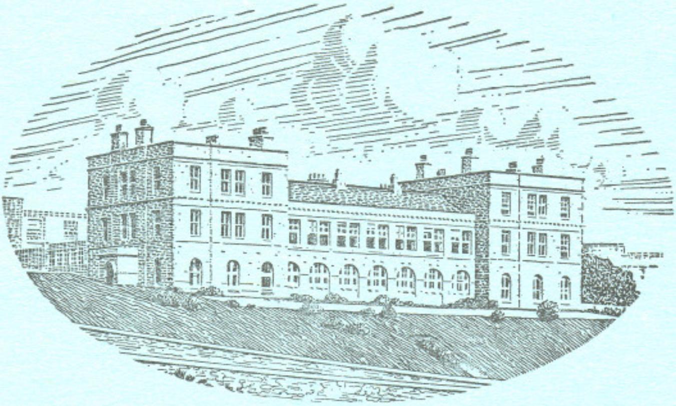
JOURNAL OF THE
MARINE BIOLOGICAL ASSOCIATION
OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME 39, No. 2

(issued June 1960)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1960

Price Sixty-two shillings net

(U.S.A. $10.50)

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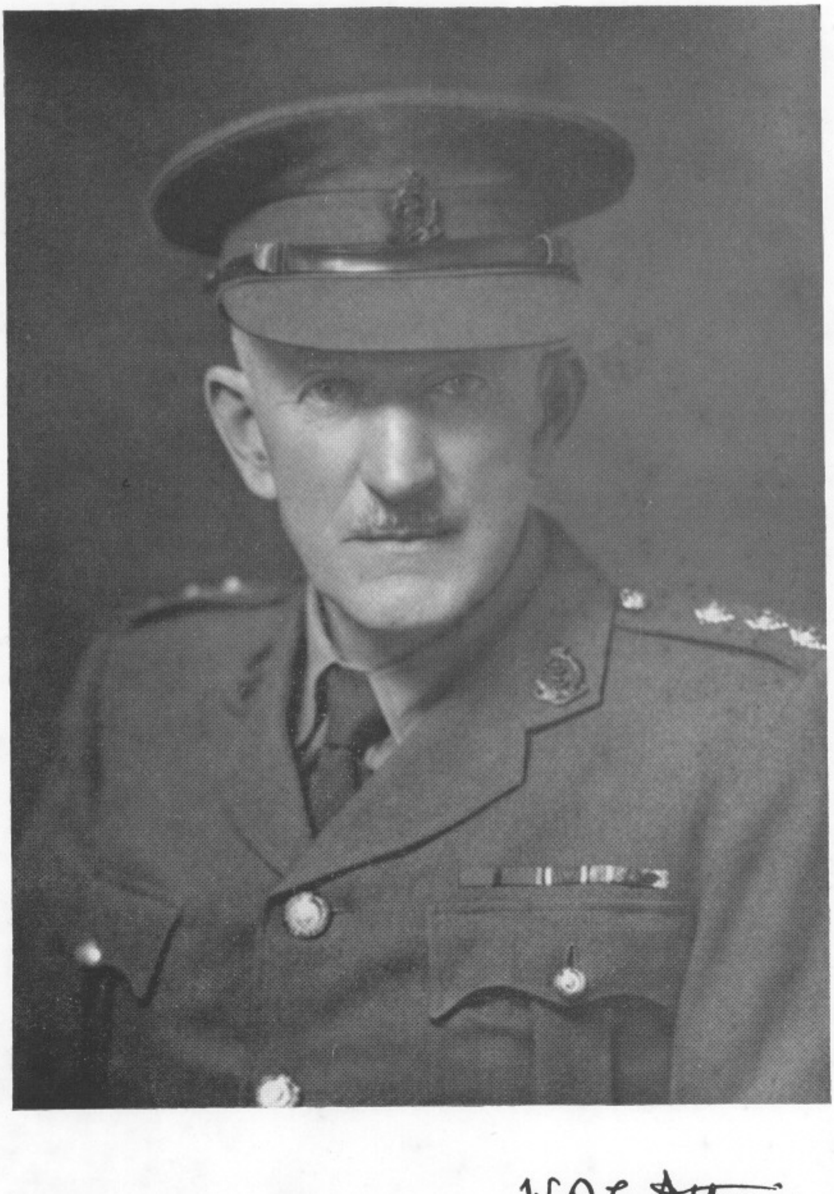
June 1960



W. R. G. Atkins.

OBITUARY

W. R. G. ATKINS, C.B.E., O.B.E.(Mil.), SC.D., F.R.I.C., F.INST.P., F.R.S.

1884–1959

William Ringrose Gelston Atkins was appointed Head of the Department of General Physiology at the Plymouth Laboratory in February 1921 at the age of 36 having already at Trinity College, Dublin, applied widely the methods of physics and chemistry to the problems of biology, particularly botany. He was very well equipped to study the physics and chemistry of sea water as an environment for marine life. He served with great distinction at Plymouth, apart from the years of the Second World War, until he retired from the staff in March 1955 and enjoyed only four years of leisure before his death on 4 April 1959.

Atkins may be said to have borne the same relationship to chemical oceanography that V. M. Goldschmidt did to geochemistry. Each saw the problems of the waters or of the rocks broadly, drew on all the apparatus of research available in their day and founded each a new branch of science. They became close friends, mainly by correspondence and cross-fertilized each other. They differed in temperament, whereas Goldschmidt founded schools, Atkins preferred to work with his own hands or with those of his trusted assistants, Mr F. J. Warren and Miss Pamela Jenkins (Mrs L. Hummerstone). The greater part of his sea work was done on the 'Salpa', described when she arrived a few months after Atkins himself, as a powerful sea-boat and much more capable of facing rough weather than her predecessor. Powerful for her time she may have been but uncomfortable she certainly was, to an extent which those who work on our present vessels may find it hard to understand. It was on this ship that so much of Atkins's work, which became classical, was carried out. Her master, Captain Vivian Lord, was an individualist like Atkins himself. Each held the highest regard for the other for their personal integrity and competence at their respective jobs.

The chemical study of the sea as a biological environment started in Germany but the analytical methods of the day were not equal to the task. Matthews at Plymouth had introduced methods of improved accuracy but too slow for the considerable surveys which were necessary. Atkins's great gift was to realize the value of new techniques and then with great energy and care to apply them to problems which he was the first to define clearly. The credit for the first effective application of colorimetric, or as we prefer to say to-day, absorptiometric chemical analysis to oceanography is his.

He formulated clearly the problems of the biological productivity of temperate seas and started, following Benjamin Moore, by studying the carbon cycle, using measurement of pH as his tool. His results were clear-cut but he quickly realized that the answers he sought could be more surely obtained by studying phosphate. This he achieved by applying Denigès's colorimetric method to sea water. His technique was simple but effective and could be used on ocean-going research ships. During the years that followed he devised methods for a number of other constituents of sea water of biological importance, and applied them extensively.

Atkins quickly saw that production in the sea depended in equal measure upon the availability of nutrients and upon a sufficiency of light. As early as 1924 he entered upon a famous partnership with Dr H. H. Poole of the Royal Dublin Society which combined two acute minds with different gifts and opportunities to attack the intractable problem of the manner, the extent and the consequences of the penetration of light in the sea. As joint authors they wrote over forty papers, many of which have become classics. They found that though the photo-electric cell was much the best tool for the job, the early models could be treacherous. Much meticulous work was carried out to track down sources of error, many still with us, so that young men entering this field of research would be well advised to read for themselves how these sources of error were recognized and overcome.

One result of this intimate knowledge of photo-electric cells and their failings was that in his other main field of study, absorptiometric analysis, he remained to the end of his days an advocate of visual methods and rejected photo-electric methods. Possessed himself of exceptional powers of colour discrimination and memory he found it hard to realize that few shared his gifts or that the fatigue and failings of a modern photo-electric cell might be less serious than those of most human eyes. He was ever ready to give from his wide experience and one consequence was the application of his work in terrestrial environments, as in soils and woods all over the world.

For many years he continued work on the preservation of nets and ropes which developed from his earlier work in Egypt on fabrics. This was typical of the way in which he applied his discoveries in one branch of science to the problems of another.

An account of the many honours he received and of his work at Dublin and elsewhere during the two world wars will be found in the Obituary Notices of the Royal Society and in *Nature* (2 May 1959).

Atkins was a man of strong and forthright character, often stern in his support of causes which he felt to be just. He expected high standards of experimental competence and scientific integrity from his staff and from workers visiting the Laboratory. He was a very kindly man with a strong social conscience. Much of the good work that he did was known only to those who were very near to him. In his private life he was devoted to home and garden. To Mrs Atkins and their married son, all who knew them—and they were many—will extend deep sympathy.

L. H. N. COOPER

J. mar. biol. Ass. U.K. (1960) 39, 155–171
Printed in Great Britain

SOME THEOREMS AND PROCEDURES IN SHALLOW-WATER OCEANOGRAPHY APPLIED TO THE CELTIC SEA

By L. H. N. Cooper

The Plymouth Laboratory

(Text-figs 1–5)

CONTENTS

Twenty years ago the Plymouth Laboratory investigated the spawning of mackerel and pilchard in the Celtic Sea. The physical background for their work, which the late Dr G. A. Steven and Mr P. G. Corbin sought, could not be provided since waters with similar temperatures and salinities evidently had very different physical and biological histories.

Thus any study of the physical and chemical oceanography of the Celtic Sea, as of other waters around Britain, is an industrial rather than a fundamental research. Answers are needed for practical ends so that an imperfect answer today may be as useful as a thorough understanding tomorrow. In such circumstances oceanographers fall back on intuitions, which they cannot defend, to amplify inadequate observation. Since my own views about the Celtic Sea were so largely intuitive they have never been published. In 1948, an attempt at rationalization was made, much in the form to be presented here. Some of the theorems were used as working hypotheses when the 1950 programme was designed and proved compatible with the observations (Cooper, 1960, and in preparation), others remained shelved awaiting opportunity for tests which have never come. Now that 9 more years have passed, these theorems may help to build a bridge with findings in the same area by the Lowestoft Fisheries Laboratory. No more is claimed than that no theorem is in conflict with observations some of which will be published in a paper now in preparation.

In order to understand the water circulation better, it is essential to appreciate the pattern of winds over the area and what they are likely to do to the sea, to understand the effects of the physiography of the sea bed and of the neighbouring land on currents, and to eliminate the effect of latitude on temperature. These problems have been examined and some conclusions drawn. Their importance is that if they are indeed true, then they may always be true and applicable on occasions when only few observational records are available.

PATTERNS OF WIND-INDUCED CURRENTS

There is little doubt that west of a line drawn from Waterford through the Scilly Isles to a point 30 miles west of Ushant and within a line drawn 20 miles north-east and east of the continental edge, the currents are mainly wind-induced and are as variable as the winds. Rarely will the distribution of mass have time to approach equilibrium with the wind stress before this changes in strength and direction. This failure to reach an equilibrium state may account for failure during work spread over 20 years to find a satisfactory fit between a dynamic approach to the whole region and the information given by a study of nutrients and plankton indicators. Now that geometrical models of limited scope have been devised, short-lived equilibrium states may be recognized and studied with more hope of success.

Any steady wind over deep water should produce, in accordance with Ekman's (1905) theory, a surface current 45° to the right of the wind direction. In shallow water unrestricted by any land mass this angle will be smaller the less the depth of water and the stronger the wind. In summer the thermocline acts as a false bottom so that above a thermocline or above any discontinuity layer the current will run more nearly in the direction of the wind. In Fig. 1 the system of currents that should result in the Celtic Sea and English Channel from winds from six directions are presented for winter conditions.

Over a fairly small sea area such as the Celtic Sea, it should be possible to compute the torque exerted on the surface of the Celtic Sea from wind records at coastal observatories. For the 5 weeks preceding the cruise of April 1950, the pattern of winds at three well-placed exposed meteorological stations has been examined, viz. Scilly, St Ann's Head in Pembrokeshire, and Valentia in County Kerry. The period has been broken down into five parts each with a well-defined wind pattern (Table 1) and then summed up for the whole period. Vector addition has been used.

