11 | 51° 08·0′ N., 01° 57·0′ E. | 29. vii. 48 | 0·111 | 0·109 | 15 | *D* | — | 15·9 | 15·7 | + |
| 12 | 51° 11·5′ N., 02° 41·5′ E. | 30. vii. 48 | 0·321 | — | 5½ | *B* | — | 18·0 | 17·9 | + |
| 13 | 50° 46·2′ N., 01° 34·0′ E. | 5. viii. 48 | — | — | 3 | *A* | — | 18·2 | 18·0 | + |
| 14 | 50° 47·0′ N., 01° 12·0′ E. | 10. viii. 48 | 0·247 | — | 6¾ | *B* | 35·40 | 14·6 | 14·7 | 0 |
| 15 | Beachy Head 7 miles 332° true | 11. viii. 48 | — | — | 7 | *B* | 35·18 | 14·9 | 14·7 | + |
| 16 | 50° 36·0′ N., 0° 03·2′ W. | 14. viii. 48 | 0·123 | 0·110 | — | *C–D* | — | 16·0 | 15·5 | + |
| 17 | 50° 21·0′ N., 0° 34·0′ W. | 15. viii. 48 | — | — | 12 | *D* | — | — | — | – |
| 18 | 50° 0·0′ N., 0° 38·0′ W. | 16. viii. 48 | 0·136 | 0·097 | 10 | *C–D* | 35·30 | 15·2 | 15·2 | 0 |
| 19 | 49° 45·0′ N., 01° 0·0′ W. | 16. viii. 48 | 0·128 | 0·082 | 10 | *C–D* | — | 16·0 | 15·9 | + |
| 20 | 2 miles due North Alderney lighthouse | 20. viii. 48 | — | — | 11½ | *C* | — | 14·7 | 14·5 | + |
| 21 | 50° 23′ N., 01° 51′ W. | 21. viii. 48 | 0·136 | 0·137 | 10 | *C* | — | 15·0 | 14·9 | + |
| 22 | 50° 16·5′ N., 01° 33′ W. | 24. viii. 48 | 0·108 | 0·098 | 13½ | *D* | — | 15·2 | 15·2 | 0 |
| 23 | 50° 07·5′ N., 02° 21·5′ W. | 24. viii. 48 | 0·084 | 0·079 | 13 | *D* | — | 15·1 | 15·1 | 0 |
| E 1 | 50° 04·0′ N., 04° 22·0′ W. | 6. ix. 48 | 0·123 | 0·122 | 9 | *C* | 35·33 | — | — | – |
| 24 | 49° 47·5′ N., 02° 01·0′ W. | 9. ix. 48 | 0·215 | 0·208 | 7¼ | *B* | — | — | — | – |

*Note.* The opacity of the water (seventh column of Table) has been graded as follows: *A*, extinction coefficient >0·8, Secchi disk <4 m.; *B*, extinction coefficient 0·2–0·8, Secchi disk 5–8 m.; *C*, extinction coefficient 0·11–0·2, Secchi disk 9–12 m.; *D*, extinction coefficient <0·11, Secchi disk >12 m. When the two depths fall into a different grade, both letters are given, that for 0–10 m. being put first. At station No. 5 the Secchi disk reading 3¼ m. was taken in an opaque patch, other readings at this station were taken in clear water.

close inshore off Lowestoft which gave a value of 1·24); while in the English Channel values ranged between 0·24 and 0·079.

On the whole, the agreement between the 0–10 and 0–20 m. readings is close, though a difference of some 45% of the mean value was found at station no. 19. There the surface layer was the more opaque. An extreme instance of the same effect was visible at station no. 5, as mentioned already (p. 767).

On the other hand, at station no. 9, in the vicinity of the Sandetti bank, the water became decidedly more opaque below 10 m. This was presumably due to suspended matter being taken off the top of the bank, but not mixing with the upper layers. Station no. 8, in the vicinity of the Hinder Sand, also shows an inversion of the extinction coefficient with depths, but to a smaller extent than at station no. 9.

The extinction coefficients at station nos. 6–11 are surprisingly low, as these stations are in shallow water, where there are currents of the order of 2½ knots, which would be expected to keep a great deal of matter in suspension.

TABLE III. SECCHI DISK DATA

| Station no. | Date | Secchi disk reading (m.) | Photoelectric current ratio | Sea conditions | Weather conditions |
|---|---|---|---|---|---|
| 1 | 15. vii. 48 | 1¼ | 21·5 | Calm | Intermittent sun |
| 8 | 24. vii. 48 | 13½ | 21·5 | Oily | No sun, hazy |
| 9 | 25. vii. 48 | 11½ | 24·5 | Slight swell, ruffled surface | Bright sun |
| 10 | 28. vii. 48 | 14½ | 23·0 | Very slight swell and sea calm | Bright sun (10.00 G.M.T.) |
| 11 | 29. vii. 48 | 15 | 16·1 | Slight swell and sea calm | Bright sun, haze (15.00 G.M.T.) |
| 12 | 30. vii. 48 | 5½ | 18·7 | Very slight sea swell | Bright sun (low), haze (07.30 G.M.T.) |
| 14 | 10. viii. 48 | 6¾ | 17·0 | Slight sea and swell | No sun |
| 18 | 16. viii. 48 | 14 | 17·3 | Heavy swell, smooth surface | No sun, grey sky |
| 19 | 16. viii. 48 | 10 | 25·0 | Sea rough, swell short | Intermittent sun 5/10 cloud. Wind force 3–4 |
| 21 | 21. viii. 48 | 10 | 20·0 | Sea calm | Intermittent sun |
| 22 | 24. viii. 48 | 13½ | 18·0 | Oily surface, moderate swell | No sun, 10/10 cloud |
| 23 | 24. viii. 48 | 13 | 23·9 | Small waves | Mist and drizzle |
| 24 | 9. ix. 48 | 7¼ | 19·2 | Sea calm, turbulent | Bright sun |
| E 1 | 9. ix. 48 | 9–8½ | 23·5 | Sea moderate, medium swell | Intermittent sun |

*Note.* When the sun is shining, its altitude and relative bearing would probably affect the Secchi disk reading, but it cannot be said with certainty whether more consistent results would have been obtained if these had also been considered. However, it is safe to say that in calm weather the Secchi disk depth is greatest when there is no sun and least when the sun is shining brightly, and in rough weather the Secchi disk depth is less than in calm weather. These observations are consistent with what might be concluded from considerations of surface reflexion under the respective weather conditions.

## CONCLUSIONS

The results show that it is possible to carry out opacity observations with an accuracy depending on the weather conditions. The table of Secchi disk results probably gives the best guide to the accuracy of the other opacity results. It is not possible to calculate the overall accuracy, as the random error of the depth of the instrument plays such an important part. The main feature of these results is that they show continuous sets of readings from which the extinction coefficient can be calculated, and changes in the transmission of light with depth observed down to 20 m. The quantity that has been measured by the ratiometer is not an absolute measurement of the ratio of light at depth to light at surface but is a quantity proportional to this ratio and has been called transmission ratio. The results are probably of the order of 15% greater than the absolute ratio.

If an accurate depth-meter could be fitted to the submarine instruments, one of the largest sources of random error could be reduced and more satisfactory results obtained.

## SUMMARY

During a cruise in the southern North Sea and English Channel in 1948 a series of measurements on light penetration was secured.

The apparatus used has been described, and methods of handling it discussed. A description of the experiments for determining the transmission curve of the filters used in the photometers, has been included.

Of the systematic and random errors to which the photometer measurements were liable the most serious lay in not knowing the precise depth of the sea cell.

Extinction coefficients have been determined from the gradients of logarithmic transmission-ratio/depth graphs, and the results tabulated for each station.

Temperature gradients were never large, usually of the order of 0·02 degrees per metre, the temperature usually dropping with increased depth, frequently there was no gradient at all.

An attempt has been made to correlate Secchi disk readings with extinction coefficients, as far as the data permit.

Sea-water samples from ten stations show that generally the salinity is higher in areas of low opacity, the Beachy Head vicinity being the main exception to this.

The opacity results show clearer water than might be expected at certain stations (Nos. 6, 7, 8, 10 and 11) in the southern North Sea.

## REFERENCE

ATKINS, W. R. G. & POOLE, H. H., 1933. The photo-electric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc.* B, Vol. CCXXII, pp. 129–64.

# APPENDIX

## I

As specimens of the raw data, the particulars of six of the stations are given herewith:

### Station No. 8

*Time:* 13.45 G.M.T. *Date:* 24 July 1948. *Position:* 51° 36·1′ N., 02° 41·2′ E.
*Conditions:* excellent, hazy atmosphere, no direct sunlight, oily sea, slight swell.
*Secchi disk:* 13½ m.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) |  | Temperature (° C.) |  |  |
|---|---|---|---|---|---|
|  | Down | Up | Resistance | Temp. (R) | Temp. (Hg) |
| 0 | 97·5 | 96·5 | 7·58 | 15·93 | 15·5 |
| 1 | 79·5 | 78·8 | — | — | — |
| 2 | 69·5 | 70·0 | — | — | — |
| 3 | 61·7 | 60·5 | — | — | — |
| 4 | 54·0 | 51·2 | — | — | — |
| 5 | 47·8 | 45·5 | 7·53 | 15·79 | — |
| 6 | 44·0 | 42·0 | — | — | — |
| 7 | 41·25 | 38·0* | — | — | — |
| 8 | 37·0 | 35·5* | — | — | — |
| 9 | 34·0 | 32·5 | — | — | — |
| 10 | 31·25 | 29·5 | 7·52 | 15·76 | — |
| 11 | 27·0 | 28·0 | — | — | — |
| 12 | 24·0 | 25·5 | — | — | — |
| 13 | 22·0 | 23·0 | — | — | — |
| 14 | 20·0 | 21·0* | — | — | — |
| 15 | 18·8 | 19·2* | 7·52 | 15·76 | — |
| 16 | 17·4 | 17·4 | — | — | — |
| 17 | 16·5 | 16·8 | — | — | — |
| 18 | 15·5 | 15·0 | — | — | — |
| 27 | 6·2 | — | 7·50 | 15·71 | — |

* Possibly turbulence.

*Calculation of extinction coefficients*

From graph:

$$P_5 = \frac{2{\cdot}3\,(\log 72 - \log 30)}{10} = 0{\cdot}23\,(1{\cdot}875 - 1{\cdot}478) = 0{\cdot}0875,$$

$$P_1 = \frac{2{\cdot}3\,(\log 30 - \log 12)}{10} = 0{\cdot}23\,(1{\cdot}478 - 1{\cdot}080) = 0{\cdot}0915.$$

### STATION NO. 9

*Time:* 11.00 G.M.T. *Date:* 25 July 1948. *Position:* 51° 12′ N., 01° 54′ E. *Sea depth:* 15 fathoms.

*Conditions:* very fine, bright sun, horizon hazy, light breeze, slight swell, negligible sea, wind went flat calm during photoelectric experiments, ship rolling.

*Secchi disk:* 11½ m.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) | | Temperature (° C.) | |
|---|---|---|---|---|
| | Down | Up | Resistance thermometer | Check (Hg) temp. |
| 0 | 94 | 100 | 15·5 | 15·5 |
| 1 | 87·5 | 90 | — | — |
| 2 | 75 | 79·5 | — | — |
| 3 | 69 | 71 | — | — |
| 4 | 61 | 66 | — | — |
| 5 | 52 | 58 | — | — |
| 6 | 49 | 56·5 | 16·1 | — |
| 7 | 44 | 52·5 | — | — |
| 8 | 39 | 42·5 | — | — |
| 9 | 31 | 37·5 | — | — |
| 10 | 30·5 | 35·5 | — | — |
| 11 | 25 | 28·3 | — | — |
| 12 | 21 | 25·2 | — | — |
| 13 | 19·5 | 22·5 | — | — |
| 14 | 17·0 | 19·5 | — | — |
| 15 | 15·4 | 17·5 | 16·1 | — |
| 16 | 13·2 | 15·5 | — | — |
| 17 | 12·0 | 14 | — | — |
| 18 | 11 | 13 | — | — |
| 26·5 | 3·5 | — | — | — |

*Note.* Bright sun would be expected to fatigue deck cell and cause sea cell to appear more sensitive on upward path. Readings of opacity support this.

*Extinction coefficients (calculated as above)*: $P_5 = 0{\cdot}101$. $P_{15} = 0{\cdot}124$.

### STATION NO. 12

*Time:* 07.30 G.M.T. *Date:* 30 July 1948. *Position:* 51° 11·5′ N., 02° 41·5′ E.

*Conditions:* weather fine, bright sunlight, very hazy, horizon visibility 1 mile, wind force 1 north, very slight sea and swell.

*Secchi disk:* 5½ m.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) | | Temperature (° C.) | | |
|---|---|---|---|---|---|
| | Down | Up | Resistance | Temp. (R) | Temp. (Hg) |
| 0 | 91 | 100 | 8·49 | 18·37 | 18·0 |
| 1 | 76·5 | 75·0 | 8·48 | 18·35 | — |
| 2 | 60·0 | 59·0 | 8·47 | 18·32 | — |
| 3 | 45·0 | 43·5 | 8·47 | 18·32 | — |
| 4 | 31·5 | 28·0 | 8·47 | 18·32 | — |
| 5 | 22·0 | 20·0 | 8·46 | 18·29 | — |
| 6 | 16·0 | 14·5 | 8·46 | 18·29 | — |
| 7 | 11·5 | 10·5 | 8·45 | 18·27 | — |
| 8 | 8·5 | 7·5 | 8·45 | 18·27 | — |
| 9 | 6·5 | 6·5 | 8·45 | 18·27 | — |
| 10 | 4·34 | 4·04 | 8·45 | 18·27 | — |
| 11 | 2·94 | 2·80 | — | — | — |
| 12 | 2·13 | 2·02 | — | — | — |
| 13 | 1·08 | — | 8·44 | 18·24 | — |

*Extinction coefficient (calculated as above)*: $P_5 = 0{\cdot}321$.

### STATION NO. 23

*Time:* 15.45 G.M.T. *Date:* 24 August 1948. *Position:* 24 miles south of Portland Bill, 50° 07·5′ N., 02° 21·5′ W.

*Conditions:* misty, drizzle, sea ruffled, small waves, measurements easy, Galvo spot steady.

*Secchi disk:* 13·0 m.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) Down | Transmission ratio (%) Up |
|---|---|---|
| 0 | 105·5 | 103 |
| 1 | 82 | 80 |
| 2 | 70 | 69 |
| 3 | 59·5 | 59 |
| 4 | 52·0 | 53 |
| 5 | 48·0 | 49 |
| 6 | 44 | 43·5 |
| 7 | 39 | 38 |
| 8 | 35·8 | 37·5 |
| 9 | 33 | 33 |
| 10 | 31 | 31 |
| 11 | 28·2 | 30·5 |
| 12 | 26 | 26·2 |
| 13 | 23·8 | 24 |
| 14 | 21·8 | 21·0 |
| 15 | 20·5 | 20 |
| 16 | 18 | 18·8 |
| 17 | 17 | 18 |
| 18 | 16·2 | 17 |
| 23 | 8·8 | — |
| 26 | 7·5 | — |

*Extinction coefficients (calculated as above)*

$P_5 = 0{\cdot}0842$. $P_{15} = 0{\cdot}0792$.

### STATION NO. E 1

*Time:* 14·00 G.M.T. *Date:* 6 September 1948. *Position:* 50° 04′ N., 04° 22′ N.

*Conditions:* very bad, sun casting awkward shadows, too much wind, ship never stationary, continually turning and rolling.

*Secchi disk:* 9·0 m. before experiments; 8·5 min. after experiments, at 15.45 G.M.T.

*Photocells:* initial comparison on deck, 105 %; cell ready to lower, 101·5; deck cell also wet, 104; deck cell dry, 101.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) | | | | | |
|---|---|---|---|---|---|---|
| | Down | Up | Checks | | | |
| 0 | 101 | 103 | — | — | — | — |
| 1 | 75 | 80 | 84 | — | — | — |
| 2 | 67 | 69 | — | — | — | — |
| 3 | 60 | 54·5 | 53·8 | 51 | 55 | — |
| 4 | 50 | 44 | 42·5 | 41 | 42 | — |
| 5 | 45·5 | 35·5 | 35·5 | 36 | 35 | — |
| 6 | 34·5 | 28 | 29 | — | — | — |
| 7 | 30·5 | 26·0 | 25·5 | 25 | — | — |
| 8 | 27·0 | 22·5 | 23·5 | — | — | — |
| 9 | 25·0 | 21·0 | 19·5 | 18 | — | — |
| 10 | 20·5 | 19·0 | 17·8 | 17 | 17 | 18·5 |
| 11 | 18·0 | 16·8 | 16·5 | — | — | — |
| 12 | 15·0 | 14·0 | 15·0 | — | — | — |
| 13 | 13·0 | 13·0 | 13·0 | — | — | — |
| 14 | 13·0 | 11·0 | 11·5 | — | — | — |
| 15 | 10·5 | 10·5 | — | — | — | — |
| 16 | 8·5 | 8·8 | 8·5 | — | — | — |
| 17 | 7·5 | 8·5 | 8·0 | — | — | — |
| 18 | 7·5 | 8·5 | 5·5 | — | — | — |
| 26½ | 3·0 | — | — | — | — | — |

*Extinction coefficients (calculated as above)*

$P_5 = 0{\cdot}1225$. $P_{15} = 0{\cdot}1220$.

### STATION No. 24

*Time:* 10.40 G.M.T. *Date:* 9 September 1948. *Position:* north-east end of race of Alderney. 49° 47·5′ N., 02° 01·0′ W. drifting north-east.
*Conditions:* sea very turbulent, wind light, bright sun.
*Secchi disk:* $7\frac{1}{4}$ m.

*Photoelectric measurements*

| Depth (m.) | Transmission ratio (%) | |
|---|---|---|
| | Down | Up |
| 0 | 97 | 100 |
| 1 | 84 | 82 |
| 2 | 63 | 65·5 |
| 3 | 52·5 | 52 |
| 4 | 45 | 45 |
| 5 | 34·5 | 35 |
| 6 | 27 | 28 |
| 7 | 20 | 21 |
| 8 | 17 | 17 |
| 9 | 12·5 | 13 |
| 10 | 11 | 11·5 |
| 11 | 9 | 9·8 |
| 12 | 7·5 | 7·7 |
| 13 | 5·5 | 6·0 |
| 14 | 4·2 | 4·8 |
| 15 | 3·5 | 4·17 |
| 16 | 3·2 | 3·31 |
| 17 | 3·0 | 2·37 |
| 18 | 2·5 | 1·805 |
| 26 | — | 0·322 |

Turbulence less noticeable on 'up' path. Turbulence most noticeable at 4 and 5 m.

*Extinction coefficients (calculated as above)*

$P_5 = 0{\cdot}215$. $P_{15} = 0{\cdot}208$.

## II

*The transmission ratio at depths at which the Secchi disk disappears under different weather conditions.*

Readings were extracted from Table II as follows:

*Bright sun and rough sea*

| Station no. | Transmission ratio* |
|---|---|
| 19 | *c.* 25·0 |
| E 1 | *c.* 23·5 |
| | Mean = 24·3 |

*Bright sun and calm sea*

| Station no. | Transmission ratio* | Deviation* |
|---|---|---|
| 1 | *c.* 21·5 | *c.* + 1·1 |
| 9 | *c.* 24·5 | + 3·1 |
| 10 | 23·0 | + 2·6 |
| 11 | 16·1 | − 4·3 |
| 12 | 18·7 | − 1·7 |
| 21 | 20·0 | − 0·4 |
| 24 | 19·2 | − 1·2 |
| | Mean = 20·43 | — |
| | $\sigma$ = 2·83 | $\sigma_m$ = 1·07 |

*No sun and rough sea*

| Station no. | Transmission ratio* |
|---|---|
| E 1 | 23·5 |
| 23 | 23·9 |
| 19 | 25·0 |

*No sun and calm sea*

| Station no. | Transmission ratio* | Deviation* |
|---|---|---|
| 8 | 21·5 | *c.* + 2·7 |
| 18 | 17·3 | − 1·5 |
| 14 | 17·0 | − 1·8 |
| 21 | 20·0 | + 1·2 |
| 22 | 18·0 | − 0·8 |
| | Mean = 18·8 | — |
| | $\sigma$ = 1·92 | $\sigma_m$ = 0·86 |

| *All 'rough sea' stations* | *All 'calm sea' stations* |
|---|---|
| (19, 23, E 1) | (1, 8, 9, 10, 11, 12, 14, 18, 21, 22, 24) |
| Mean 24·1 (± *c.* 1·7) | Mean 19·7 ± 0·80 |
| $\sigma$ — | $\sigma$ 2·66 |

* Current ratio at Secchi disk depth.

# NOTES ON PLYMOUTH MYSIDACEA

## By Olive S. Tattersall

Whilst working recently at the Plymouth Marine Laboratory[1] I was, very kindly, given the opportunity of examining the mysids captured during a night cruise carried out by Mr P. G. Corbin around the Eddystone Lighthouse on 26/27 August 1936.

Eight 30 min. standard oblique hauls were taken with a 2-metre stramin ring trawl, at stations situated in a circle around the lighthouse, starting 2 miles due north-east at 8.17 p.m. The second haul was taken 2 miles due east and so on, passing from station to station in a clockwise direction, the last haul being taken due north at 4 a.m. The weather was fine and clear, with a clear half-moon which set at 15 min. past midnight.

The collection included nine species, only four of which—*Anchialina agilis*, *Leptomysis gracilis*, *Gastrosaccus normani* and *Schistomysis ornata*—were present in any numbers, whilst the other five were represented by only a few isolated individuals.

Adult mysids in the open ocean live by day, for the most part, either on the bottom or swimming about in the lowest levels of the water just clear of the bottom. It has been shown by many workers (e.g. Russell, 1925, 1927, 1928, 1931; Tattersall, 1936, 1938; Fage, 1933) that many species of mysids perform regular migrations to higher levels during hours of darkness, and sometimes actually reach the surface. Shortly before dawn they begin to move downward again, and by daylight all but immature animals have regained their habitat at the bottom. In addition to this nightly upward movement, many mysids become markedly planktonic during their breeding season, and in many species the females rise to the surface to release the young. These juvenile animals remain pelagic but gradually seek deeper water as they approach maturity (Fage, 1932, 1933; Tattersall, 1938).

In oblique hauls such as were used on the Eddystone cruise, it is not possible to say at which levels the animals were mainly taken, but certain points arise which bear out the observations of earlier workers. The first haul was taken before daylight had completely faded and the upward migration had not yet begun, for only five specimens were taken. At 9.14 p.m., when the second haul was taken, 458 mysids were captured, of which more than half were immature. Hauls 3 and 4 showed a steady increase in numbers but, for some reason, the numbers in hauls 5 and 6 fell considerably, rising again sharply in hauls 7 and 8.

The hauls are analysed in Table I. Hauls 4 to 8 were sub-sampled, one-tenth being counted.

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[1] I should like to express my gratitude to the Director, Mr F. S. Russell, F.R.S., and to Mr G. M. Spooner, for all the help they have so kindly given me.

The majority of the mysids collected during the night were immature and practically all the adults were actively breeding, the males large and well developed and the females with full brood-pouches. The proportion of adults increased markedly in the later hauls. Whilst sorting the collection I was particularly struck by the preponderance of males among the adults. The numbers of the sexes were counted in *Gastrosaccus normani*. I found that in the early part of the night there was an average of three adult males to every adult female, with the sexes more or less evenly balanced in the juveniles. In the later hauls more females appeared and the males outnumbered them by only two to one, while the juveniles were again present in almost equal numbers.