The direction of the mean wind measured over the whole 5 weeks at St Ann's Head was over 30° greater than at Scilly—251° as compared with 218°. Moreover, a similar difference showed up on each of the five shorter periods with winds from east through south to west-north-west. However, the difference in wind direction may be due to differences of latitude, or

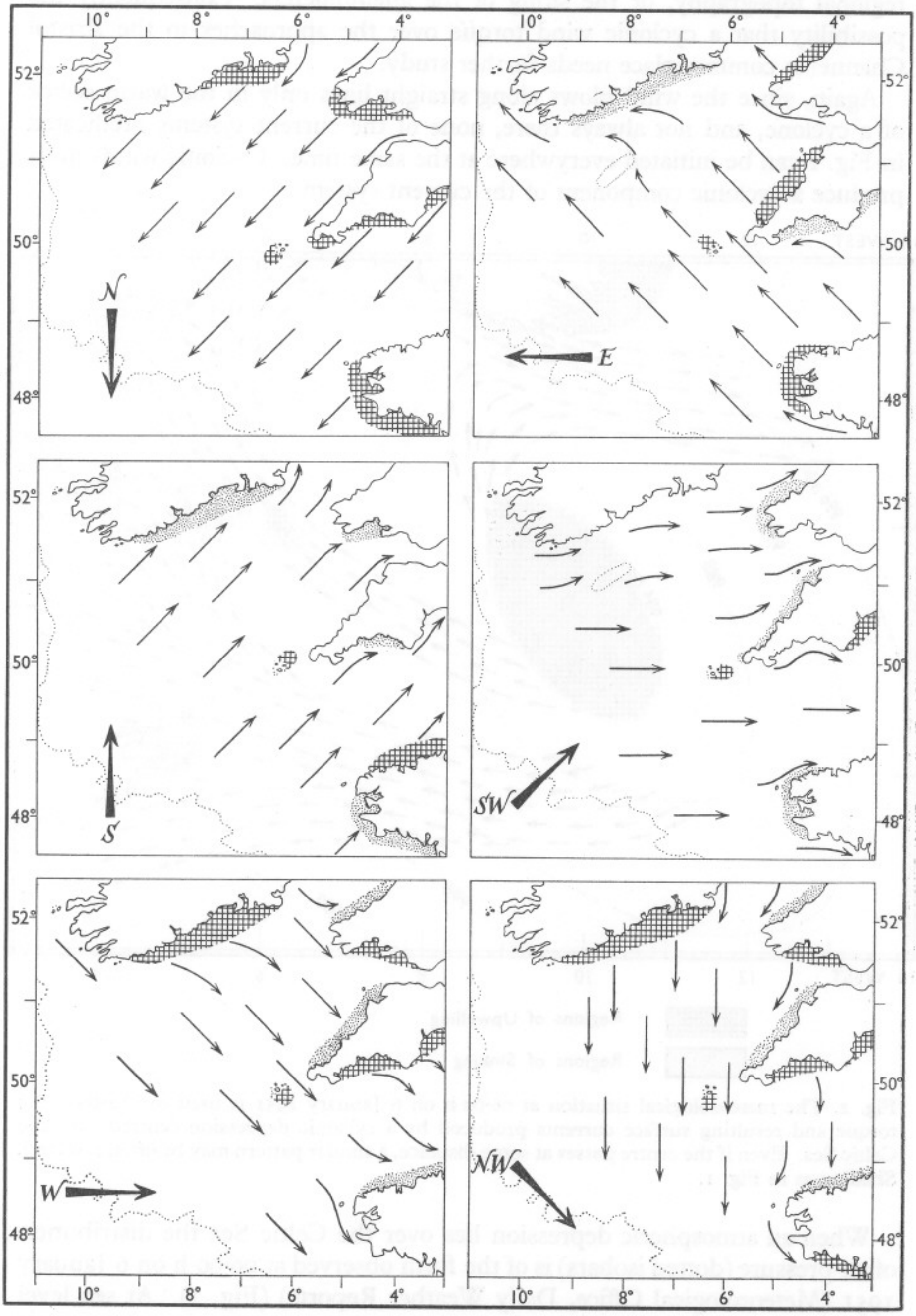


Fig. 1. Hypothetical system of surface currents induced in the Celtic Sea by winds in winter. The direction of the wind is shown by the heavy arrow in the bottom left-hand corner. Areas where upwelling should be favoured are cross-hatched. Areas where water must escape by sinking or by strong coastal flows are stippled.

regional topography, or the siting of the anemometers. Consequently the possibility that a cyclonic wind torque over the approaches to the Bristol Channel is commonplace needs further study.

Again, since the wind blows along straight lines only in the warm sector of a cyclone, and not always there, none of the current systems predicated in Fig. 1 can be initiated everywhere at the same time. Cyclonic winds must produce a cyclonic component of the current system.

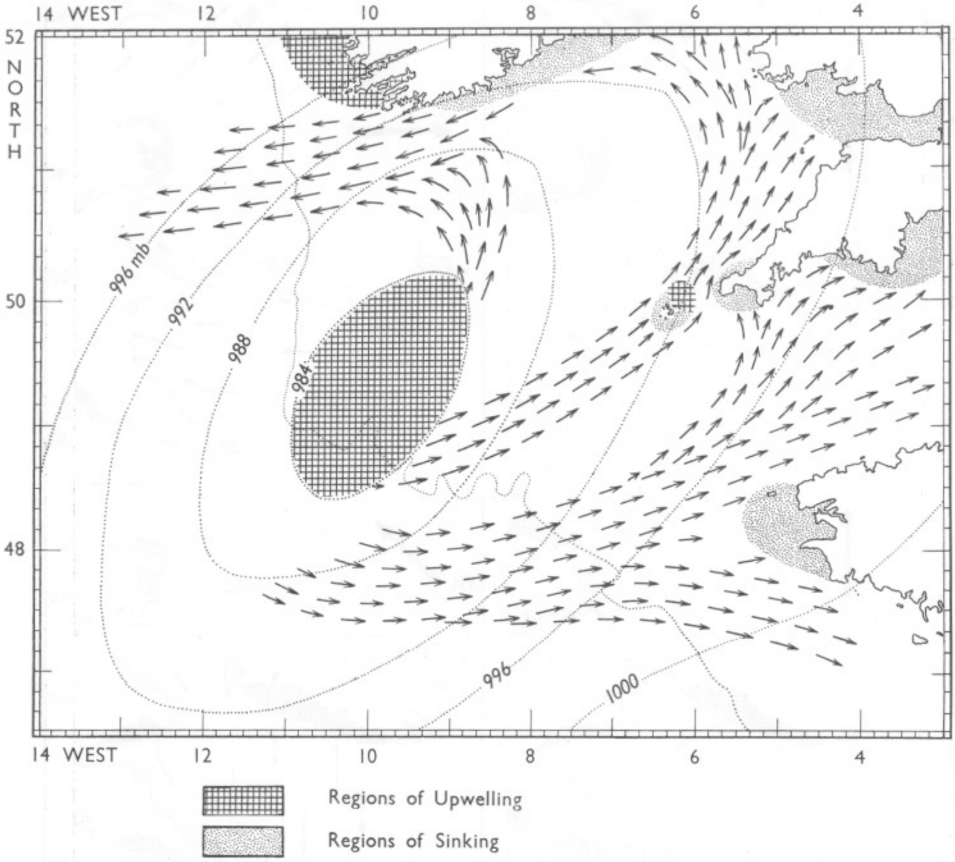


Fig. 2. The meteorological situation at 06·00 h on 6 January 1951 is used to illustrate the torque and resulting surface currents produced by a cyclonic depression centred over the Celtic Sea. Even if the centre passes at some distance, a similar pattern may be often resolved. Shading as in Fig. 1.

When an atmospheric depression lies over the Celtic Sea the distribution of air pressure (dotted isobars) is of the form observed at 06·00 h on 6 January 1951 (Meteorological Office, Daily Weather Reports) (Fig. 2). At sea level the resulting cyclonic wind was blowing across the isobars inwards towards the centre. Since the surface water current at every point would be initiated to the right of the surface wind direction, the surface currents will diverge a few degrees to the right of the isobars. Under the centre of the depression, a vortex will tend to form, accompanied by upwelling and diverging surface currents. In compensation, bottom water must converge on the vortex. Its course will be much influenced by the bottom topography.

The land constrains the current system absolutely so that the atmospheric pressure system on the morning of 6 January 1951 would have initiated a current system such as that in Fig. 2.

Such an atmospheric pressure distribution ought therefore to produce a torque on the sea surface, and it is this over-all torque and not the wind direction and strength at any one position which may produce the cyclonic circulation of the Celtic Sea.

TABLE 1. INTEGRATED MEAN WIND DIRECTIONS AT THREE METEOROLOGICAL STATIONS BORDERING THE CELTIC SEA

Period 1950	No. of observations	Mean wind direction: St Ann's Head	Mean wind direction: Scilly	Mean wind direction: Valentia	Difference: St Ann's Head − Scilly
14 March, 00.00 h–24 March, 06.00 h	42	233½°	202°	179°	+31½°
24 March, 12·00 h–29 March, 12.00 h	21	118°	66°	134½°	+52°
29 March, 18.00 h–5 April, 06.00 h	27	306½°	281°	300°	+25½°
5 April, 12.00 h–7 April, 24.00 h	11	205½°	164°	193°	+41½°
8 April, 06.00 h–17 April, 24.00 h	40	292°	278°	283°	+14°
14 March, 00.00 h–17 April, 24.00 h	141	251°	218°	226°	+33°

The centre of a cyclonic depression passes over the Celtic Sea not very often and when it does it stays there not very long. Occasions when a simple circulation such as that in Fig. 2 may be initiated may be rare. Nevertheless, when a depression passes over or near the British Isles, and that is often, a cyclonic torque may be resolved from the depression and will be operative over the Celtic Sea as a whole and it is this torque rather than a south-westerly wind off Ushant or a north-easterly one off southern Ireland which produces the observed circulation. It may therefore often prove necessary to combine two or more of the charts in Fig. 1 for different parts of the area to evaluate a real occasion.

In summer when the thermocline forms, the arrows in Fig. 1 all require to be rotated in an anticlockwise direction. A study of the currents around Ushant (Cooper, 1960) has shown that just such a change in current direction occurred there after the thermocline had formed in the summer of 1950. If the conclusion may be generalized, as probably it may, it could be of importance for studies on the seasonal drift of fish eggs anywhere.

VORTEX LANES IN THE SEA AND PLANKTON PRODUCTION

Beneath the centre of a depression a vortex will be created in the sea to a considerable depth. Under extreme conditions the water in this vortex may be carried upwards into the air as a waterspout. In winter the vertical column approaches homogeneity so that the vortex can do little by further mixing the water column but, even then, it may have an effect by disturbing bottom deposits. When the water is stratified, as often in summer, the passage of a deep depression in the atmosphere may produce, by upwelling in the sea beneath it, a 'vortex lane' of surface enrichment. Along this vortex a summer outburst of phytoplankton may possibly ensue.

The upwelling vortex in shallow seas is likely to create considerable disturbance of light bottom deposits and occluded dissolved products of regeneration and to suck these towards the surface. A vortex lane should become characterized by a high content not only of total phosphorus, silicate and bacteria but also of chemical substances which affect the growth of plants and animals. This phenomenon should be especially marked over mud bottoms. Phytoplankton outbursts in a vortex lane are therefore likely to consist of a few species which find conditions especially favourable. Similarly animals which spawn into a vortex lane will find exceptional conditions (cf. Wilson, 1951; Cooper, 1951) which may be favourable to some. The zooplankton which subsequently develops may possibly include characteristic indicator species.