Amongst the specimens of *G. normani* I was interested to find three adults which possessed reflexed lobes on the posterior margin of the carapace but which, in every other particular, conformed with the published descriptions of the species. My husband (Tattersall, 1912, p. 41) recorded similar specimens from the west coast of Ireland, and among his unpublished notes I find a record that he had examined a male and a female specimen from Plymouth, both with reflexed lobes, but which were 'undoubtedly *G. normani*'. It was at one time thought that the presence of reflexed lobes was constant for certain species, and that they never occurred in *G. normani*. Acting on this assumption, Kossmann (1880, p. 95) founded the genus *Haplostylus* for those species which had no lobes on the posterior margin of the carapace, and he placed *G. normani* in this genus. Since it is now clear that the character upon which the genus was founded is variable the name *Haplostylus* (ἁπλόος = simple) ceases to have any significance and the species must be referred to Sars's original genus *Gastrosaccus*.

TABLE I. NUMBERS OF MYSIDACEA SPECIES CAPTURED IN EACH HAUL OF THE EDDYSTONE CRUISE

| Haul ... | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Time ... | 8.17–8.56 | 9.14–9.45 | 10.01–10.34 | 10.58–11.34 | 00.55–01.31 | 01.51–02.22 | 02.50–05.26 | 04.01–04.36 |
| *Anchialina agilis* | 1 | 63 | 181 | 790 | 580 | 480 | 1290 | 1430 |
| *Schistomysis ornata* | — | 59 | 36 | 120 | 130 | 320 | 260 | 370 |
| *Leptomysis gracilis* | 3 | 146 | 136 | 510 | 270 | 280 | 740 | 1160 |
| *Gastrosaccus normani* | 1 | 24 ♂<br>9 ♀<br>20 juv. | 52 ♂<br>17 ♀<br>83 juv. | 18 ♂<br>7 ♀<br>23 juv. | 11 ♂<br>4 ♀<br>11 juv. | 12 ♂<br>7 ♀<br>19 juv. | 20 ♂<br>11 ♀<br>15 juv. | 13 ♂<br>7 ♀<br>9 juv. |
| *Erythrops elegans* | — | 1 | — | — | — | 2 | 6 (1 with parasite) | 8 (2 with parasite) |
| *Siriella norvegica* | — | 2 | 1 | — | 1 (♀ 23 m.) | 1 | — | 1 (juv.) |
| *S. jaltensis* | — | 1 | — | — | 1 (juv.) | — | — | — |
| *Mysidopsis gibbosa* | — | 2 | 1 | — | 1 | — | — | — |
| *M. angusta* | — | 6 | — | — | — | — | 1 | — |

In the material from haul 7, I found an adult female of *Erythrops elegans*, bearing a large male specimen of the parasitic copepod *Aspidoecia normani* Giard & Bonnier attached by a short stalk to the middle of the dorsal surface of the first abdominal somite. In haul 8, I found two more specimens of *Erythrops elegans* which were parasitized by the same species. One of the *Aspidoecia* was a male attached to the dorsal surface of the second abdominal somite, and the other was a large female with eight to nine ovisacs attached to the first abdominal somite. Among about twenty specimens of *Erythrops elegans* dredged off Rame Head on 6 June 1948, I found one adult female bearing a female *Aspidoecia normani* on the dorsal surface of the second abdominal somite. Only one of the hosts was a male which appeared to be fully developed. It is significant that although unparasitized females captured at the same time all had their brood-pouches full of eggs or embryos, all the parasitized females had empty brood-pouches.

*A. normani* has been recorded from Norwegian waters on five species of *Erythrops*. Scott (1902, p. 480) recorded it from the Firth of Forth on *E. elegans* and *E. microps* (= *E. goësii*) but, although its host species are known from many localities around our coasts, I can find no further record of it from British waters. Its occurrence in two gatherings taken nearly 12 years apart suggests that it may occur regularly in the Plymouth area.

Although the Eddystone cruise yielded representatives of only nine species, there have, up to the present, been no fewer than twenty-six species of mysids recorded from the Plymouth area. I have therefore drawn up a key for the identification of the genera to which they belong, with supplementary keys[1] from which it should be possible to identify any of the species mentioned. I have included among these a few species which have not yet been recorded from the Plymouth area, but which may reasonably be expected to be found there.

Descriptions of genera and species may be found in the standard works of Sars (1870–9) and Zimmer (1909). The keys given by Zimmer (1933) for the North and Baltic Seas, and in particular the sketches which accompany them, are also very useful.

The nomenclature here conforms with that adopted in the Ray Society Monograph (Tattersall, in Press).

## KEY TO THE MYSIDACEA FOUND IN THE PLYMOUTH AREA

### Genera

1. Telson cleft. . . . . . . . . . . . . 2
   Telson entire (one species with very small naked incision). . . . 8
2. Scale setose all round. Carpus and propodus of third thoracic limb fused, much enlarged and not subdivided. *Heteromysis* S. I. Smith [see p. 785]
   Scale with outer margin without setae. Third carpopropodite subdivided into three or more segments, not much enlarged. . . . 3
3. Exopod of uropod with spines arming outer margin. . . . . 4
   Exopod of uropod setose all round. . . . . . . 5

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[1] The supplementary keys are given in taxonomic order.

4. Short robust form. Posterior margin of carapace transverse and straight. Inner margin of endopod or uropod with many spines in series right to distal end. Telson with many spines in series. Carpopropodus of thoracic endopods subdivided into three or four segments. *Anchialina* Norman & Scott [*A. agilis* (G. O. Sars)]

Long slender form. Posterior margin of carapace emarginate. Few large spines on inner margin of endopod of uropod. Few spines on lateral margins of telson, not in series. Carpopropodus of thoracic endopods subdivided into many segments. *Gastrosaccus* Norman [see p. 788]

5. Scale ovate, with proximal part of outer margin naked and not ending in a thorn. *Hemimysis* G. O. Sars [*H. lamornae* (Couch)]

Naked portion of outer margin of scale ending in a thorn or spine. . . 6

6. Scale long, slender, with naked outer margin terminating in articulated spine; its apex little, if at all, longer than spine. Fourth pleopod of male with exopod very long, styliform, seven-segmented; distal segment terminating in a knob, armed a short distance from its apex with dense, spirally arranged spinules, but no 'pincer' setae. *Praunus* Leach [see p. 787]

Scale oval, its apex extending far beyond terminal thorn. Fourth pleopod of male very long; armed distally with two long setae which form a weak kind of 'pincers'. . . . . . . . . . . 7

7. First subsegment of carpopropodus of thoracic limbs short, swollen, very setose and cut off obliquely from more distal joints. *Paramysis* Czerniavsky [see p. 787]

First subsegment of carpopropodus of third to eighth thoracic limbs longer than more distal segments, not swollen and cut off by transverse articulation. *Schistomysis* Norman [see p. 787]

8. Scale with outer margin naked and ending in a thorn. . . . . . 9

Scale setose all round. . . . . . . . . . 10

9. Telson short, triangular, lateral margins naked, apex narrow, transverse, armed with 2–4 strong spines. Eye pigment very red. *Erythrops* G. O. Sars [see p. 786]

Telson long, linguiform with rounded apex; armed all round with many spines usually arranged in series. Exopod of uropod two-segmented; inner margin of endopod with many spines. *Siriella* Dana [see p. 785]

10. Tarsus, three- to four-segmented. Pleopods of male biramous, natatory, with only setae modified. (Telson long.) . . . . . . 11

Tarsus six- to eight-segmented. Pleopods of male rudimentary; fourth pair long, with modified setae. . . . . . . . . . . 12

11. Scale very slender and rather long. Telson more parallel-sided, armed with many spines in series. (Carpopropodus of third to eighth thoracic limbs three-segmented.) *Leptomysis* G. O. Sars [see p. 786]

Scale lanceolate. Telson triangular, tapering to narrow truncate or rounded apex (one British species has small unarmed median notch); lateral margins armed with small spines not in series. (Telson hollowed into a trowel-shape.) *Mysidopsis* G. O. Sars [see p. 786]

12. Scale long and narrow. Telson long, tapering, with many spines arming lateral margins and apex. Fourth pleopods of male very long, armed distally with two equal setae. . . . . . . . . . . . 13

Scale small and narrow. Telson short, lateral margins unarmed, each ending distally in large spine; apex rounded, armed with dense comb of regular spines. Fourth male pleopod long, with 'pincer' setae. (Eye-stalks long, cylindrical.) *Mesopodopsis* Czerniavsky [*M. slabberi* (van Beneden)]

13\. Distal end of scale acutely pointed. *Acanthomysis* Czerniavsky [*A. longicornis* (Milne Edwards)]

Distal end of scale rounded. *Neomysis* Czerniavsky [*N. integer* (Leach) (=*vulgaris* J. V. Thompson)]

## **Siriella** Dana, 1850

1\. Rostrum long and tapering, extending to distal end of second segment of antennular peduncle. Apex of telson with four (rarely three) spinules between the two large apical spines. *S. armata* (Milne-Edwards)

Rostrum short and pointed, reaching only half-way along the first segment of antennular peduncle. Telson with three apical spinules. . 2

2\. Terminal spinules of telson of equal length. Distal segment of exopod of uropod not twice as long as broad. *S. clausii* G. O. Sars

Terminal spinules of telson in form of trident with median one considerably longer than the other two. Distal segment of exopod of uropod twice (or nearly) as long as broad. . . . . . . . . . 3

3\. Outer margin of exopod of uropod with 9–15 spines. Spines arming inner margin of endopod of uropod increasing evenly in size distally without smaller spines between. *S. jaltensis* Czerniavsky

Outer margin of exopod of uropod with 11–12 spines. Spines arming inner margin of endopod of uropod arranged in series proximally with the 8–10 distal spines equal and no small ones between. (Rostrum curved downward and appearing short in dorsal view.) *S. jaltensis* var. *brooki* Norman

Outer margin of exopod of uropod with 15–23 spines; spines on inner margin of endopod arranged in series throughout. Very like *S. clausii* in general appearance but nearly twice as large. *S. norvegica* G. O. Sars

## **Gastrosaccus** Norman, 1868

Posterior margin of carapace with fringe of eight to ten delicate prolongations. Antennular peduncle without conspicuous setae. Apex of scale equal in length to terminal spine of outer margin. Telson with 6–8 large spines on each lateral margin. Fifth abdominal segment laterally compressed with median dorsal keel produced into a spine posteriorly. *G. spinifer* (Goës)

Posterior margin of carapace usually with two reflexed lobes. Inner margins of second and third segments of antennular peduncle, each with three to five long plumose setae. Apex of scale shorter than spine terminating outer margin. Telson with 6 spines on each lateral margin. (Endopod of uropod with 6 spines on inner margin.) *G. sanctus* (van Beneden)

Posterior margin of carapace usually without reflexed lobes. Inner margins of second and third segments of antennular peduncle each with a single plumose seta. Apex of scale longer than terminal spine of outer margin. Telson with about 10 spines on each lateral margin. (Endopod of second pleopod of male sigmoid and not natatory. Eyes small.) *G. normani* G. O. Sars

### **Erythrops** G. O. Sars, 1869

1. Outer margin of antennal scale serrated. Inner margin of endopod of uropod minutely serrulated under the setae. . . . . . . . . . 2

   Outer margin of antennal scale not serrated. Inner margin of endopod of uropod usually not serrulated. . . . . . . . . 3

2. Distal serration of outer margin of scale longer than apex of scale. Endopod of eighth thoracic limb variable in length, but not extending beyond posterior margin of abdomen. *E. serrata* (G. O. Sars)

   Distal serration of outer margin of scale shorter than apex of scale. Endopod of eighth thoracic limb reaching beyond distal tip of uropod. *E. abyssorum* G. O. Sars

3. Inner margin of endopod of uropod minutely serrulated. . . . . . 4

   Inner margin of endopod of uropod without serrulation. (Endopod of eighth thoracic limb extending to posterior end of fifth abdominal segment. Eyes large, close together; short, linguiform rostrum produced forward between the eyes; antennal scale considerably longer than antennular peduncle.) *E. erythrophthalma* (Goës)

4. Eyes large, set well apart, antennal scale a little longer than antennular peduncle. Endopod of eighth thoracic limb usually short, barely reaching end of fourth abdominal segment. (Animals small and comparatively robust.) *E. elegans* (G. O. Sars)