THE EFFECT OF THE PHYSIOGRAPHY OF A LAND MASS, SOUTHERN IRELAND

The currents in the northern Celtic Sea may be much influenced by the physiography of southern Ireland. Between Dungarvan Harbour and Cape Clear the coast runs E.N.E.–S.S.W. Winds from south-south-west will tend to initiate currents along the coastline (cf. Fig. 1). Winds between south-west and north-west will tend to cause a similar coastal current but with an off-shore set at the surface.

The main drainage of south-western Ireland runs in deeply cut valleys from west to east or vice versa (Fig. 3). Although several of the original west–east rivers have been captured by others which have cut south across the ridges, the original valleys will channel surface winds from between north-west and south-west, so that they reach the coast in the neighbourhood of Waterford, Dungarvan and Youghal harbours more nearly from due west. There they should tend to produce a series of parallel off-shore currents setting between east-south-east and south-east. Waterford Harbour not only receives the Suir from the west, connected by a low watershed to the valley of the Shannon estuary, but the Barrow which has cut for itself a deep valley running for 50 miles practically due south along the meridian 6° 57′ W. This will similarly channel northerly winds which, whilst they blow, should initiate a current setting south-south-west or south-west off Waterford Harbour.

These are upwelling situations likely, when the wind is favourable, to initiate productive centres, particularly off Waterford at about 51° 40′ N., 7° W. This effect of physiography has been used by Cromwell (1956) to explain the productivity of the Gulf of Tehuantepec on the Pacific coast of southern Mexico. There strong or gale force northerly winds blow through the low and narrow Tehuantepec Pass on to the Gulf to produce an upwelling situation.

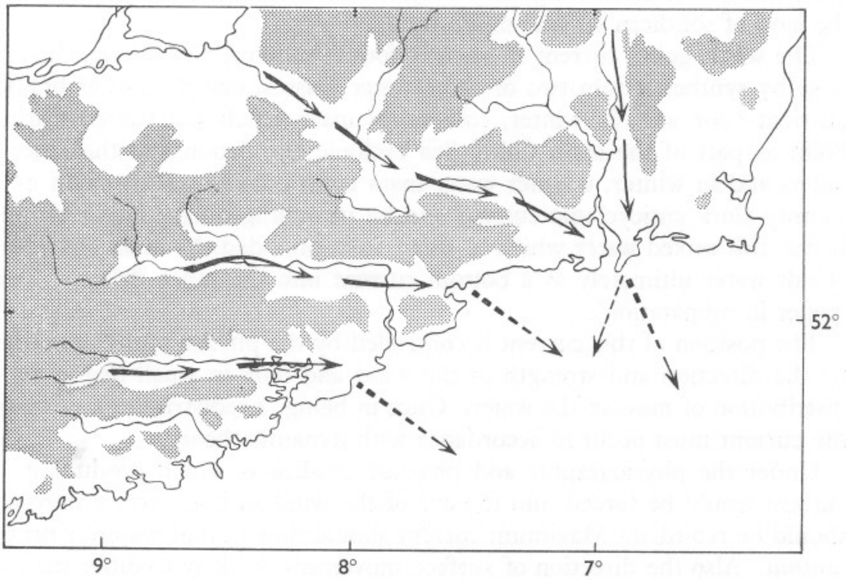


Fig. 3. To illustrate the effect of the prevailing westerly and south-westerly winds combined with the physiography of southern Ireland on currents and upwelling in the northern Celtic Sea. The effect of northerly winds channeled by the Barrow valley is also shown.

The prevailing winds of southern Ireland, which often blow with gale force, should therefore tend to create coastal currents towards the east often trending away from the coast.

To oppose this current system, the Coriolis force operating on the main cyclonic circulation system of the Celtic Sea and favoured by the light coastal belt of water of low salinity will tend to create a coastal current setting west or west-south-west along the length of southern Ireland. Moreover, the two opposed tendencies are produced by much the same winds and may therefore be in frequent conflict. The conflict can only be relieved by a current setting south away from the coast and this seems most often to occur in 7° W., the longitude of Waterford Harbour. This may be pictured as a large-scale rip current (Shepard, 1948). The analogy should not be pressed too far and the term 'rip' should not be transferred. Such a current shows the site of a surface divergence. A cyclonic wind system may therefore produce an anticyclonic current south of County Cork which may force the main cyclonic circulation into a narrow ellipsoidal figure lying east of 8° W. long.

The main cyclonic eddy is much the greater and contains much more water and momentum than the County Cork anticyclonic current. Consequently as soon as the westerly or south-westerly winds die down the main cyclonic current should become dominant, spreading westwards, becoming more nearly circular and creating a westerly coastal current of the usual type with the land of southern Ireland on its right.

The south-going current frequently found in about 7° W. long. thus may arise by synthesis from two or three water masses, one the rather brackish, nutrient-poor and, in winter, cold water mass which has passed Carnsore Point as part of the main Celtic Sea cyclonic circulation and the other the salter, and in winter, warmer water mass contributed from the west by the County Cork anticyclonic current and by upwelling during northerly gales. It was this mixed water which in April 1950 provided the main recruitment of salt water ultimately as a bottom current into the inner Bristol Channel (paper in preparation).

The position of this current is controlled by the physiography of the land, by the direction and strength of the wind and only in small degree by the distribution of mass in the water. Once in being, a redistribution of mass in the current must occur in accordance with dynamic theory.

Under the physiographic and physical conditions which produce it, this current would be forced into the eye of the wind so that surface movement should be retarded. Maximum current should flow in mid-water or near the bottom. Also the direction of surface movement is likely to differ markedly from that near the bottom. Surface movement should trend south-west, mid-water south-east, and bottom movement east towards the Bristol Channel. The Ekman spiral would seem not to apply to such a current forced to flow against the direction of the wind. Under such conditions no help in sketching its course is to be expected from charts of dynamic height anomalies (geopotential topographies).

THE NATURE OF THE BOTTOM DEPOSITS OFF SOUTHERN IRELAND

The topography of the bed of the Celtic Sea has been contoured and described by Robinson (1952). Matthews (1914) pointed to the importance of the weak tidal streaming and small scour in favouring deposition of mud between about 51° N., 6° W. and the coast of County Waterford.

Much information as to the nature of the bed of the Celtic Sea is given on old charts published privately and by the Hydrographic Office. Off the south coast of Ireland in depths of about 35–40 fm. there are many references to 'mud' and 'ooze'. Along the south coast of Cornwall, which in its physiography and exposure to wind has much in common with southern Ireland, no such deposits of mud and ooze were reported nor, indeed, are found by our research ships.

Again, off southern Ireland, there are many records of 'muddy stones', 'muddy gravel', or 'mud' with 'stones' nearby at a similar depth. The picture one has is of an area of what on land would be called boulder clay, deposited during the southernmost extension of glaciation in Ireland. If so the stones have lain there uncovered for at least 10,000 years. Much of the mud, therefore, can be no more than a veneer. If the area was one of strong unidirectional residual currents, as the south coast of Cornwall seems to be, detritus would be swept away to be deposited somewhere else. It would not collect even as a veneer.

If this interpretation as an area of boulder clay overlain by a veneer of mud is correct, we have an equilibrium system: (*a*) the area is one of weak currents which enable mud to be deposited or of horizontal or vertical eddies which tend to concentrate detritus to settle on the bottom beneath, but (*b*) the area is also one where the muddy deposits are creamed off probably intermittently as the result of storm action to be redeposited further south or west. Coring work in this region is badly needed.

A solution may be approached in two ways. Detritus, even organic detritus, is heavier than water, and so tends to settle on the bottom. Our prevailing winds tend to produce an upwelling situation along the south coast of Ireland. Detritus caught up in such a situation will tend to undergo a cyclic movement. Material inshore near the bottom may rise with the upwelling water to be carried seaward in the surface offset. From this it would settle into the deeper water some of which will be drawn back towards the site of upwelling.

Although by itself this mechanism would be insufficient to build up a muddy deposit, it would seem to be a necessary component of one that might. Its biochemical implications need also to be considered. If the detritus should consist of a pure clay mineral it would have no nutrient value and would reduce the amount of light available for photosynthesis. Its effect would be adverse. The clay might carry adsorbed materials which have value to plants. The important part of the detritus, sometimes called seston, would be organic material resulting from death and defaecation and capable of yielding breakdown products essential for the subsequent success of plants and animals in the water. Such organic detritus, only slightly heavier than water, cycling in this way, is particularly likely to provide an explanation of the richness established along the south coast of Ireland by the Lowestoft and Plymouth research vessels in 1958–59.

This mechanism would also favour the concentration of zooplankton which undergo vertical migration from surface to bottom. It would, however, do them no good unless they found food to live on.

This argument would apply equally to much of the south coast of Cornwall, particularly off the Helford River. I know of no evidence for it there. There is, however, a second line of argument which complements the first.

In general, in the northern hemisphere, the outflow of rivers tends to build up a zone of brackish coastal water which, except sometimes at the time of minimum temperature, creates a band of light water which flows with the coast on its right. Along the south coast of Ireland, this current would flow from east to west. However, the direction of the prevailing winds combined with the physiography of the area may, as we have seen, require a current along this coast in the opposite direction, west to east. Evidence for its existence in April 1950 will be produced in a later paper. When these tendencies cancel each other to produce no residual current in a region where tidal currents are weak, the load of detritus may be dropped.

At the Daunt light vessel off Cork Harbour, the table of the tidal stream given on Admiralty chart no. 2049 bears this annotation: 'Wind has so much effect on the direction and rate of the tidal streams at this position that the above table can only be looked upon as approximate and the stream may sometimes be found running even in the contrary direction to that given for any hour in the table'. South of the Daunt light vessel Imray's old chart shows many entries for mud.

By combining the two arguments the difference between the bottom deposits off the south coasts of Ireland and of Cornwall, which otherwise have so much in common, may be explained.

A study of these muddy bottoms may, therefore, for several reasons have a proper place in fisheries research.

THE EFFECT OF THE LABADIE BANK

The Labadie Bank, 20 miles long but only 3 miles wide, extends in a direction south-west by west and lies about 60 miles off the Irish Coast. It rises 40 m from the sea bed in 110 m and is connected by deeper spurs with the Cockburn and Great Sole Banks lying more than 60 miles to the south-west. This system of banks may exert some control over currents in their neighbourhood and tend to make them conform to a north-easterly–south-westerly pattern.

The Bank lies athwart the general south-easterly and southerly trend of the County Cork anticyclonic current. Both the Coriolis force and the pressure of the main Celtic Sea cyclonic circulation tend to turn this current to the right or south-west in line with the constraint imposed by the Bank. On many occasions the Labadie Bank may provide the southern limit of the County Cork anticyclonic system.

The degree of permanence of this anticyclonic system has not yet been assessed but it is likely that on occasion it may last long enough to become markedly enriched from the mud deposits of the Labadie area (Cooper, 1951) and off the south coast of Ireland, not only with inorganic nutrients but with growth-affecting substances as well. Then distinctive chemical composition may lead in time to the development of characteristic biological indicator species.

THE EFFECT OF THE SCILLY ISLES

The Scilly Isles comprise a few small inhabited islands and a large number of rocks rising from an elevation of the sea floor about 11 miles long and 5 miles wide. The surrounding sea floor lies at 70–80 m, whereas the depth of water within the islands ranges from 15 to 45 m. There can be but little land drainage to affect the density of the water.

When air temperature is below sea temperature, as frequently in autumn and winter, the water within the island group will be cooled further and become heavier than in the adjacent sea (Cooper & Vaux, 1949). It will therefore sink and flow out by the deepest channels, North Channel and Broad Sound on the western side of the Isles. To replace this loss, surface water will be drawn in through the many surface channels so that a cyclonic current will be created round the Isles (Sandström, 1918, fig. 41*a*).

When air temperature is above sea temperature or much solar radiation is being received, the sea surface will warm up everywhere but, due to the rugged bottom topography of the Isles, vertical mixing there would be expected to extend deeper than in the adjacent open sea. Although the surface water may become slightly cooler, the vertical water column as a whole should become lighter than outside. A rising centre has come into being so that there will be a tendency for water to be drawn in through the two deepest channels and ejected at some depth between the surface and the depth of the thermocline outside.

These conditions are more complicated than those associated with cooling but the net effect would seem to be to create a divergent anticyclonic current round the Isles at or just above the level of the thermocline.

It is not considered that these trends will ever be dominant but that they will modify currents near the Isles due to other causes. Carruthers, Lawford & Veley (1951) have found that at the Seven Stones Light Vessel, 9 miles E.N.E. of the islands, the current sets on the average towards 110° true. On this view during cold weather this current should set more nearly east, whereas in warm sunny weather it should set more nearly south. When such fluctuations are actually observed they may need to be interpreted not in terms of a major change in the current system of the Celtic Sea, but as no more than a local effect due to the presence of the Scilly Isles.

ELIMINATION OF THE LATITUDE EFFECT IN PLOTTING TEMPERATURES

In these investigations charts and sections of temperature did not at first prove helpful. It is not easy to deduce currents with a meridional component from plots of temperature because as a current moves southward it is warmed by insolation to a greater extent than it loses heat by radiation and evaporation. Such a current is also continuously warming up by lateral mixing with warm water through which it flows.

When, as in our April 1950 cruise, the lay-out of the sections is latitudinal, it is worth while to eliminate the effect of latitude. Calculating along the fiftieth parallel, as shown in Table 2, the effect of uneven spacing of the stations is eliminated. Between Lands End and a point north of Scilly, stations were 7 miles apart, whereas to the westward the interval was 30 miles. Proper weight is given to the length of the section which each station must represent.

TABLE 2. MEAN TEMPERATURES ALONG 50° N. (FIRST APPROXIMATION) 10·17°

Station	Lat. (°N.)	Long. (°W.)	Limits represented by station (long. °)	Minutes of long. ($\Delta\lambda$)	Observed temp. °C (T)	$\theta = T - 10°$	$\theta\Delta\lambda$	Temp. correct to 50° 00′ N.
			9° 15′					
20	49° 57′	9° 06′		20′	9·99	−0·01	−0·20	9·97
			8° 55′					
21	49° 56′	8° 45′		17′	10·15	0·15	+2·55	10·12
			8° 38′					
22	49° 58′	8° 31′		25′	10·17	0·17	+4·25	10·16
			8° 13′					
23	50° 03′	7° 55′		30½′	10·33	0·33	+10·07	10·35
			7° 42½′					
24	50° 00′	7° 30′		29½′	10·20	0·20	+5·90	10·20
			7° 13′					
25	49° 58′	6° 56′		28′	10·16	0·16	+4·48	10·15
			6° 45′					
26	50° 04′	6° 34′		17½′	10·20	0·20	+3·50	10·23
			6° 27½′					
27	50° 04′	6° 21′		9½′	10·10	0·10	+0·95	10·13
			6° 18′					
28	50° 04′	6° 15′		7′	10·08	0·08	+0·56	10·11
			6° 11′					
29	50° 04′	6° 07′		7½′	10·17	0·17	+1·28	10·20
			6° 03½′					
30	50° 04′	6° 00′		7′	10·08	0·08	+0·56	10·11
			5° 56½′					
31	50° 04′	5° 53′		7½′	10·22	0·22	+1·65	10·25
			5° 49′					
32	50° 04′	5° 45½′		7′	10·24	0·24	+1·68	10·27
			5° 42′					
				213′			37·03	

$$\theta_{\text{mean}} = \frac{\Sigma\theta \,.\, \Delta\lambda}{\Sigma\Delta\lambda} = \frac{37{\cdot}03}{213} = 0{\cdot}17°.$$

Assuming that all stations lay precisely on the fiftieth parallel the calculation gave as a first approximation a mean latitude temperature of 10·17° C. However, some stations deviated 4′ from the parallel. A similar calculation for latitude 49° 30′ N. had given the mean temperature for that latitude as

10·48° C. It was therefore possible to apply a correction of 0·01° per minute of latitude to correct each observed temperature along each latitude to 50° 00′ N. or to 49° 30′ N. precisely. This refinement increased the mean latitude temperature along 50° N. by a mere 0·01° C. This figure was used for further development.

By similar means the mean temperature was computed for other lines of latitude where enough observations were available (Table 3, column 4).

In order to use all the available observations and to distribute error and random deviations, it was assumed that the rate of decrease of temperature was linear with latitude. A least mean square of calculation then gave the relation

$$T = 10{\cdot}46 - \frac{0{\cdot}712}{100}(\Phi - 2970),$$

where Φ is the station latitude and 2970 is the latitude 49° 30′, each expressed in minutes of arc.

The final column in the Table shows the mean temperature for latitude computed in this way.

For a depth of 10 m, at each of the 57 stations worked during the cruise of April 1950, the latitude temperature was then computed. Finally, the difference of each observed temperature from the computed latitude temperature was evaluated and plotted on a graph as in Fig. 4. The information will be used in a paper in preparation.

TABLE 3

Lat. (°N.)	Limits of long. (W.)	No. of observations	Mean temp. for lat.: Observed on lat. only	Mean temp. for lat.: Mean square calc. from whole area
51° 20′	5° 05′–9° 00′	5	9·65	9·68
51°	4° 45′–9° 15′	5	9·87	9·82
50° 35′	5° 20′–9° 05′	6	9·98	10·00
50° 00′	5° 42′–9° 15′	13	10·18	10·25
49° 30′	4° 45′–9° 15′	9	10·49	10·46

It will be seen that, strictly speaking, the development has added nothing which could not have been deduced by careful drawing and study of a conventional chart of isothermal contours. However, to use a simile from electronics, the required information has been raised above the level of the background noise. The enclave of water north of Cornwall shows this well.

The technique has another application. One often needs to decide whether the sea at any time is warmer or colder than at some other time. Inevitably oceanographic observations are untidy and heterogeneous. Elimination of the ‘Latitude Effect’ should enable a lot of scattered observations to be summarized in a compact and convenient equation in standard form and to be used for practical ends. One such is fog forecasting where the forecaster

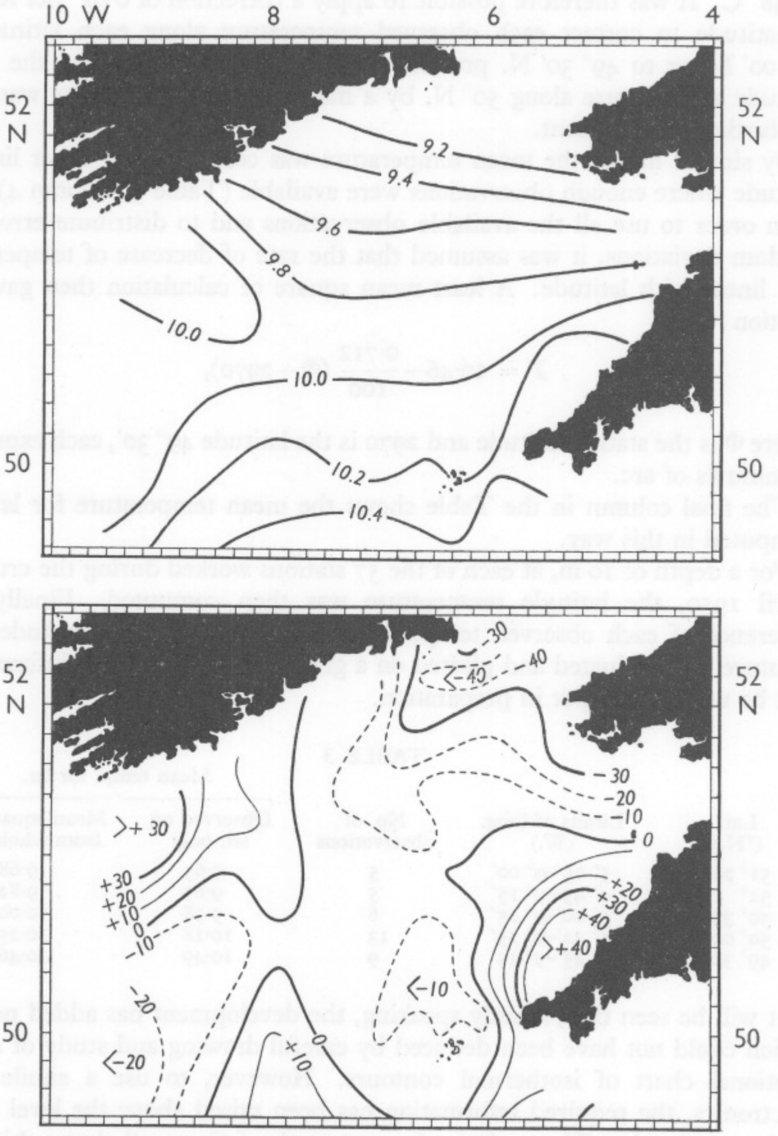


Fig. 4. Two ways of presenting sea temperatures in the Celtic Sea, 19–30 April 1950 at 10 m depth. Upper panel as conventional isotherms, lower panel as deviations from the latitude mean.

needs much more information that he is every likely to get for all of the time and all of the area for which he needs it.

In an investigation where observations have been made in a symmetrical pattern, the calculation may be much curtailed. One could proceed straight into a least-mean-square calculation using all the data. But if some of the stations are clustered, as in April 1950 around the Scilly Isles, bias would be introduced by this short-cut.

THE USE OF GEOPOTENTIAL TOPOGRAPHIES IN SHALLOW-WATER OCEANOGRAPHY

In common practice geopotential topographies are drawn only in oceanic areas where there is a probability of a level surface at a depth in which no motion may reasonably be assumed. The lead set by Harvey (1929) for shallow water work has been rarely followed.

In shallow seas there can be no level surface of no motion. Nevertheless, in our own shallow-water work in the Celtic Sea we have always drawn geopotential topographies and have found them to have diagnostic value. Any deductions which may be drawn must always be consistent with the continuity of conservative and semi-conservative properties of the water.

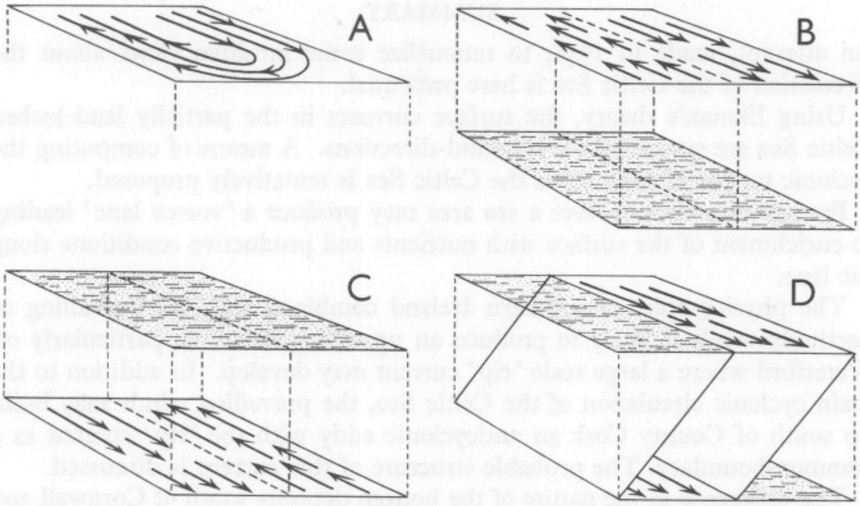


Fig. 5. Interpretations of a tongue in a geopotential topography.

Tongues on geopotential topographies (Fig. 5A) are usually interpreted as geostrophic surface flow along the isolines (Fig. 5B); similarly to geostrophic winds on a meterological isobaric chart. Occasionally, they may be interpreted as a precisely opposite bottom flow, the surface being considered a layer of no motion (Fig. 5C). There is, however, another possibility (Fig. 5D) which may often be important in shallow-water oceanography when water piled up against a coast by wind has to escape as a bottom or mid-water current flowing against the wind at the surface. In this the two halves of the geopotential topography may be interpreted oppositely, so that a picture emerges of a unidirectional current sloping from the surface where the conventional arrows face towards the tip of the tongue to the bottom where they face away from it. The maximum strength may well be in mid-water beneath the axis of the tongue.