   Eyes small, set widely apart; antennal scale short, subequal in length to the antennular peduncle. Endopod of eighth thoracic limb reaching to posterior end of telson. *E. microps* (G. O. Sars)

### **Leptomysis** G. O. Sars, 1869

1. Integument covered with scales which are upturned distally, giving the animals a hispid appearance. Rostrum acutely pointed with convex sides and a deep notch at each side at its base. (Animals very transparent and slender. Marked constriction in telson marking insertion of distal pair of long marginal spines. Statocyst large.) *L. gracilis* (G. O. Sars)

   Integument smooth. Rostrum without lateral notches. . . . . . 2

2. Animals longer and more slender. Body covered all over with fine branches of brown pigment. Rostrum with straight sides. (Limbs stouter and statocyst smaller than in *L. gracilis*. No marked constriction in the telson.) *L. mediterranea* G. O. Sars

   Animals much shorter, more compact and robust than other two species. Colour milky, pale rosy markings. Rostrum short, with curved margins. (Eyes closely set, thick and short. Telson short and broad without constriction distally.) *L. lingvura* (G. O. Sars)

### **Mysidopsis** G. O. Sars, 1864

1. Telson with no trace of median cleft. . . . . . . . . 2

   Apex of telson with short unarmed notch. (Lateral margins of telson armed with 14–18 spines which increase in size distally. Cleft wedge-shaped without plumose setae.) *M. angusta* G. O. Sars

2. Rostrum broadly triangular. Telson triangular, rather long; lateral margins straight, converging to narrow truncate apex with a large spine at each

corner; 8–10 spines on each lateral margin. Carapace without median swellings. *M. didelphys* (Norman)

Rostrum very small, in form of very obtuse triangle. Telson short, with lateral margins concave, narrowing to rounded apex armed with two small median spinules; spines on lateral margins very small. Two conspicuous median swellings on carapace appearing as humps in lateral view. *M. gibbosa* G. O. Sars

## **Paramysis** Czerniavsky, 1882

Short robust form; length 7 mm. Uropod armed along whole length of inner margin with 28–30 spines arranged in series. Telson narrow, with narrow cleft not widely open. *P. arenosa* (G. O. Sars)

Longer and more slender form; length 11 mm. Endopod of uropod with 9–10 subequal spines along distal two-thirds of inner margin. Telson wider, cleft widely open with sides nearly straight. *P. helleri* (G. O. Sars)

## **Schistomysis** Norman, 1892

*Note.* The spines arming the inner margins of the endopods of the uropods are fewer and less crowded, and the cleft of the telson less deep in immature animals than in adults in this genus. As a result there may be some difficulty in identifying immature specimens.

1. Eyes long and narrow. Carpopropodus with nine subsegments. (Body very slender, expecially anteriorly. Cleft of telson fairly wide with straight sides. Spines arming inner margin of endopod of uropod very dense.) *S. spiritus* (Norman)

Eyes not long and narrow. Carpopropodus with five to six subsegments. . 2

2. Eyes short and thick and large, not extending much beyond lateral margin of carapace. Spines arming inner margin of endopod of uropod not dense; one situated terminally, then a space, then 1 spine, then another space and then regular row to statocyst. Carpopropodus with five subsegments (rarely six). (Body robust. Cleft of telson deep with convex margins.) *S. ornata* (G. O. Sars)

Eyes nearly globular, moderately large. Endopod of uropod markedly curved, armed on inner margin with 1 very long terminal spine, then a gap to about half-way along margin, then 3–4 very long slender spines, and then a close row of spines in series back to the statocyst. Carpopropodus with six subsegments (rarely five). *S. parkeri* Norman

A fourth species, *S. kervillei* (G. O. Sars), has not yet been recorded from Plymouth, though it has been taken in the mouth of the Seine and off the coast of Kent. It is very closely similar to *S. ornata* and appears to have similar habits to that species. Although certain of its characters are quite constant, and the two species may be distinguished when they are together, it is extremely difficult to set out shortly any definite characters whereby they may be distinguished. The most reliable guide is in the arrangement of the chromatophores.

## **Praunus** Leach, 1814

*Note.* The specific characters differentiating the species of this genus are not attained until the animals are fully grown, though they may be sexually mature. The proportions of the antennal scale, the number of sub-segments in the tarsus of the thoracic limbs and the depth of the cleft of the telson vary considerably with age, and it is very difficult to distinguish between specimens of *P. flexuosus*, which are not fully mature, and specimens of *P. neglecta*. The only reliable guide lies in the distribution of the chromatophores, which remains constant throughout life (Keeble & Gamble, 1904, p. 331).

1. Apex of scale shorter than terminal spine of outer margin. (Body long and slender. Eyes well developed with long cylindrical eye-stalks; whole of cornea and part of eye-stalks extending well beyond lateral margins of carapace. Scale very long and slender, seven to nine times as long as broad; more than twice as long as antennular peduncle. Telson cleft to one-sixth of total length. Endopod of uropod with 10–12 spines on inner margin. Tarsus of third to eighth thoracic limbs usually with six subsegments, eighth with five.) *P. flexuosus* (Müller)

2. Apex of scale longer than terminal spine of outer margin. Somewhat smaller than *P. flexuosus*, but very similar in form. Antennal scale five times as long as broad; less than twice as long as antennular peduncle. Apex slightly longer than terminal spine. Endopod of uropod with 12 spines on inner margin. Telson cleft to one-fifth of total length. Tarsus of thoracic limbs five-segmented (eighth four-segmented). *P. neglectus* (G. O. Sars)

   Body shorter and less slender than preceding species. Antennal scale four times as long as broad, and about one-third longer than the antennular peduncle. Apex produced beyond terminal spine to about two to three times length of spine. Endopod of uropod with 6–7 spines on inner margin. Telson cleft to nearly one-third of total length. Tarsus of thoracic limbs four-segmented. *P. inermis* (Rathke)

## **Heteromysis** S. I. Smith, 1874

1. Telson with spines only on the distal portion of the lateral margins. . . 2

   Telson with spines (18–20) along whole length of lateral margins; apical lobes with 2 spines, the inner longer than the outer. Endopods of uropods with spines along whole length of inner margin. *H. armoricana* Nouvel

2. Endopod of uropod with 17–20 spines along whole of inner margin. Lateral margins of telson with 14–18 spines on distal portion; apical lobes with 2 spines, the inner longer than the outer. Eye not very small. *H. formosa* S. I. Smith

   Endopod of uropod with single spine near statocyst. Lateral margins of telson armed distally with 9–13 spines; apical lobes narrow and acute, armed with 2 spines, the outer twice as long as the inner. Eyes very small. *H. microps* (G. O. Sars)

## SUMMARY

The mysid fauna of eight night hauls made near the Eddystone Lighthouse is analysed.

Keys are given for the identification of Mysidacea which have been recorded from, or are likely to occur in, the Plymouth area.

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# THE FOOD OF THE DOGFISH, *SCYLIORHINUS CANICULUS* L.

By Nellie B. Eales, D.Sc.

Zoology Department, University of Reading

During the past eight years records have been kept of the contents of the stomachs of all dogfish dissected in the Zoology Department of Reading University. The specimens, numbering about 450 altogether, came from Swansea Docks, and were caught off the west coasts of the British Isles. Students were asked to spread out the contents of the stomach of the fish they were dissecting in a dish, and to make notes of those animals they could identify. I then, as far as was possible, checked the identifications, and removed for more detailed investigation any specimens of particular interest. In the circumstances it was impossible to make accurate numerical records of each species, or to work out fragments from partially digested material, but the rare specimens were recorded by numbers. Sometimes a record of one means one perfect specimen.

The records showed a remarkable uniformity, indicating either a habit on the part of the fish of hunting over certain bottom areas, or a selective search for palatable food. Six phyla were represented, and despite partial digestion, the genus and sometimes the species could be determined. Details are given in Table I.

Comparing these records with those of Ford (1921), there is a close resemblance in the nature of the food, allowing for variations due to the location of the feeding grounds. Several points of interest may be noted:

(i) Fish comprise only a part of the food of the dogfish and consist of small specimens. As Ford points out, dogfish are bottom feeders, and the presence of pelagic fish in the stomach is largely accidental.

(ii) Ford's records do not include the horse mackerel, which in my records for 1948 and 1949 were almost as numerous as herring. The scutes on this fish retard digestion and it is therefore easy to identify.

(iii) In the Invertebrate groups we have many records in common—some of relatively rare animals, e.g. *Atelecyclus* and *Gonoplax*, and others indicating a selective feeding habit, e.g. *Upogebia*, *Thyone*, Gephyrean worms.

(iv) Molluscs, except for *Buccinum*, are not well represented. How does the dogfish tackle a whelk? Does it swallow it whole, and dissolve the shell? I have found lamellibranch shells and even cuttlebone undigested, but have never seen a trace of a whelk shell, though opercula are frequently found. Are the opercula scooped up from dead material on the sea bottom? Similarly, does the dogfish swallow the shell containing the hermit crab—for again, no trace of the shell remains, though the crab itself forms a large proportion of the food in some fish?

TABLE I. SPECIES RECORDED FROM STOMACHS OF *Scyliorhinus caniculus*

| | 1942 | 1943 | 1944 | 1945 | 1946 | 1947 | 1948 | 1949 |
|---|---|---|---|---|---|---|---|---|
| Phylum Chordata: class Pisces | | | | | | | | |
| *Clupea harengus* (6 or more records) | × | × | × | × | × | × | . | × |
| *Trigla lucerna* | . | . | . | 1 | . | . | . | . |
| *Limanda limanda* | . | . | . | . | . | . | 1 | . |
| *Cottus bubalis* | . | . | . | . | . | . | . | 1 |
| *Caranx trachurus* | . | . | . | . | . | . | 3 | 4 |
| *Nerophis lumbriciformis* | . | . | . | . | . | . | . | 1 |
| Egg capsule of dogfish | . | 1 | . | . | . | . | . | . |
| Phylum Annelida: Chaetopoda, Polychaeta | | | | | | | | |
| *Aphrodite aculeata* | . | . | . | 5 | . | . | . | . |
| *Nereis* sp. | . | . | . | 2 | . | . | . | . |
| *Nephthys* sp. | . | 1 | . | . | . | . | . | . |
| *Glycera lapidum*? | 1 | . | . | . | . | . | 10 | 4 |
| *Lumbriconereis latreilli* | . | . | 1 | . | . | . | 5 | . |
| Phylum Gephyrea | | | | | | | | |
| *Phascolosoma* sp. | . | . | . | . | . | . | 1 | 1 |
| Phylum Echinodermata: class Holothurioidea | | | | | | | | |
| *Thyone fusus* | 2 | . | 3 | 8 | . | . | . | 3 |
| Phylum Arthropoda: class Crustacea | | | | | | | | |
| *Hippolyte varians* | . | . | . | 1 | . | . | . | . |
| *Leander serratus* | . | . | . | . | . | . | . | 2 |
| *Crangon vulgaris* | 1 | 1 | 1 | . | . | . | 1 | . |
| *Homarus vulgaris* (small) | . | 6 | . | . | . | . | . | . |
| *Nephrops norvegicus* | . | . | . | . | . | . | 1 | 20 |
| *Galathea* spp. | . | . | . | . | . | . | . | 1 |
| *Upogebia stellata* | . | . | 3 | . | . | . | . | . |
| *Eupagurus bernhardus* (many) | × | × | × | × | × | × | . | × |
| *Portunus*, mainly *depurator* | . | 3 | . | . | . | . | . | . |
| *Atelecyclus septemdentatus* | . | . | . | . | . | . | 2 | . |
| *Gonoplax rhomboides* | . | 1 | . | . | . | . | . | 3 |
| Phylum Arthropoda: class Pycnogonida | | | | | | | | |
| *Pycnogonum littorale* | . | 1 | 7 | . | . | . | . | . |
| Phylum Mollusca: class Lamellibranchia | | | | | | | | |
| *Mya truncata* (siphons) | . | . | . | 2 | . | . | . | . |
| *Ensis ensis* (shell and siphons) | . | . | . | 1 | . | . | . | . |
| Phylum Mollusca: class Gastropoda | | | | | | | | |
| *Buccinum undatum* (opercula) | Many | . | . | Many | . | . | . | . |
| Phylum Mollusca: class Cephalopoda | | | | | | | | |
| *Sepia officinalis*—small | . | . | 2 | . | . | . | 1 | . |
| beaks of adults | . | . | . | Many | . | . | Many | . |
| *Loligo forbesii* | . | . | . | . | . | . | 1 | . |
| *Octopus* (acetabula) | Many | . | . | . | . | . | . | . |

(v) There is no mention of *Nephrops norvegicus* in Ford's records. This is not surprising, for his fish came from the English Channel where there are none of the extensive muddy bottoms which these lobsters require. In fact, *Nephrops* is not recorded in the Plymouth Fauna list. In my records, it appeared for the first time in 1948, and in 1949 was abundant. I wrote to the fish merchant from whom the fish were obtained, asking for information concerning the fishing grounds. He replied that only during the past two years had the usual grounds, closed on account of mine fields during the war, been re-opened. Recently fish had been caught in the Irish Sea and off the extreme west coat of Ireland, to a distance of 400 miles west of Swansea. Muddy areas are present to the north and west of the British coasts, and the dogfish were evidently feeding on these grounds.