Lateral mixing is usually considered as occurring across a more or less vertical boundary. Allowing for the vertical exaggeration of scale, the present interpretation of geopotential topography may require that the boundary between a current and its envelope of stationary water shall dip beneath the surface at an angle of only 1° or so with the horizontal.

Studies of eddy diffusion and eddy viscosity in such a situation take a different form when horizontal and vertical coefficients require to be replaced by oblique coefficients.

This theorem may be illustrated by the events in the Celtic Sea in April 1950, described in a paper in preparation.

SUMMARY

An attempt, made in 1948, to rationalize some intuitive views about the circulation of the Celtic Sea is here presented.

Using Ekman's theory, the surface currents in the partially land-locked Celtic Sea are suggested for six wind-directions. A means of computing the cyclonic torque of gales upon the Celtic Sea is tentatively proposed.

Passage of a cyclone over a sea area may produce a 'vortex lane' leading to enrichment of the surface with nutrients and productive conditions along the lane.

The physiography of southern Ireland combined with the prevailing or northerly winds is likely to produce an upwelling situation, particularly off Waterford where a large scale 'rip' current may develop. In addition to the main cyclonic circulation of the Celtic Sea, the prevailing winds may build up south of County Cork an anticyclonic eddy with the 'rip' current as a common boundary. The probable structure of this current is discussed.

The difference in the nature of the bottom deposits south of Cornwall and south of Ireland, regions with much in common, is considered in relation to the current régime and to biological productivity.

It is suggested that the Labadie Bank may affect the direction of currents, especially the intermittent County Cork anticyclonic eddy.

In both winter and summer it is suggested that events within the Scilly Island group may affect the currents in the neighbourhood, as at the Seven Stones Light Vessel.

A method is given of eliminating the latitude effect from a study of temperature in a limited sea area.

A profitable method of applying information from geopotential topographies in shallow seas is described.

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Printed in Great Britain

THE WATER FLOW INTO THE ENGLISH CHANNEL FROM THE SOUTH-WEST

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The Plymouth Laboratory

(Text-figs. 1–17)

CONTENTS

ON CURRENTS AROUND HEADLANDS

The physical oceanography of the shallow seas south-west of the British Isles is much influenced by the exchanges of waters around headlands between neighbouring areas of the sea. These are:

Bay of Biscay (south-west of Brittany)–*Ushant*–English Channel
English Channel–*Lands End*–Bristol Channel
Bristol Channel–*St David's Head*–St Georges Channel
St Georges Channel–*Carnsore Point*–Celtic Sea (south of Co. Waterford)

This paper discusses the first of these, the recruitment of water from south and west of Ushant into the English Channel. Exchanges of water around the other headlands, together with the recruitment into the English and Bristol Channels of 'western' or 'elegans' waters will be discussed in a further paper now in preparation.

Off the Island of Ushant (I. d'Ouessant) the coast falls steeply to a peneplain at about 110 m. Tides are very strong and the coastline very rugged. Twenty-five miles to the south the Chaussée de Sein (The Saints shoal) projects about 15 miles to seaward and must cause much mixing in coastal water which may flow northwards along the coast of Brittany towards Ushant. Here in summer the surface layers often become cooler and the deeper layers warmer than at corresponding depths in the sea to the westward. The distribution of mass is then such as to encourage the north-going current round the island to flow most strongly not at the surface but at a level around 20–30 m corresponding to that of the thermocline in the sea to the westward. If no other forces were operating the current at surface and near the bottom would flow southward from the English Channel into the Bay of Biscay.

However, in summer, after wet weather, land drainage contributes to the epithalassa and only slowly to the hypothalassa by vertical mixing against a density gradient. The density of the surface water becomes further decreased so that it should acquire a tendency to flow with the coast on the right. In general, summer or winter alike, rivers entering the sea in the northern hemisphere show a tendency to mix away to the right on the surface.

Dietrich (1950, 1951) applied a powerful thermodynamic approach to the circulation of the English Channel as a whole. This was based upon the increase in heat content of the water of the English Channel from its minimum in winter to its maximum in summer. The characteristic feature of thermodynamics is that it deals with the energy changes of a physical or chemical process without requiring a knowledge of the mechanism by which the process occurs. Correctly drawn conclusions are independent of hypothesis, a great advantage since such conclusions remain true even if some of our views about mechanism should undergo radical change. There are converse and very considerable disadvantages to a thermodynamic approach. Without help from other disciplines it cannot give information about mechanism. Consequently it is essential clearly to separate Dietrich's treatment into two parts, that which is strictly thermodynamic and that which is not so.

The unassailable part of Dietrich's paper (his Abbildung 4) is his conclusion that an area on the southern side of the Channel from immediately northwest of Ushant towards the north of the Cherbourg peninsula has a far greater range of temperature than can be accounted for by local exchanges of heat. There must be currents which bring much heat into the area or take it away.

As so often in physics and in physical chemistry, advance is fastest when thermodynamics can be complemented by another approach using, for example, kinetics or continuity of properties. Such methods admit of accurate study of detail, but first attempts at generalization, leaning all too heavily on analogy and intuition, may appear to conflict.

West of the meridian 3° W., the eastern limit of this study, there appears no conflict between my findings, as set out below, and the 13 figures published by Dietrich. Unfortunately those parts of Dietrich's interpretation which are not thermodynamic do not always agree well with mine. In particular, in stratified water north and west of Brittany, this investigation suggests that the residual current at depth sets to the left of that in the upper water. Hansen (1950) produced evidence with which Dietrich concurs that for tidal currents in similar circumstances mass transport tends towards the coast (i.e. to the right) in the bottom layers and away from it in the upper layers.*

THE USHANT CURRENT IN THE SPRING OF 1928

Let us now consider the current around Ushant in late winter and spring following prolonged heavy rain over France. Events in 1928, already briefly discussed by Poole & Atkins (1929, p. 318), illustrated the nature of this flow. Further information was published by the Conseil International (1929, *a*, *b*).

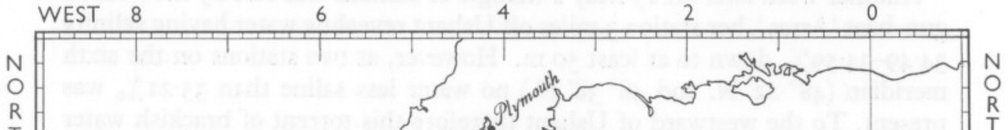

Fig. 1. A chart to illustrate the spread of run-off from the Loire watershed during the spring of 1928.

Early in that year very heavy rainfall occurred in the basin of the Loire, exceeding the normal for the 3 months January–March by 55%, whereas in England it was unexceptional. The heavy run-off spread northwards from the neighbourhood of St Nazaire (Fig. 1), so providing a label enabling its subsequent movement to be followed. Water of somewhat reduced salinity had begun to enter the English Channel by 22 February, the salinity at E3 being 35·01–35·09‰. By 24 March water of exceptionally low salinity (34·06‰)

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* Of Carruthers's (1927) drift bottle results, the few that are relevant to this enquiry support the views of Dietrich and of Hansen rather than my own.

was still present off Ushant at position *A*. In the following 11 days this brackish water spread out for over 30 miles north of Ushant (4 surface salinities on line *AC* 34·74–34·85‰). It had also reached eastward along the French coast to the Hurd Deep in 3° W.

By 5 May the stream of low-salinity water north of Ushant had widened by a further 13 miles to include the position *D* (five salinities between 34·41 and 34·88‰). On 9 May it was sampled by R.V. 'Salpa' at E3 when the uppermost 15 m had a salinity of 34·8‰.

Another week later on 15 May a triangle of stations was run by the French gun-boat 'Arras', her station 3 miles off Ushant revealing water having salinity 34·49–34·59‰ down to at least 50 m. However, at two stations on the sixth meridian (48° 22′ N. and 48° 38′ N.) no water less saline than 35·21‰ was present. To the westward of Ushant therefore this torrent of brackish water was not more than 30 miles wide. It may have been much less. To the northward of Ushant, it would seem that the momentum of the water mass was sufficient to carry it onward within an arc, centred on Ushant, of 40 miles radius. As the northward momentum fell away, the resulting mixed water mass moved up-Channel on the French side.

By 26–27 March the water had nowhere crossed the fiftieth parallel but in the next 5 days it did so. On 31 March it covered the whole of the line from Plymouth to Guernsey, and sometime before 19 April it had moved westward along the English side as far as station E1. During April and May the low-salinity water spread throughout the central and eastern parts of the Channel from which it was not displaced until October–November. By early June, however, the movement of low-salinity water past Ushant was over. No more was observed there.

The brackish water from off Plymouth approached Land's End from the east, arriving at the Seven Stones Light Vessel about 29 April, but was not there felt in full strength until 5 June. The main spate occurred during June and was over by 1 July. There were minor recurrences of less saline water (< 35·1‰) close into Land's End in the corner current until September but at the Seven Stones Light Vessel (50° 04′ N., 6° 05′ W.) this influence was not again detected. It is clear that the corner current around Land's End (50° 04′ N., 5° 43′ W.) was carrying a considerable volume of Loire and Seine watershed water even though the influence at the light vessel, which lies 14 miles west of the promontory, was undetectable. The Land's End corner current was quite narrow.

It is clear that during 1928 we experienced a hydrographical event of considerable magnitude, the whole of the English Channel being affected. It is probable, though not completely proved, that the Biscayan water diluted by run-off from the Loire watershed turned Ushant as a quite narrow current, not more than 30 miles wide and for most of the time probably much narrower. It took 10 weeks to reach Land's End at a rate of 3 miles a day by the route followed. When it did its tendency was to enter the Bristol Channel as a current snugging the headland and not to spread out to include the Seven Stones Light Vessel in its path. Added water alters both density and the consequent pattern of currents, particularly near Ushant. The spring of 1928 may therefore provide a pattern for the circulation of the western English Channel in spring only in years when rainfall over central and western France has been above average.

To understand the behaviour of any of these corner currents it is necessary to have very close stations in the offing and to have one as close to the headland as prudent navigation will allow.

It may not be chance that 1928 and 1929 provided very poor year-classes of hake. Hickling (1935) sought a correlation with the reduced run of the wind to the eastward during the breeding season, but the presence of much fresh water and a consequent pattern of currents may have played a part.

CURRENTS WEST OF USHANT IN THE SUMMER OF 1950

The English Channel and Celtic Sea were exceptionally thoroughly surveyed in the summer of 1950 (Conseil International, 1954) by the Lowestoft research vessel 'Sir Lancelot' and by our own vessel, 'Sabella'. Valuable information was also collected by R.R.S. 'Discovery II' and R.R.S. 'William Scoresby'. The vessels worked in informal but close association. Only observations relevant to currents west and north of Ushant are here considered (Fig. 3).

The important line of surface observations between Land's End and Ushant (no. 10) also requires special comment. This is operated on fortnightly schedules out and home by two ships which often pass each other in the mouth of the Channel. In the early months of 1950 serious discrepancies between temperature observed by each ship and those observed at the Seven Stones Light Vessel and by R.V. 'Sabella' were noted. By such comparison and by scrutinizing the times of observation, we have had good reason to reject observations from one ship for the whole year and from the second ship for the months of January, February and March. Observations from the second ship have been accepted for the following dates and are included in the isopleth (Fig. 2). It is understood that the Lowestoft Laboratory have arrived at a similar conclusion.