Collating the above information, it appears that the favourite food of the dogfish consists of a mixture of whelks, shrimps, hermit crabs, cuttlefish, *Thyone*, and small fish of various species. They are general feeders on benthic and pelagic animals, scooping some up from the bottom and catching others while swimming. There is no evidence that they are a serious danger to the food fishes.

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# THE OCCURRENCE OF BRITISH *APLYSIA*

By Ursula M. Grigg[1]

From the Plymouth Laboratory

(Plates I and II and Text-figs. 1–3)

## INTRODUCTION

On 13 November 1947 a specimen of the sea hare, *Aplysia depilans* L., which had been trawled in Babbacombe Bay, was sent to the Plymouth Laboratory. When it was realized that the animal was not the common *A. punctata* Cuv., collecting trips to likely places were undertaken in the hope of finding more. No others were found, but on one of the expeditions Dr D. P. Wilson picked up a specimen of *A. limacina* L.

Both *A. depilans* and *A. limacina* are found in the Mediterranean and on the west coast of Europe: *A. depilans* has been found in British seas before, but so far as is known *A. limacina* has not.

These occurrences provide the main reason for publishing this study. The paper also includes an account of the distribution of aplysiids in British waters and a review of the controversy over the identity of large specimens. As the animals are not usually described in natural history books, notes on the field characters are added.

I would like to thank the Director of the Plymouth Laboratory for affording me laboratory and collecting facilities and for his interest in the work. I am most grateful to Dr G. Bacci, who went to much trouble to send me specimens from Naples; to Dr W. J. Rees, who arranged for me to have access to the British Museum collection; to Dr D. P. Wilson, who has provided the photographs of *A. punctata* (Pl. I) and *A. limacina* (Pl. II); and to D. J. Slinn, who prepared the map. The distribution records were compiled with the help of many members of other marine laboratories and university zoology departments, and I am indebted to them for their kind co-operation in answering my queries.

I am greatly indebted to the Director of the Stazione Zoologica, Naples, for allowing me to spend a fortnight at the Stazione in September 1949, and providing me with living specimens of *A. limacina*.

This study was undertaken during the period of tenure of a D.S.I.R. grant.

## RECENT OBSERVATIONS

### *Aplysia depilans*

The specimen of *A. depilans* was trawled by a Teignmouth fishing vessel in Babbacombe Bay on 12 November 1947. It was brought to the Plymouth Laboratory on 13 November in a rather damaged condition.

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[1] Tucker Price Research Student, Girton College.

When crawling the animal measured 24 cm. and was therefore a large specimen. It was a purplish fawn colour, with darker and lighter mottlings. The lips, gills and genital aperture were pale fawn. The eyes were very small and black, each surrounded by an area of pale blue. No dye was ejected, even when the animal was handled. It was put in a tank with circulating seawater, and crawled a short distance very slowly, without attempting to feed. The footsole was broad and non-contractile, and the head was not lifted or stretched out. The parapodia, which were low and exposed the visceral hump, were not undulated. The slight side to side swaying of the head and neck as the animal advanced was more reminiscent of a hippopotamus than a hare.

After the death of the specimen two days later, dissections showed that the head and visceral mass were much bruised. The shell was torn at the apex, which did not appear to have been pronounced. The anal indentation was also shallow. The shell was 5·7 cm. long and 4·5 cm. broad, measurements being taken from the apex to the farthest margin, and from the shoulder to the opposite margin at right angles to the first measurement. Only the hyaline layer of the shell was present. The radula was of the spade-shape characteristic of the species and carried over 70 rows of teeth; the formula was not determined. There was no recognizable food in the oesophagous or gizzard.

The photograph (Pl. I), which was taken when the animal was dying, is included to show the shape of the head and parapodia. The bloating of the footsole is not characteristic of a healthy specimen.

### *Aplysia limacina*

The specimen of *A. limacina* was collected at L.W.S.T. on the Salstone, Salcombe Estuary, on 15 February 1949. It measured 20 cm. extended, which is small for the species.

The animal was a dark purple, the skin having a velvet lustre. The edges of the parapodia, tentacles and mouth-lappets were violet, as was the dye, which was ejected copiously whenever the animal was disturbed. The eyes were black.

This *Aplysia*, though sluggish, could be made to crawl by handling or by warming the water slightly. When it was at rest, the parapodia were folded over one another, and exhibited slow waving movements. A water current flowed from front to back through the cavity thus formed above the mantle. When crawling, the animal held the parapodia partially or fully stretched up, undulating the edges. The mouth-lappets and rhinophores were also in constant motion, but the head was never lifted and held out as in *A. punctata*. The footsole was narrow and the animal sometimes gripped the substratum with the posterior end only, as *A. punctata* does, but was not capable of the active extension and contraction of that species.

Specimens in the Naples Aquarium also folded their parapodia across their mantles when at rest and passed water over the visceral mass by undulating the parapodia. When an animal was crawling the parapodia were partially extended, while in swimming they waved vigorously, propelling the *Aplysia* forward. The long axis of the body was held nearly vertical when the animal swam across the tank with the head slightly advanced and the tail bent back, giving a graceful sigmoid curve to the foot. When the animal swam a short distance over the tank floor the foot was horizontal.

Though the Salcombe specimen browsed on *Ulva lactuca* when first caught, it lost weight rapidly and was killed 3 weeks later. The shell had both hyaline and calcareous layers, and the apex and anal indentation were pronounced. It measured 3·5 cm. long by 2·8 cm. broad. The radula was of the typical square shape with abrupt tip, but was rather short, measuring only 0·8 cm. long by 0·9 cm. broad (Text-fig. 2C). There were 28 rows of teeth, and the formula across the broadest part was 20.1.20. The long dagger-like cusps on the lateral teeth were very well developed, which suggests that it was a young specimen. There was no recognizable food in the gut.

Dr Wilson's photograph (Pl. II) was taken while the animal was crawling with parapodia partially extended.

## HISTORY

Although *Aplysia punctata* is the only aplysiid common in British seas, it has been described under several names on account of the great variation between individuals. Owing to their lack of skeletal structure compared with most shell-bearing molluscs, all aplysiids can assume many shapes, a faculty increased in *A. punctata* by its power of extension, which exceeds that of most other members of the family. The colour varies from a dark purple to a pale olive green, always with well-defined spots of black or white, and occasionally with the parapodia bordered with blue. Young specimens may be a delicate leaf-green or rose pink, the latter phase being *A. rosea* of Rathke and *A. nexa* Thompson. These colour variations probably depend upon the colour of the weed on which the individuals are living.

In the radula the number of tooth rows and the number of lateral teeth in each row increase as the animal grows larger. Hunt (1878) gives a table of radula formulae in which the numbers range from 4.1.4 to 15.1.15. Though the shape of the radula does not change, the teeth in large specimens are blunt, and rarely have the regular and distinctive shapes of most published diagrams. The shells of large animals show the same phenomenon, being generally coarser and less easy to define than those of small ones. Comparable changes are found in all members of the family.

All these factors have contributed to confuse the synonymy of *A. punctata*, and it is not surprising that on the rare occasions when extra large specimens appeared some naturalists were unwilling to assign them to another species. It was not until descriptions were published from regions where several species were common that the identifications could be made with certainty.

Pennant (1812) gives two species of *Aplysia* in his British list. These he calls *A. depilans* L. and *A. mustelina* Davies. He separates them on the gill shape, and mentions that *A. mustelina* had a crimson patch on 'that part which by its situation corresponds with what Bohadsch deems the lungs in his subject'. Mazzarelli (1893) considers Pennant's *A. depilans* to be *A. punctata*, and his *A. mustelina* to be *A. depilans* Cuv., presumably on the strength of the crimson patch. *A. mustelina* is usually taken to be a synonym for *A. punctata*.

Forbes & Hanley (1853), in their *British Mollusca*, include only one species, which they call *A. hybrida* Sowerby (= *A. punctata*). Jeffreys (1869), while supporting their view that *A. punctata* is the common species, records two specimens of *A. depilans*, one from Guernsey, and one collected by Gosse in Torbay.

In 1870 Couch described two specimens under the name of *A. melanopus*. His types are in the British Museum and are undoubtedly *A. depilans*.

In the autumn of 1875 A. R. Hunt, who had made a collection of shells and radulae of *A. punctata* from Torbay, found several *A. depilans*. He published an account of these (Hunt, 1877), and discussed their identity. While considering the possibility that they might be *A. depilans*, he remarked that 'too much reliance is perhaps placed on specific differences deduced from the very flexible shells and varying odontophores of these gastropods', and pointed out that 'an examination of a series of specimens of different sizes will prove conclusively that the odontophores develop gradually with the growth of their owners'. After collecting more in the winter of 1877–78 he published a paper (Hunt, 1878) on the growth of aplysiids, in which he came to the conclusion that the specimens were overgrown *A. punctata*. This paper includes an ingenious theory to account for the fact that all these large specimens were found in the winter when *A. punctata* was not present, and that there were no specimens within the size range of *A. punctata* which could be considered as the young of another species. He therefore suggested that *A. punctata* could only reach maximum size when protected from rough seas and provided with abundant food. These conditions were fully met near Torquay, which was sheltered naturally from the north and west and where artificial breakwaters of various kinds provided additional protection. Ample food was to be found on the *Ulva* beds growing round the sewage outflow at Tor Abbey. The animals were therefore able to live longer than they would otherwise have done, and to attain a large size. Hunt went on to remark that 'as the large Aplysiae have not been taken in deep water...it is probable that they do not make their way back to the greater depths from which they originally came and that the race is kept up by partially grown individuals'. Apparently he did not realise that *Aplysia punctata* comes inshore to spawn. He did not comment on the different external appearance and lack of contractility of his large animals as compared with *A. punctata*, though he mentioned that they very rarely ejected dye.

Garstang (1890), who discussed the subject with Hunt and examined his specimens, was equally inclined to regard them all as *A. punctata*, but he said: 'I trust that the subject may receive more conclusive treatment in the hands of a naturalist upon a coast where large Aplysiae are more common than they are with us in England.'

This treatment was supplied when Mazzarelli published his monograph (Mazzarelli, 1893) describing the anatomy, field characters, distribution and habits of six aplysiids including the three considered here. He recognized three records of *A. depilans* for the British coast. These are Gray (reference not given), Pennant (1812), and Couch (1870). He did not include Britain in his list of localities for *A. limacina*.

In the second edition of the list of British marine mollusca published by the Conchological Society of Great Britain and Ireland in 1902, *A. punctata* and *A. depilans* are both included, but in the later list compiled by Winckworth (1932) only *A. punctata* appears.