Southbound	Northbound	Southbound	Northbound
(1) 11–12 April	17–18 April	(8) 22–23 July	2–3 August
(2) 23–24 April	29 April	(9) 16–17–18 Sept.	—
(3) 7 May	12–13 May	(10) 30 Sept.–1 Oct.	8–9 October
(4) 22–23 May	29 May	(11) 15 October	22–23 October
(5) 3–4 June	10–11 June	(12) 12–13 November	20 November
(6) 17–18 June	24–25 June	(13) 26–27 November	3 December
(7) 1–2 July	14–15 July	(14) 12–13 December	21–22 December

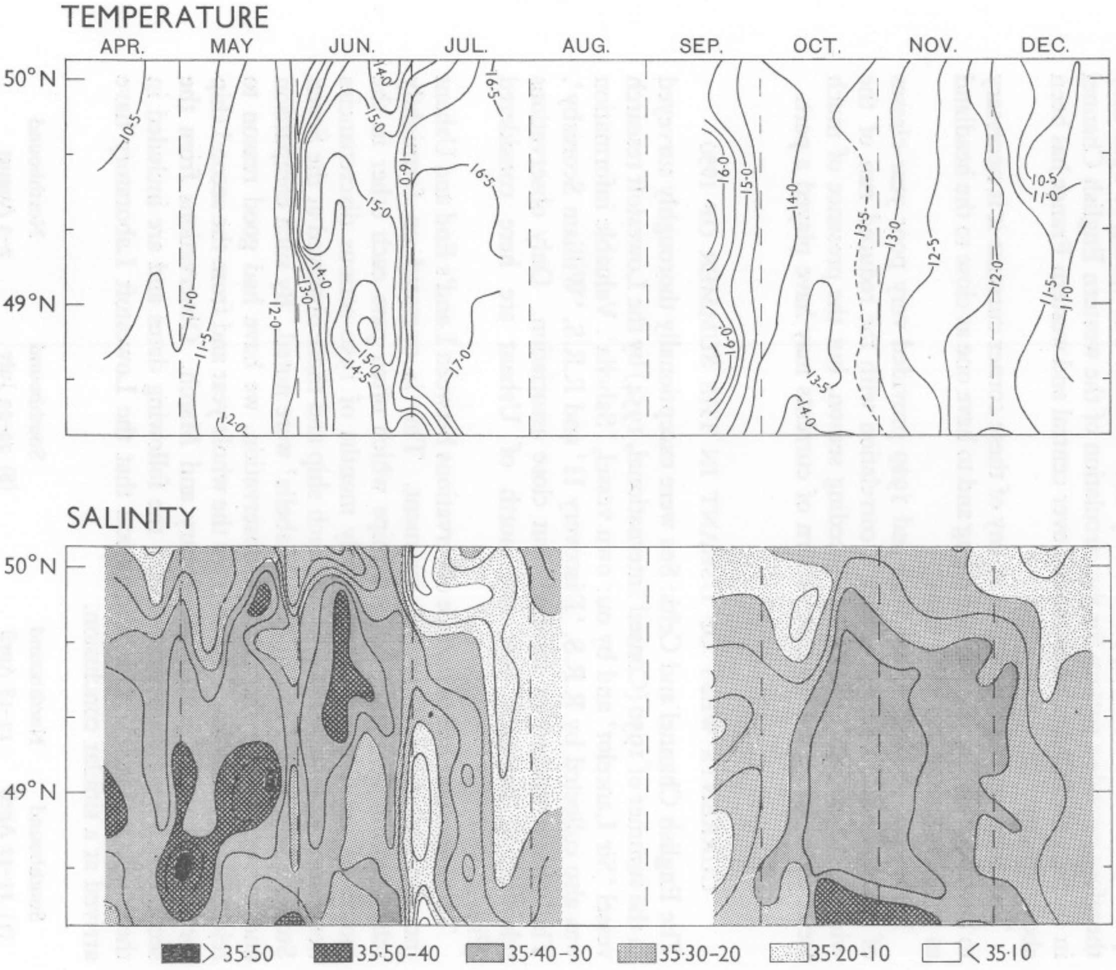

Fig. 2. Selected surface observations of temperature (°C) and salinity (‰) along line no. 10 between Land's End and Ushant. Time (April–December 1950) plotted against latitude.

'*Sir Lancelot's' observations in August* 1950

In August R.V. 'Sir Lancelot' worked a line of stations west of Ushant at even closer intervals than those of R.V. 'Sabella' in June and additionally made highly critical observations north of north-western Brittany (Fig. 3).

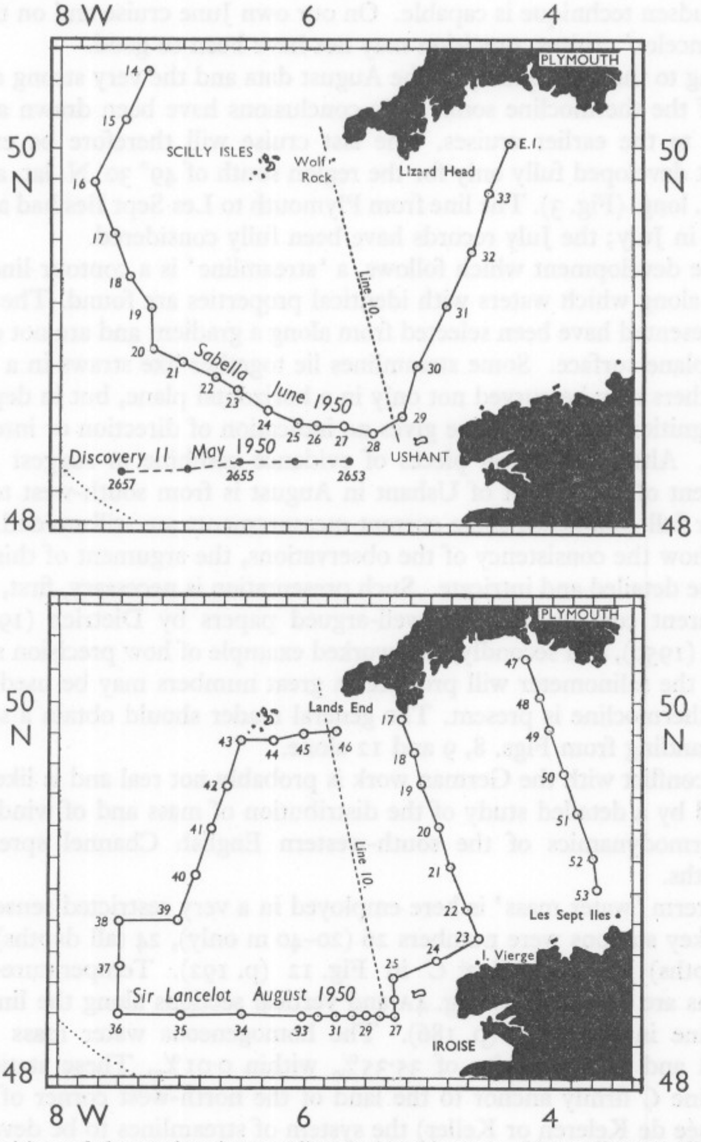

Fig. 3. Positions of observations in 1950 discussed in this paper. Upper diagram, 'Discovery' stations 2653–57 on 11 May and 'Sabella' stations 16–33 on 12–14 June. Lower diagram, 'Sir Lancelot' stations 17–53 on 6–13 August. Surface observations on line 10 are indicated.

The homogeneity of the August observations when plotted on temperature and salinity (T–S) diagrams was very good. Such few errors in salinity as there may have been were relatively gross (of the order ± 0·1 ‰ salinity), suggesting leaky stoppers. Otherwise it would seem that the analyses, made in the Government Chemists' Laboratory, attained the highest precision of which the Knudsen technique is capable. On our own June cruise and on the other 'Sir Lancelot' cruises, precision may not have been so good.

Owing to the high quality of the August data and the very strong development of the thermocline some basic conclusions have been drawn and then applied to the earlier cruises. The last cruise will therefore be examined first but developed fully only for the region south of 49° 30′ N. lat. and west of 4° W. long. (Fig. 3). The line from Plymouth to Les Sept Iles had also been worked in July; the July records have been fully considered.

In the development which follows, a 'streamline' is a contour line within the sea along which waters with identical properties are found. The streamlines presented have been selected from along a gradient and are not confined to any plane surface. Some streamlines lie together like straws in a sheaf of corn, others may be curved not only in a horizontal plane, but in depth also.

Recognition of a streamline gives no indication of direction or intensity of current. Although several pieces of evidence combine to suggest that the movement of water west of Ushant in August is from south-west to north-east, for full confidence some current measurements are still needed.

To show the consistency of the observations, the argument of this section has to be detailed and intricate. Such presentation is necessary, first, because of apparent conflict with the well-argued papers by Dietrich (1950) and Hansen (1950), and secondly, as a worked example of how precision salinities such as the salinometer will produce in great numbers may be used when a strong thermocline is present. The general reader should obtain a sufficient understanding from Figs. 8, 9 and 12 alone.

The conflict with the German work is probably not real and is likely to be resolved by a detailed study of the distribution of mass and of wind, and of the thermodynamics of the south-western English Channel spread over 12 months.

The term 'water mass' is here employed in a very restricted sense.

The key stations were numbers 26 (20–40 m only), 24 (all depths) and 22 (all depths) on streamline *C* in Fig. 12 (p. 192). Temperature–salinity diagrams are displayed as Fig. 4A and vertical sections along the line of the streamline in Fig. 7, *C* (p. 186). The homogeneous water mass is there stippled and has a salinity of 35·35‰ within 0·01‰. These stations and streamline *C* firmly anchor to the land of the north-west corner of Ushant (Chaussée de Keleren or Keller) the system of streamlines to be developed.

The water at station 26, at 75 m and deeper (salinity 35·37–35·39‰, temperature 12·1°) was not moving east into the English Channel, neither was the water at 0 and 10 m depth where the salinity of 35·32‰ was not elsewhere recognized. Our interest rests on the water between 20 and 50 m with a salinity of 35·35‰ precisely and a range of temperature between 12·05 and 14·4° C. This water passed between station 25 and the Island of Ushant. Indeed there is no doubt that with the help of the strong tide it suffered considerable vertical mixing as it passed over the bottom in 38–50 fm. (70–90 m), between the steep-to submarine cliff of the Chaussée de Keleren and the off-lying submarine fosse to become the water mass observed at station 24. Here the salinity was unchanged and the range of temperature was reduced by mixing to 13·35–13·85° C at 10–90 m depth. All the water at station 24 proceeded unchanged to station 22 where it was found between 20 m and the bottom at 97 m.

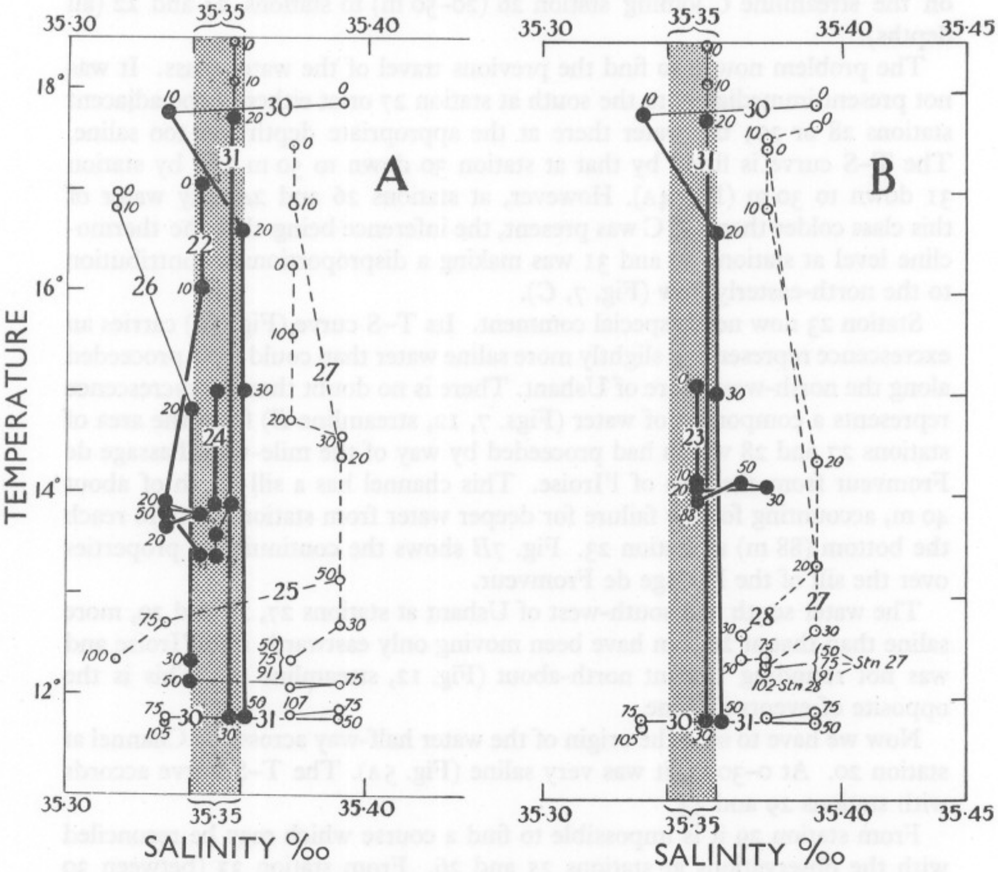

Fig. 4. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed: A, streamline *C*; B, streamline *B*. Cf. Figs. 7B, C and 9. To display the many points with salinity 35·35‰, the vertical line has been expanded into the shaded band.

The warmer water at station 22 (0–10 m) had been subjected to solar insolation. Its properties are compatible with a flow of water from station 30 (15–25 m deep) 15 miles west of Ushant.

On Fig. 4A, T–S curves (pecked) for stations 25 and 27 are included to show that the waters there were quite markedly different from that on the streamline *C* joining station 26 (20–50 m) to stations 24 and 22 (all depths).

The problem now is to find the previous travel of the water mass. It was not present immediately to the south at station 27 or at either of the adjacent stations 28 or 29; the water there at the appropriate depth was too saline. The T–S curve is fitted by that at station 30 down to 50 m and by station 31 down to 30 m (Fig. 4A). However, at stations 26 and 24 only water of this class colder than 15° C was present, the inference being that the thermocline level at stations 30 and 31 was making a disproportionate contribution to the north-easterly flow (Fig. 7, *C*).

Station 23 now needs special comment. Its T–S curve (Fig. 4B) carries an excrescence representing slightly more saline water than could have proceeded along the north-west shore of Ushant. There is no doubt that the excrescence represents a component of water (Figs. 7, 12, streamline *B*) from the area of stations 27 and 28 which had proceeded by way of the mile-wide Passage de Fromveur from the area of l'Iroise. This channel has a sill depth of about 40 m, accounting for the failure for deeper water from station 27/28 to reach the bottom (88 m) at station 23. Fig. 7*B* shows the continuity of properties over the sill of the Passage de Fromveur.

The water south and south-west of Ushant at stations 27, 28 and 29, more saline than that at 26, can have been moving only eastwards into l'Iroise and was not rounding Ushant north-about (Fig. 12, streamline *A*). This is the opposite of events in June.

Now we have to seek the origin of the water half-way across the Channel at station 20. At 0–30 m, it was very saline (Fig. 5A). The T–S curve accords with stations 29 and 33.

From station 29 it is impossible to find a course which may be reconciled with the observations at stations 25 and 26. From station 33 (between 30 and 45 m depth) the course (Fig. 12, streamline *E*) fits with the story that has still to be told.

Below 30 m at station 20 a different water mass was present. An origin from a position half way between stations 28 and 29 (not here illustrated) fits the T–S diagrams but is inconsistent with other stations or the pattern of geopotential anomalies. The vertical column at station 20 has therefore to be fitted by a surface sloping from a depth of about 28 m at station 32 (which sinks to the bottom at station 20) and 40 m at station 33 (which rises to 30 m at station 20). That is between stations 33/32 and 20, the T–S surface executed what an aviator would call a roll through more than a right-angle

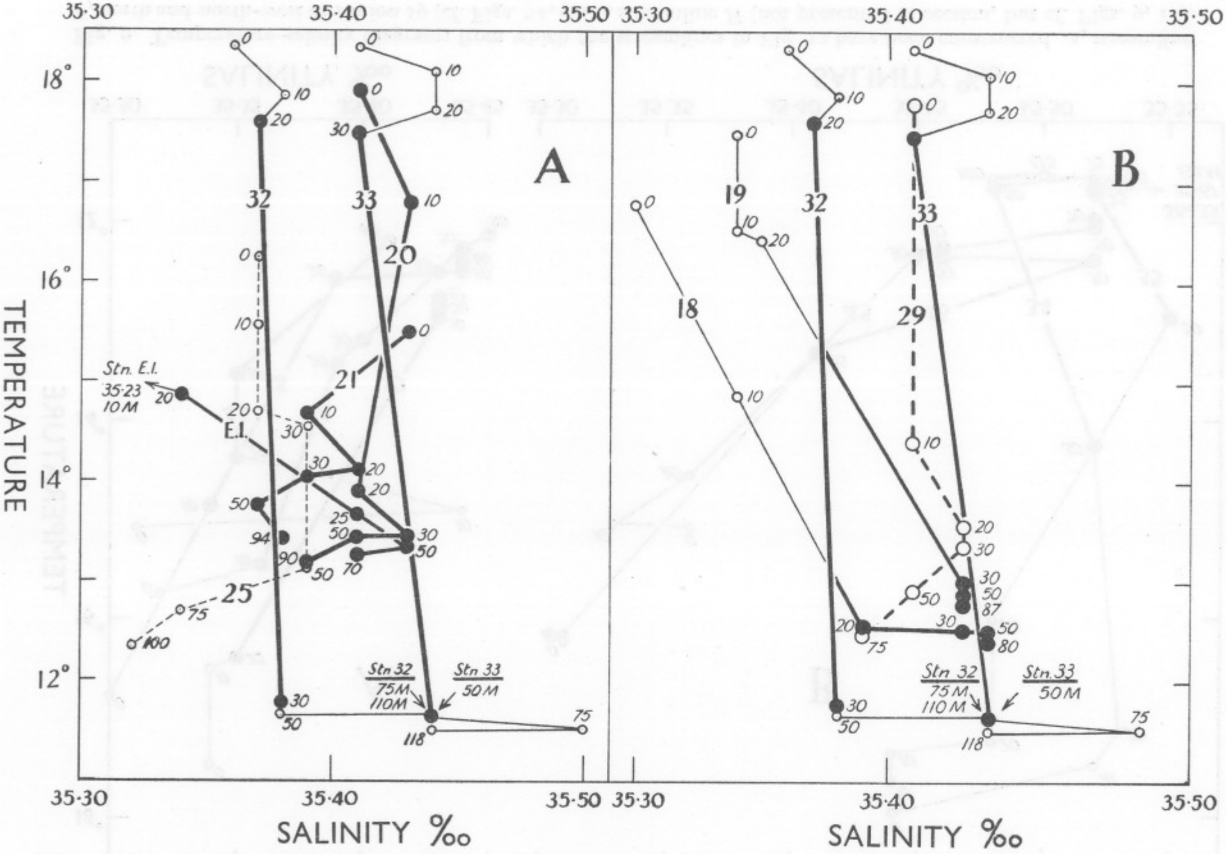

Fig. 5. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed: A, streamlines *D* and *E* (cf. Figs. 7D, 8, 9); B, streamline *F* as far as station 18 (cf. Figs. 7F, 9).

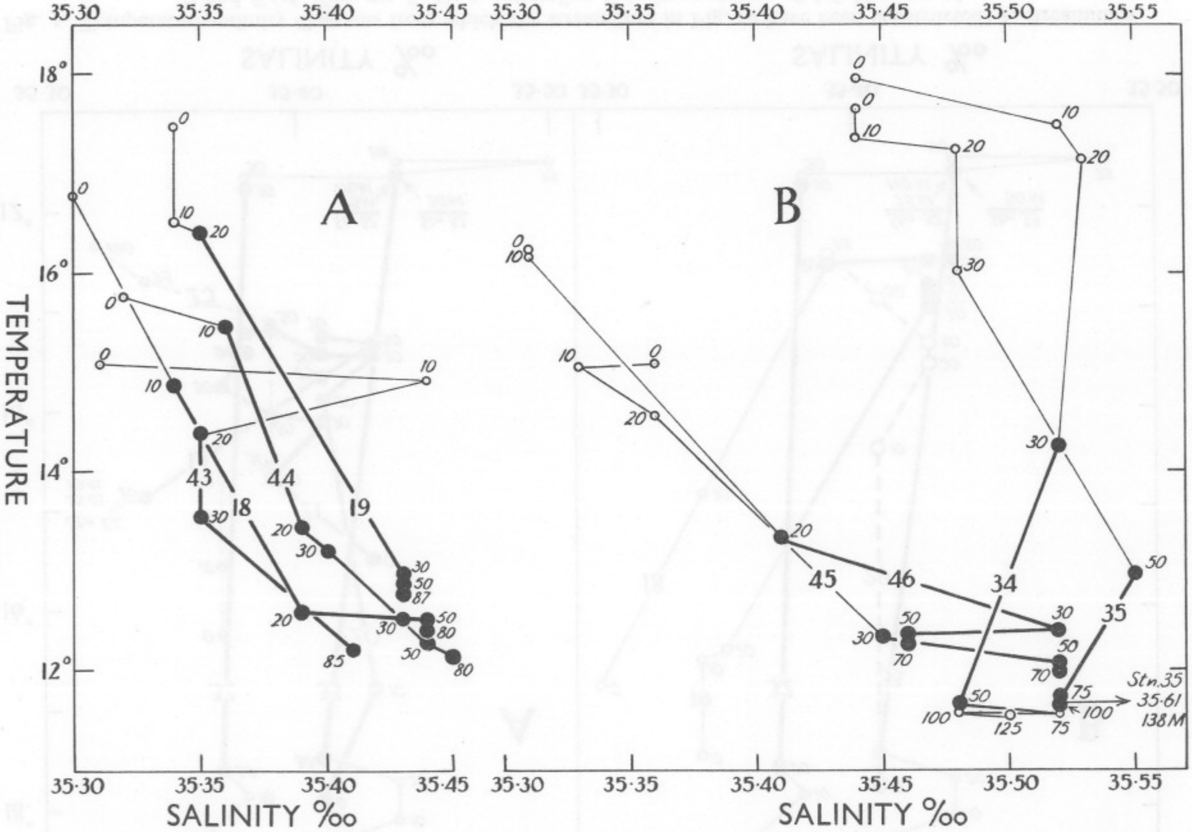

Fig. 6. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed. A, streamline *F*, north and north-west of station 19 (cf. Figs. 7F, 9); B, streamline *H* (not presented in section, but cf. Figs. 9, 12).

(Fig. 8). The direction of the roll was clockwise as the water advanced. In this deduction, temperature may legitimately be treated as a near-conservative quantity, since the water mass always remained subthermocline; Fig. 8 is necessarily somewhat schematic. It is not practicable to present this helical movement for every streamline though the tendency is present on all of them. Streamline *E* can be followed to 'Sula's' station E1 worked on 23 August (Figs. 5A, 8 and 12).

The water from station 32 (about 28 m depth), following streamline *E* in Fig. 12 passed station 25 at a depth of 50 m (Fig. 8) on its way to the bottom (90 m) at station 20, undercutting streamline *D*. Streamlines *D* and *E* at all points lay to the seaward of streamline *C* but north-west of Ushant by only a few miles.

Station 21 (Figs. 5A, 7) shows a similar history to station 20, but a larger proportion of the water came from the neighbourhood of station 32 and less from that of station 33. Moreover, the subthermocline water at station 21 was half a degree warmer than that at station 20 and consequently was somewhat higher within the thermocline at station 32.

A probable crossing-over between streamlines *D* and *E* represents water from station 32 which has passed station 25 at 50 m and then undercut somewhat shallower water on passage from midway between stations 32 and 33 at about 35 m north of station 25 to 21 (40–90 m). For clarity it has been eliminated from Fig. 12. It is not easy to represent the fanwise spreading and interlacing of these waters on plane diagrams.