## DISTRIBUTION

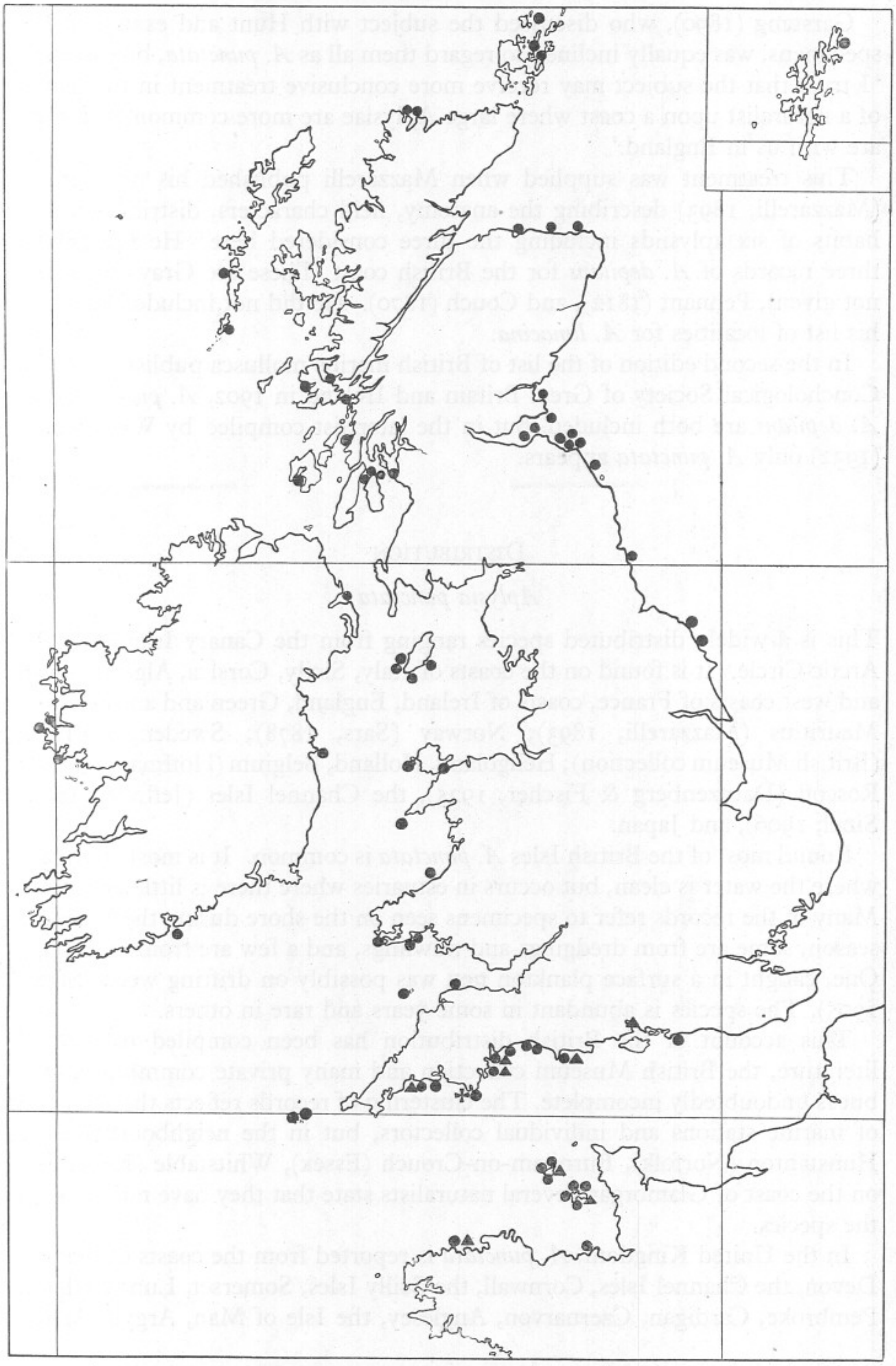
### *Aplysia punctata*

This is a widely distributed species ranging from the Canary Islands to the Arctic Circle. It is found on the coasts of Italy, Sicily, Corsica, Algeria, south and west coasts of France, coasts of Ireland, England, Greenland and possibly Mauritius (Mazzarelli, 1893); Norway (Sars, 1878); Sweden, Portugal (British Museum collection); Heligoland, Holland, Belgium (Hoffmann, 1926); Roscoff (Dautzenberg & Fischer, 1925), the Channel Isles (Jeffreys, 1869; Sinel, 1906), and Japan.

Round most of the British Isles *A. punctata* is common. It is most abundant where the water is clean, but occurs in estuaries where there is little pollution. Many of the records refer to specimens seen on the shore during the breeding season, some are from dredgings and trawlings, and a few are from crab-pots. One, caught in a surface plankton net, was possibly on drifting weed (Sikes, 1905). The species is abundant in some years and rare in others.

This account of the British distribution has been compiled from local literature, the British Museum collection and many private communications, but is undoubtedly incomplete. The clustering of records reflects the activities of marine stations and individual collectors, but in the neighbourhoods of Hunstanton (Norfolk), Burnham-on-Crouch (Essex), Whitstable (Kent) and on the coast of Glamorgan several naturalists state that they have not yet seen the species.

In the United Kingdom, *A. punctata* is reported from the coasts of Dorset, Devon, the Channel Isles, Cornwall, the Scilly Isles, Somerset, Lundy Island, Pembroke, Cardigan, Caernarvon, Anglesey, the Isle of Man, Argyll, Arran,



Text-fig. 1. Records of British *Aplysia*. ●, *A. punctata*; ▲, *A. depilans*; ✠, *A. limacina*.

Islay, Mull, Cumbrae, the Outer Hebrides, Sutherland, the Orkneys, the Shetlands, Moray Firth, Banff, Aberdeen, Fife, the Firth of Forth, East Lothian, Berwick, Northumberland and Yorkshire. For the seas between Scarborough (Yorkshire) and Selsey Bill (Sussex) no records have been found; there is one doubtful record for Hampshire depending on a specimen identified in a boat and subsequently lost. On the French coast of the Channel it certainly occurs at Dinard and Roscoff.

Thompson (1856) says that the species is common all round the coast of Ireland. More explicit records are for Belfast Lough (Thompson, 1856) and the coasts of Dublin (Colgan, 1908), Cork and Galway (Sikes, 1905).

### *Aplysia depilans*

This species is recorded from the coasts of Italy, Sicily, Corsica, England, Madeira, the west coast of France and the Cape of Good Hope (Mazzarelli, 1893). It is also found on the coasts of Spain and Portugal (British Museum collection), at Roscoff (Dautzenberg & Fischer, 1925), in the Channel Isles (Jeffreys, 1869; Sinel, 1906), and in Torbay (Gosse, recorded by Jeffreys, 1869; A. R. Hunt, 1877, 1878).

British specimens examined during the course of the present study are as follows:

British Museum specimens:

1850. 6. 17. 12, from Weymouth. This animal is interesting as it measures 9 cm. preserved, and is therefore small enough to be directly comparable with specimens of *A. punctata*. It shows very clearly the characters which help to distinguish the two species.

1860. 11. 28. 1, a very large specimen from Ichen, Southampton [presumably the river Itchen].

1870. *A. melanopus* Couch, type specimens, from Polperro.

Other specimens:

The animal from Babbacombe recorded above (p. 796).

### *Aplysia limacina*

Mazzarelli lists this species from the coasts of Italy, Sicily, Corsica, Algeria and the south and west coasts of France. There are specimens from the coasts of Spain and Portugal in the British Museum.

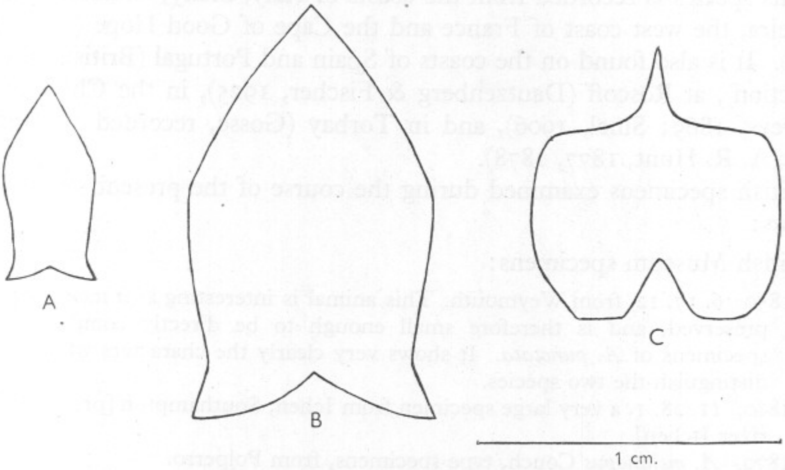
The only British animal, as far as is known, is the specimen from the Salcombe Estuary, recorded above (p. 796).

## RECOGNITION CHARACTERS

The following characters are included as means of determining the species quickly. Nearly all are external, and have been found to be adequate for the determination of both living and preserved material. The animals from which the list was made include at least two thousand *A. punctata* brought into the Plymouth Laboratory this year, and preserved material of all three species, including young, from Naples.

Colour, as indicated before, varies considerably and is not reliable. *A. punctata* is the only species which has small well-defined black or white spots, and none of the specimens that have been examined alive lacked them. *A. depilans* and *A. limacina* may be mottled, but the patches do not have such sharp edges. Neapolitan *A. limacina* were sometimes clearly enough marked to be mistaken for *A. punctata* at a first glance. *A. depilans* sometimes has patches of red, blue or yellow round the mouth, penis and gill. All the species go a dirty grey when preserved.

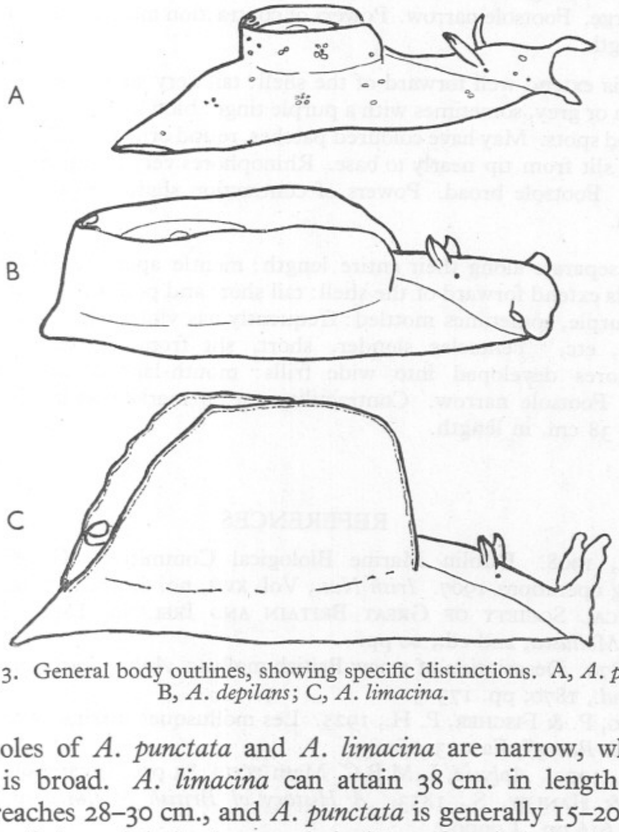
The most easily observed characters refer to the parapodia, mantle and head.



Text-fig. 2. Outlines of radulae of *Aplysia*. A, *A. punctata*; B, *A. depilans*; C, *A. limacina*. From specimens 6, 8·9 and 8 cm. long when preserved, respectively.

*A. punctata* and *A. depilans* have the parapodia fused at the posterior end. Both have a wide aperture through the mantle above the shell. In *A. punctata* (Text-fig. 3A) the parapodia surround the visceral mass closely and do not extend in front of it to any noticeable degree. As a result the neck is fairly long and there is a long pointed tail posteriorly. In *A. depilans* (Text-fig. 3B) the parapodia stand farther out, along the sides, and extend along the neck for some distance forward of the shell. They are not tall enough to conceal the shell, and the tail is very short and blunt. The parapodia of *A. limacina* (Text-fig. 3C) are separate for the whole of their extent, and there is a gap between the roots of them at the posterior end. They are much larger than in either of the other species, and fold over to conceal the visceral mass completely. The mantle aperture is in the form of a small papilla or siphon which is usually closed in life and has been closed in all preserved specimens examined. In other respects this species is intermediate between the other two, as the parapodia extend a short way in front of the shell, and there is a short pointed tail.

The mouth-lappets are least developed in *A. depilans*, and both tentacles and rhinophores are short and stout. In *A. punctata* the mouth-lappets are not very large, but the rhinophores and tentacles are slim and are capable of very great extension. The tentacles of *A. punctata* are slit at the tips only, while those of the other two species are slit from the tips nearly to their proximal ends. The mouth-lappets of *A. limacina* form large frills, confluent with similar frills on the rhinophores. The tentacles are short and slender.



Text-fig. 3. General body outlines, showing specific distinctions. A, *A. punctata*; B, *A. depilans*; C, *A. limacina*.

The footsoles of *A. punctata* and *A. limacina* are narrow, while that of *A. depilans* is broad. *A. limacina* can attain 38 cm. in length expanded: *A. depilans* reaches 28–30 cm., and *A. punctata* is generally 15–20 cm. long.

The shape of the radula is characteristic (Text-fig. 2), being long and slim with a gradually tapering tip in *A. punctata*, broader in *A. depilans*, and square with an abrupt tip in *A. limacina*. The numbers of tooth rows and of lateral teeth in each row in the radulae of adult specimens may assist in identification. Mazzarelli (1893) gives these as 38–40 rows with (15–18).1.(15–18) teeth per row for *A. punctata*, 76–80 rows with (30–33).1.(30–33) teeth per row for *A. depilans*, and 82 rows with (40–45).1.(40–45) teeth per row for *A. limacina*.

Fuller descriptions of these animals may be found in Eales (1921), and Mazzarelli (1893). The specific names used in this paper are taken from the latter, which was the original means of identifying the specimens recorded above.

### KEY TO SPECIES

Parapodia fused at posterior end: mantle aperture open.

Parapodia do not extend noticeably forward of the shell: tail long. Colour olive green, brown or purple: clusters of well-defined black or white spots. Tentacles long, tubular, each with a slit at the tip. Mouth-lappets distinct, not large. Footsole narrow. Powers of contraction marked. Reaches 20 cm. in length. *A. punctata* Cuv.

Parapodia extend well forward of the shell: tail very short and blunt. Body brown or grey, sometimes with a purple tinge: blotchy but never with well-defined spots. May have coloured patches, round orifices and gill. Tentacles blunt, slit from tip nearly to base. Rhinophores very blunt, mouth-lappets small. Footsole broad. Powers of contraction slight. Reaches 28 cm. in length. *A. depilans* L.

Parapodia separate along their entire length: mantle aperture on a papilla. Parapodia extend forward of the shell: tail short and pointed. Colour usually a dark purple, sometimes mottled: frequently has violet edges to parapodia, tentacles, etc. Tentacles slender, short, slit from tip nearly to base. Rhinophores developed into wide frills: mouth-lappets also long and waving. Footsole narrow. Contractility not so marked as in *A. punctata*. Reaches 38 cm. in length. *A. limacina* L.

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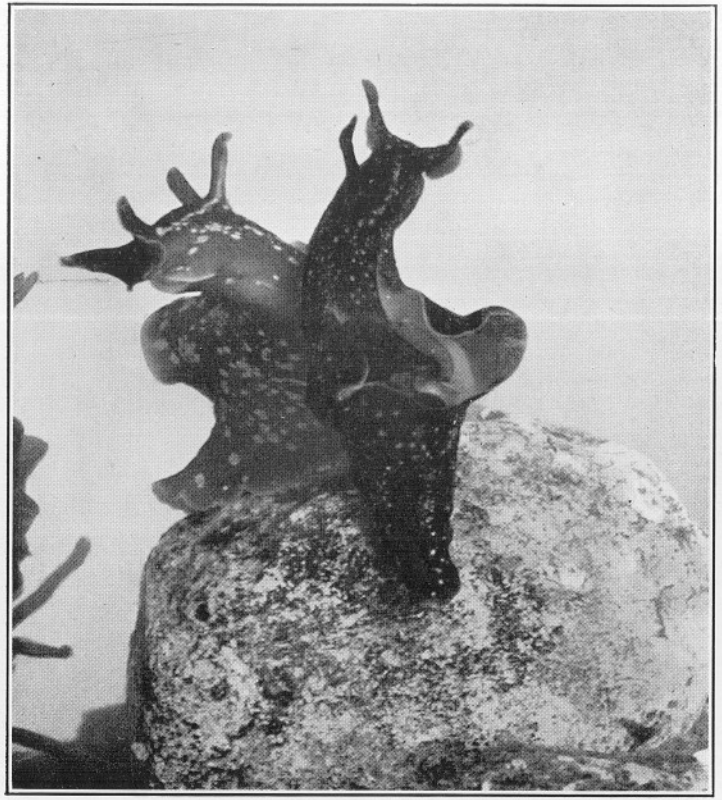
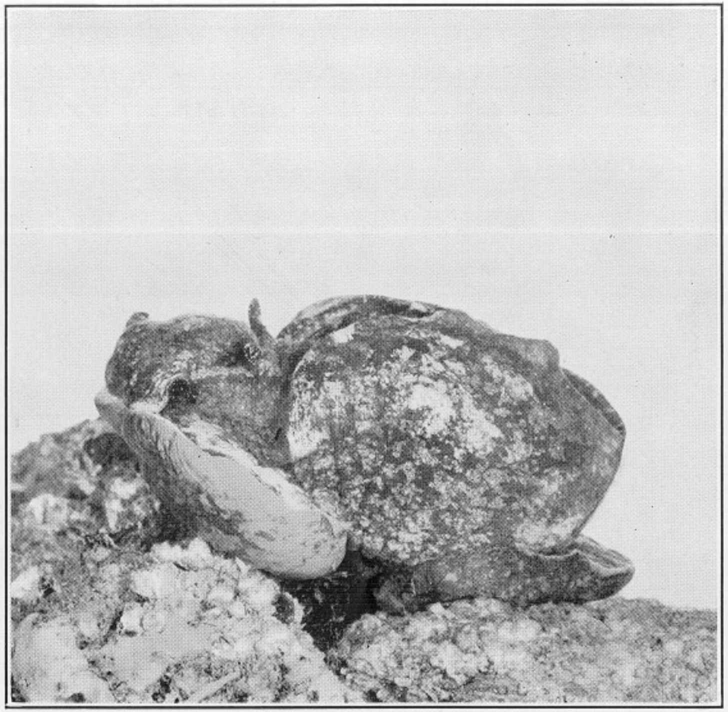


*Aplysia punctata*



*Aplysia depilans*

*Aplysia limacina*

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## EXPLANATION OF PLATES

### PLATE I

Photographs of living *Aplysia punctata* (× $\frac{1}{3}$) and *A. depilans* (× $\frac{3}{8}$).

### PLATE II

Photograph of living *Aplysia limacina* (× $\frac{1}{2}$).

# NOTES ON THE PLYMOUTH MARINE FAUNA

## CHIRONOMIDAE (INSECTA: DIPTERA)

By R. E. Hall

The following records were obtained during a fortnight at the beginning of April 1949. The localities investigated were rocky shorepools below the Laboratory, and a small area at the upper tidal limit of Tamerton Lake. In addition to imagoes collected on the wing, larvae were reared from a mud sample taken from the stream bed just below the upper limit of tidal penetration. None of the Tamerton species are marine in the strict sense adopted by Edwards (1926), but those bred out are tolerant of brackish water and belong to the estuarine fauna.

Of the species mentioned none occur in the Plymouth Marine Fauna (Mar. Biol. Assoc., 1931), but *Thalassomyia fraunfeldi* has been recorded from Wembury (Colman, 1940).

### Subfamily Orthocladiinae

*Cricotopus fucicola* (Edw., 1926)

Plymouth rocky shore pools, both intertidal and above high-water level (emergence from former observed), 15 ♂♂ and 4 ♀♀.

*Cricotopus obnixus* (Walk.)

Tamerton Lake, ♂ and ♀.

*Spaniotoma* (*Smittia*) *thalassophila* (Goet.)

Plymouth rocky shore pools, intertidal and above high-water level, 8 ♂♂ and 4 ♀♀.

*Spaniotoma* (*Smittia*) *contigens* (Walk.)

Tamerton Lake, 6 ♂♂ taken from swarm at edge of stream at head of creek.

*Metriocnemus picipes* Mg.

Tamerton Lake, one ♂.

*Metriocnemus impensus* Walk.

Tamerton Lake, pair *in coitu*.

*Tanytarsus* (*Micropsectra*) *brunnipes* (Zett.)

Tamerton Lake, adults taken in flight, and several bred from larvae living in the mud at the head of the creek.

### Subfamily Clunioninae

*Thalassomyia fraunfeldi* (Schin.)

Plymouth, shore below Laboratory, ♂ on damp seaweed about M.T.L.

### Subfamily Diamesinae

*Prodiamesa olivacea* (Mg.)

Tamerton Lake, 2 ♂♂ bred from sample of mud.

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## HALACARIDAE (ARACHNIDA: ACARINA)

By H. C. Fountain

The nomenclature follows André (1946). No Acarina were listed in the Plymouth Marine Fauna (Mar. Biol. Assoc., 1931), but *Hydrogamasus littoralis*, *Rhombognathus pascens*, *R. seahami*, and *Halacarus basteri* have since been recorded from Wembury (Colman, 1940).

Species marked with an asterisk are new records for the British Isles.

*Rhombognathus* (*s.s.*) *notops* (Gosse)

Plymouth Laboratory tank. Drake's Island.

*Rhombognathus* (*s.s.*) *magnirostris* Trouessart. Drake's Island.

*Rhombognathus* (*Rhombognathides*) *pascens* (Lohmann)

Wembury, Port Wrinkle. Seaton beach.

**Rhombognathus* (*Rhombognathides*) *trionyx* Trouessart

One, Looe Harbour at low-water level.

*Rhombognathus* (*Rhombognathopsis*) *seahami* (Hodge)

Plymouth Laboratory tank. Port Wrinkle. Seaton beach.

### Subfamily Halacarinae

*Halacarus* (*s.s.*) *ctenopus* Gosse. Duke Rock, Plymouth.

*Halacarus* (*Halacarellus*) *basteri* (Johnston). Port Wrinkle.

*Copidognathus* (*s.s.*) *fabriciusi* (Lohmann). Port Wrinkle.

**Copidognathus* (*s.s.*) *loricifer* M. André. Plymouth Laboratory Tank.

*Copidognathus* (*s.s.*) *rhodostigma* Gosse. Duke Rock, Plymouth.

*Copidognathus* (*s.s.*) *lamellosus* Lohmann. Duke Rock, Plymouth.

*Copidognathus* (*s.s.*) *glyptoderma* Trouessart
Plymouth Laboratory Tank.

*Copidognathus* (*Copidognathopsis*) *oculatus* (Hodge). Seaton Beach.

### Subfamily LOHMANNELLINAE

*Lohmannella falcata* Hodge. Duke Rock, Plymouth.

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# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### THE SYNONYMIES OF *HALICLONA ANGULATA* (BOWERBANK) AND *H. ARCOFERUS* (VOSMAER)

By Maurice Burton

*Ann. Mag. Nat. Hist.*, Ser. 12, Vol. 1, 1948, pp. 273–84

The classification of sponges must be based on the characters of the spicules, and to a larger extent this is true also of the identification of species. In identification, however, there is a certain unreliability introduced because categories of spicules, particularly of microscleres, may be sufficiently rare that they will be overlooked except in the most thorough microscopic examination. The recognition of this principle and the use of microscopic characters, as well as knowledge of the ecology, has made it possible to sort into two natural groups, corresponding to *H. angulata* and *H. arcoferus*, a long series of specimens formerly assigned to more than a dozen species belonging to different genera. M.B.

### THE ECOLOGY AND NATURAL HISTORY OF *TETHYA AURANTIUM* PALLAS

By Maurice Burton

*Ann. Mag. Nat. Hist.*, Ser. 12, Vol. 1, 1948, pp. 122–30

It is too often found that our knowledge of even the better-known species of sponges is concerned mainly with the external form and the spiculation. Details of exact distribution and ecology are given either too sparingly or omitted altogether. That these, and other details, have a value to the taxonomist is shown in the study of *Tethya aurantium*. There has, for example, been a disposition on the part of some authors to recognize geographical varieties, based mainly on size, but when the measurements of a wide series of individuals are correlated with distribution and ecology such a view is shown to be untenable. A further lack in the details attached to collected specimens has been the record of the date of collection. In the study of development—in this case of the asexual buds—the absence of such data is a great handicap.

M.B.

## The Molluscan Stomach

By Alastair Graham

*Trans. Roy. Soc. Edin.*, Vol. LXI, 1949, pp. 737–78

The internal anatomy of the stomach of sixteen species of lamellibranchs and of ten species of prosobranch gastropods is described. The trochids *Monodonta* and *Calliostoma* show a gastric structure which allows close comparison with the lamellibranchs, allowing for the effects of torsion. Within the filibranchs the genera *Glycymeris*, *Ostrea* and *Mytilus* form a series in which the gastric caecum becomes increasingly complex. *Chlamys*, *Pecten* and *Lima*, on the other hand, show a tendency towards reduction of the caecum. In the eulamellibranchs the stomach is similar, whereas in *Nucula* it is reminiscent of the archaic gastropods.

Within the gastropods the stomach becomes simpler in correlation with a macrophagous carnivorous habit and extracellular digestion. A second factor controlling its plan is a forward migration of the oesophageal aperture until in opisthobranchs and pulmonates this adjoins the intestinal opening.

The structure of the polyplacophoran and cephalopod stomach can be shown to agree with those of the lamellibranchs and gastropods.

The steps in the evolution of the crystalline style from the faecal rod found in the style sac of the stomach of protobranchs, rhipidoglossan and lower monotocardian gastropods are discussed. A.G.

## The Giant Axons of Annelids

By J. A. Colin Nicol

*Quart. Rev. Biol.*, Vol. XXIII, 1948, pp. 291–3

A review is presented of information concerning the giant axons of annelids. The term is a convenient one for certain nerve fibres relatively much larger than others in any given species. They occur in many families of polychaetes, oligochaetes, and possibly archiannelids, and their pattern in these various groups is discussed. Giant axons may be intrasegmental or intersegmental, unicellular or multicellular; in some species they are divided by segmental septa into longitudinal units. Various lines of evidence demonstrate that they are concerned with quick contractions of the entire animal, in both polychaetes and oligochaetes. Measured conduction velocities for these axons are listed, and they are shown to conduct from 2 m. per sec. in *Nereis* up to 45 m. per sec. in *Lumbricus*. Conduction velocity is a function both of axon diameter and of the myelin sheath. Their diversity of structure in different families of polychaetes and oligochaetes indicates that they have arisen independently on several occasions within the Chaetopoda. J.A.C.N.

# BOOK REVIEWS

## Sexual Endocrinology of Non-Mammalian Vertebrates

### L. H. Bretschneider and J. J. Duyvené de Wit

Monographs on the Progress of Research in Holland during the War. Published by Elsevier; Distributors: Cleaver-Hume Press. Price: 15*s*. net.

This is one of the valuable series of monographs on research performed in the Netherlands during the war. It presents results and conclusions of great interest to endocrinologists and to workers on the lower vertebrates, and demonstrates afresh the vitality and critical importance of the comparative point of view.

The book is divided into four parts. Each can be studied independently, but they are integrated by cross-references and a useful index into a lucid and comprehensive picture. While a cyprinid fish, the bitterling (*Rhodeus amarus*), is the protagonist, there is a large supporting cast of vertebrate species.

The first part describes the use made of growth of the ovipositor in the female bitterling as a quantitative assay object. After sections on technique and chemical specificity, the responses to twenty-eight different steroids are detailed. The time-course of the reaction was characteristic for each substance in a given concentration, and markedly different for the oestrane, pregnane and androstane groups. This property suggested the use of the test for the analysis of extracts of tissues and body fluids both of mammals and of other vertebrate groups. The authors themselves tested a number of these, their most spectacular claim being the presence in human urine of a new hormone, unfortunately unsuitable for pregnancy diagnosis, with effects distinguishable from those of all known steroids. Provisionally called 'luteidin', this substance was reported to be present in the pregnanediol glucuronide complex obtained from pregnancy urine. It must be noted that the bitterling test has been criticized by Van Koersveld (1948[1]) as neither regular nor specific enough for more than the qualitative detection of steroids as a group, which act at much lower concentrations than other substances.

The second part presents a far-reaching theory, based on varied evidence, of the sexual functions of the pituitary in the bitterling. This concentration on a single species gives the hypothesis a boldness and sweep that enhance its interest for the general problem of pituitary function. The evidence presented here is sometimes understandably slender—thus successful hypophysectomy is reported only in a single fish. On the basis of this result, and of quantitative studies correlating, with suitable time adjustments, the extent of basophily in a pituitary zone, the condition of the ovary and the ovipositor response, it is concluded that the steroids mentioned in the first part act indirectly, stimulating

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[1] Van Koersveld, E., 1948. *Acta Brevia Neerlandica*, Vol. XVI, Nos. 5–8, pp. 66–9.

the pituitary. This stimulation causes production of corpora lutea in the ovary, which in their turn influence the ovipositor—a signal illustration of the critical importance of hypophysectomy for the analysis of steroid and other hormone effects, particularly on lower vertebrates. (This sequence has been confirmed for other substances by Van Koersveld (1948[1]), who notes that all have a narcotic action at higher dosages.) Accounts of the blood-supply, innervation and histological changes in the bitterling pituitary lead to the elaboration of a twofold theory of secretion, embracing 'haemocrinia' and 'neurocrinia'. The most striking factual claims are the passage of a 'colloid', originating in the lobi anterior and intermedius, to the brain via the lobus posterior, and the visibly rich innervation of the lobus anterior, in contrast with its homologue in higher vertebrates (cf. review by Harris, 1948[2]). A section of this part is devoted to the homology of pituitary lobes in various vertebrate groups, especially teleosts, and to the erection of anatomical types of pituitary. It is interesting to compare this survey with parallel wartime work, experimental and anatomical, on certain of the forms discussed (e.g. Waring, 1940,[3] on *Anguilla*; Atwill, 1941,[4] on anurans; review by Waring, 1942,[5] on various species).

The third part is an almost classical illustration of the uses of comparative histology. The discovery of 'pre-ovulation corpora lutea' in the bitterling—involving in their formation the destruction of the ovum—and of their connection with ovipositor growth, led the authors and their associates to re-investigate the whole problem of follicular derivatives in forty-five species from six vertebrate groups, including man. This part contains an illustrated account of the histogenesis of the bitterling corpora lutea, a revised classification, arising out of the above survey, of normal and abnormal follicular derivatives, a tabulation of their overlapping distribution throughout the vertebrate groups, and a discussion of their histogenetic and functional significance. The hormone which the bitterling corpora lutea are inferred to produce, and which must, unlike progesterone, affect the ovipositor directly, is given the name 'oviductin'.

The last part describes studies on the sexual cycles in the females of three teleost species, *Rhodeus amarus* itself, *Zoarces viviparus* and *Lebistes reticulatus*, and in both sexes of *Bufo bufo*. It is mainly concerned with changes in the gonad, in behaviour and, in *Rhodeus*, with the ovipositor, but set against the background of pituitary activity. Among a number of interesting observations by the authors and their associates may be mentioned the cyclical nature of oestrus in *Rhodeus* and *Lebistes*, signalized by changes of ovipositor length in the former

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[1] Van Koersveld, E., 1948. *Acta Brevia Neerlandica*, Vol. XVI, Nos. 5–8, pp. 66–9.
[2] Harris, G. W., 1948. *Physiol. Rev.*, Vol. 28 (2), pp. 139–79.
[3] Waring, H., 1940. *Proc. Roy. Soc.* B, Vol. 128, pp. 343–53.
[4] Atwill, W. J., 1941. *Amer. J. Anat.*, Vol. 68, pp. 191–208.
[5] Waring, H., 1942. *Biol. Rev.*, Vol. 17, pp. 120–50.

and, it is claimed, of posture in the latter; the fact that both of these are influenced by water in which males have been kept, from which the existence of another hormone, 'copulin', is inferred; the even more bizarre fact that ovipositor development in *Rhodeus* depends on the presence of the fresh-water mussels in which the eggs are laid; the unusual follicular derivatives produced in adaptation to viviparity in *Zoarces* and *Lebistes*; and the endocrine function and response to pituitary hormones of corpora lutea in the hitherto mysterious organ of Bidder in *Bufo*. It is noteworthy that many details in the description of the sexual cycle and spawning behaviour of *Rhodeus amarus* agree very closely with the independent account by Chang (1948)[1] of the same processes in the common Chinese bitterling, *Rhodeus ocellatus*. This final part, in general, completes the biological circle, relating to the lives of particular species the reactions exposed by the preceding analysis.

The book leaves us with, if possible, an increased admiration for a people who could make such a contribution to knowledge in this field, as in so many others, during what the editorial foreword, written on V.E. day, tersely calls 'the five years of German occupation'. In this place it is proper to express the hope that this monograph, mainly concerned with fresh-water forms, will stimulate further research into the sexual endocrinology of marine vertebrates, a difficult enterprise, but one from which so much of both theoretical and practical interest may be expected. W. M. S. RUSSELL

## HYDROBIOLOGIA: ACTA HYDROBIOLOGICA, LIMNOLOGICA ET PROTISTOLOGICA

Published by Dr W. Junk, 13, van Stolkweg, The Hague, 1948, 40 guilders

*Hydrobiologia*, according to the editors' notice, 'will publish articles embodying original research in the field of Hydrobiology, Limnology and Protistology'. The field included is broad, embracing the 'biology' of marine and fresh-water plants and animals, and their systematics and taxonomy. It is truly an international journal, with editors from the Continent, the United Kingdom, and the United States of America. Two numbers have appeared, the first in August 1948; four numbers are to be published annually. The languages accepted are English, French, German, Italian and Spanish. An examination of the seventeen papers presented in these first two issues shows that fifteen are concerned with fresh-water biology, four with marine botany and phytoplankton, and one with physics (penetration of light in fresh water). Most of the papers are in English. Although authors are recommended to give a short summary in an alternative language, none has done so, and few have given any summary at all. This may not be of value for the taxonomic papers, but it certainly would be for the theoretical and experimental studies. The advance

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[1] Chang, H. W., 1948. *Sinensia*, Vol. 19, pp. 12–22.

notice for the second issue is hopelessly garbled. More attention should be directed to correcting errors in English.

Of particular interest to marine biologists are the following papers: 'Contributions to our knowledge of British algae', by F. E. Fritsch; 'Le phytoplancton estival de la "Costa Brava" catalane en 1946', by Ramón Margalef; 'Die Photosynthese des Phytoplanktons vom Gesichtpunkte der Quantenlehre', by R. Maucha. A new limnological method for the investigation of thin-layered epilithic communities, described by R. Margalef, although designed for freshwater algal deposits, probably could be adapted for marine studies. There are reviews of papers and books dealing with hydrobiology, and obituary notices. J. A. Colin Nicol

# THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

The Association was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. XV (p. 735) and Vol. XXVII (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

## TERMS OF MEMBERSHIP

| | | £ | *s.* | *d.* |
|---|---|---|---|---|
| Annual Members | per annum | 1 | 1 | 0 |
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| Founders | | 100 | 0 | 0 |
| Governors | | 500 | 0 | 0 |

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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CAMBRIDGE UNIVERSITY PRESS
LONDON: BENTLEY HOUSE, N.W.1
NEW YORK: 51 MADISON AVENUE
CANADA AND INDIA: MACMILLAN

*Printed in Great Britain at the University Press, Cambridge*
*(Brooke Crutchley, University Printer)*