Now let us consider (Figs. 5B, 7) stations 19 and 18, 24 and 14 miles S.S.E., respectively, of the Lizard. At this distance surface warming-up will have destroyed any hope of finding the history of the water above the thermocline but it would seem that temperature remained conservative below the thermocline. The very saline water (35·43–35·44‰ and temperature 12·47–12·92° C) between 30 m depth and the bottom at 82–87 m accords closely with the water in the lower part of the thermocline at station 33 (Figs. 5B and 12, streamline *F*, and the streamline *F* section in Fig. 7). Thus the water from station 33 was spreading fanwise, the upper thermocline water taking a more easterly direction than the deeper.

It would seem that 'Sir Lancelot' section between the Lizard and l'Ile Vierge, as between stations 20 and 18, lay almost along the line of movement of the current which had passed station 33 (48° 20′ N., 6° 00′ W.) at thermocline level.

This same water mass may be followed farther to station 44 south of Scilly (Fig. 12, streamline *F*, Fig. 6A, Fig. 7). Streamline *F* would seem to have passed north of stations 45 and 46, nearby the Wolf Rock. Still farther north another streamline (*G*) can be traced (Figs. 12, 6A) from station 18 (20 m, at the bottom of the thermocline there) to 43 (30 m to bottom in 85 m), i.e. along the south coast of Cornwall water which had crossed the Channel at the

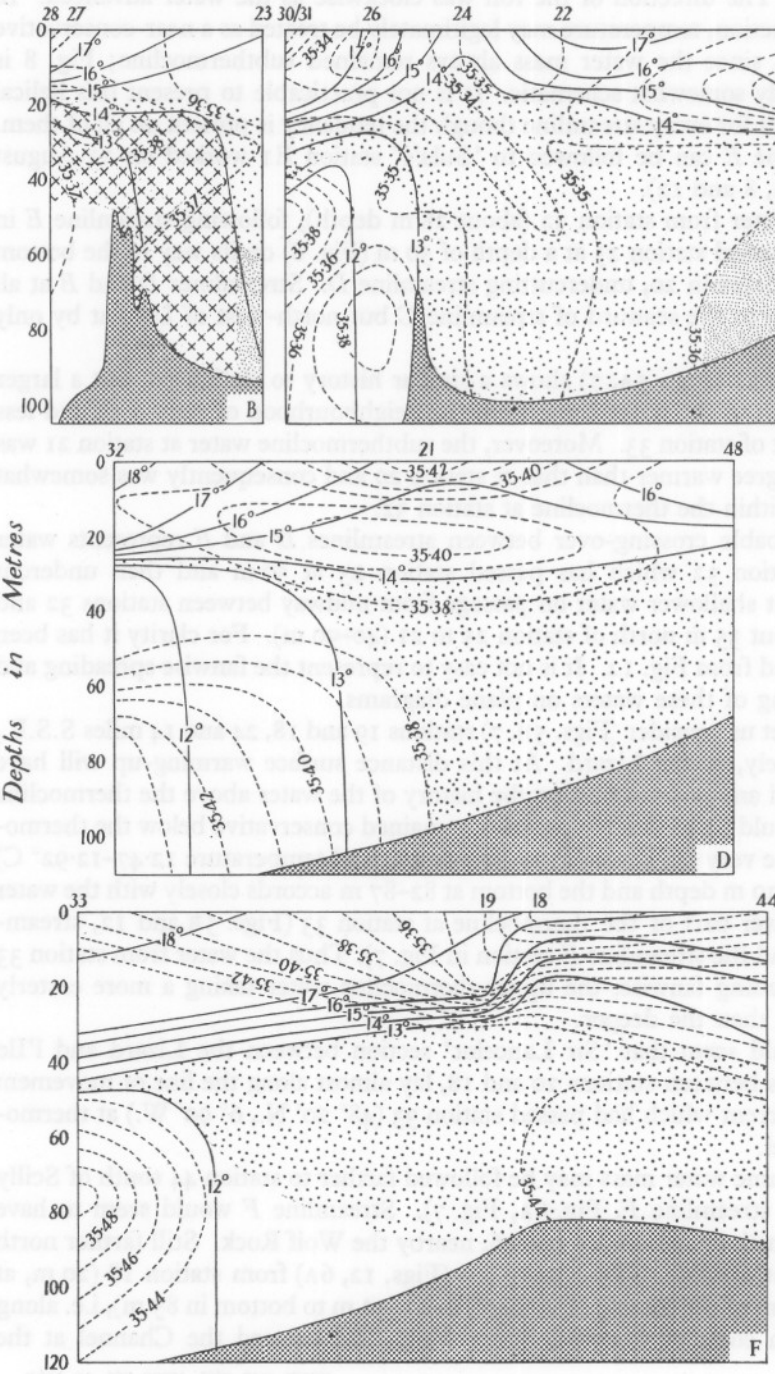

Fig. 7. For legend see opposite page.

bottom of the thermocline sank below a coastal belt of surface water to cover the submarine slope between 50 and 80 m depth.

The higher salinities at station 46 (30 m) and station 45 (49° 50′ N., south of the Land's End–Scilly Channel; at 50 and 70 m) are consistent with an origin in the lower part of the thermocline between stations 34 and 35 (48° 20′ N., 6° 45′ W., Parsons Bank area) (Fig. 12, streamline *H*, Fig. 6B).

The course of this concordant family of streamlines at the lower level is summarized in Fig. 12. They show that in the weeks preceding 6 August 1950, there had been a cyclonic circulation in the subthermocline water in the mouth of the English Channel and that most of this water had been introduced across the parallel 48° 20′ N., at thermocline level in a current there flowing east-north-east and grazing the north-west corner of Ushant. The destinations of the various parts of the thermocline structure along the parallel 48° 20′ N., are displayed in Fig. 9.

A spiral, the mirror image of the Ekman spiral, was evident west and north of Ushant, the water in the upper part of the thermocline along the parallel 48° 20′ N. proceeding to the right of that in the lower part of the thermocline there. Very little of the water truly below the thermocline moved into the English Channel. Such movement as it had was probably north-west.

So far we have examined the manner by which water which crosses the line west of Ushant within the thermocline fans out and deepens to become the subthermocline water on the line between the Lizard and l'Ile Vierge.

Legend to Fig. 7

Fig. 7. Sections along streamlines sublettered to correspond with Fig. 12.

Streamline B (area coarsely stippled) passes through the Passage de Fromveur between Ushant and the mainland of France (cf. T–S diagram, Fig. 4B). The water at 88 m at station 23 was identical with that at 8–9 m at station 24, i.e. at the top of the water in streamline *C* (next panel) which had sunk towards the east. Much of the cross-hatched water blanketing the slope of l'Ile Vierge inside of station 23 had unknown properties; to fit with the rest of this account it needed to have the properties of stations 27 and 28 between 20 and 50 m (T–S diagram, Fig. 4B, pecked lines).

Streamline C was anchored snugly to the north-west corner of Ushant (Chaussée de Keleren) (cf. T–S diagram, Fig. 4A). All but one of the points in the coarsely stippled area had a salinity precisely 35·35‰, so that only a generalized iso-line may be drawn for that salinity. The odd point was 35·34‰. The bottom water at station 49 was part of streamline *D*.

Streamline D (cf. T–S diagram, Fig. 5A, in part), lying to seaward of streamline *C*, is stippled. The elongated core of water at station 21 at between 12 and 28 m depth and having a salinity in excess of 35·39‰ had crossed the meridian 48° 20′ N. at 5° 56′ W. between stations 32 and 33 at a depth between 26 and 33 m. On Fig. 9, if inserted, it would show as a callosity on the left of streamline *D*. At station 21 it passed above section *D* and proceeded to station 51 as streamline *Q* (Fig. 10Q).

Streamline E cannot be presented as a vertical section. Its helical character is shown schematically in Fig. 8. It undercuts streamline *D* at station 25 at a depth of 50 m (cf. T–S diagram, Fig. 5A).

Streamline F (stippled) was established from a point 45 miles west of Brittany, across the mouth of the Channel, then south of Land's End and Scilly (cf. T–S diagrams, Figs. 5B, 6A).

The same process was at work in the thermocline on the Lizard–l'Ile Vierge line. Fig. 10 shows sections *P* and *Q* joining stations 22 and 52 and stations 21 and 51, where thermocline water is moving to the right of the water below the thermocline and sinking as it moves up-Channel. This is what might be expected of an anticlockwise gyral in the wide-mouth of a narrowing and shallowing channel in high summer.

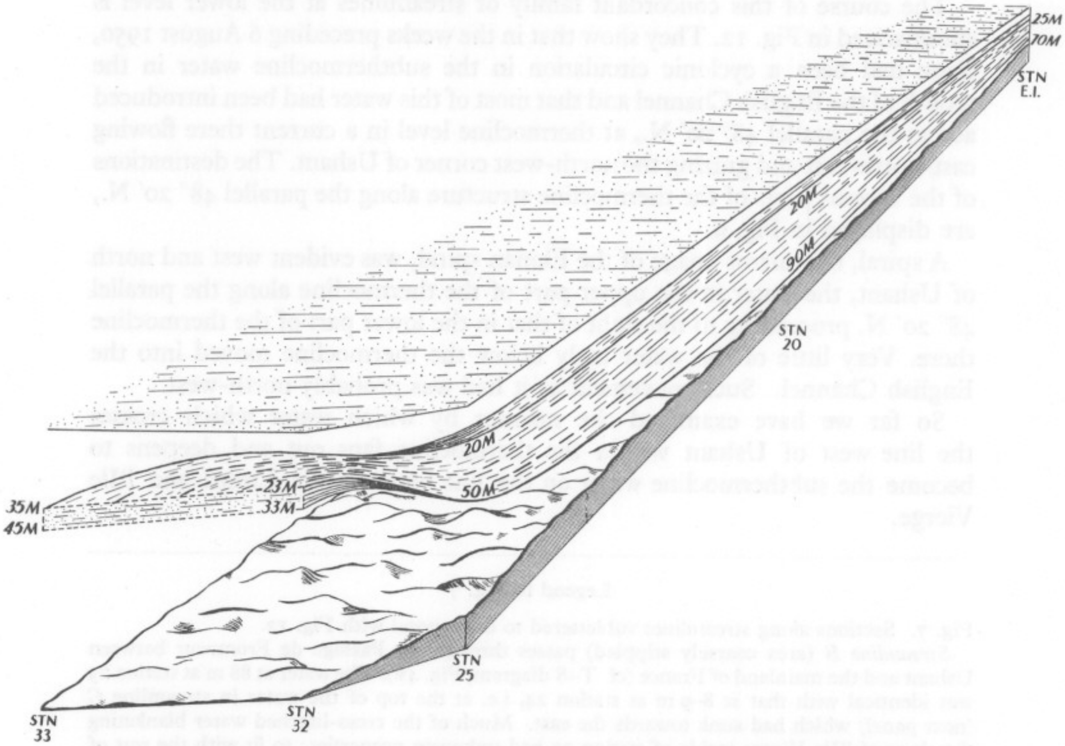

Fig. 8. A block diagram to show how water lying horizontally in the thermocline west of Ushant twists in a vertical plane through a right angle as it passes north-west of Ushant to occupy the subthermocline vertical column in mid-Channel (station 20) and at E 1. The lower contour passes through the position of station 25 at 50 m depth. The upper contour, however, passes not through station 25 but through a position some miles to the north-west. Some displacement of the isotherms and isohalines drawn in Fig. 7D is necessary but is compatible with the observations.

The course of these streamlines *P* and *Q* is also shown in Fig. 12. Streamlines *P*, *Q* and *G* lie above streamlines *C*, *D* and *F* where they cross.

The boundary between the easterly current (streamlines *P* and *Q*) and the deeper northerly or north-easterly current (streamlines *C*, *D* and *E*) was sharp. There is no evidence for water at the boundary depth at stations 20, 21 and 22 moving in an intermediate direction.

Consequently the thermocline 30 miles N.N.E. of Ushant was different

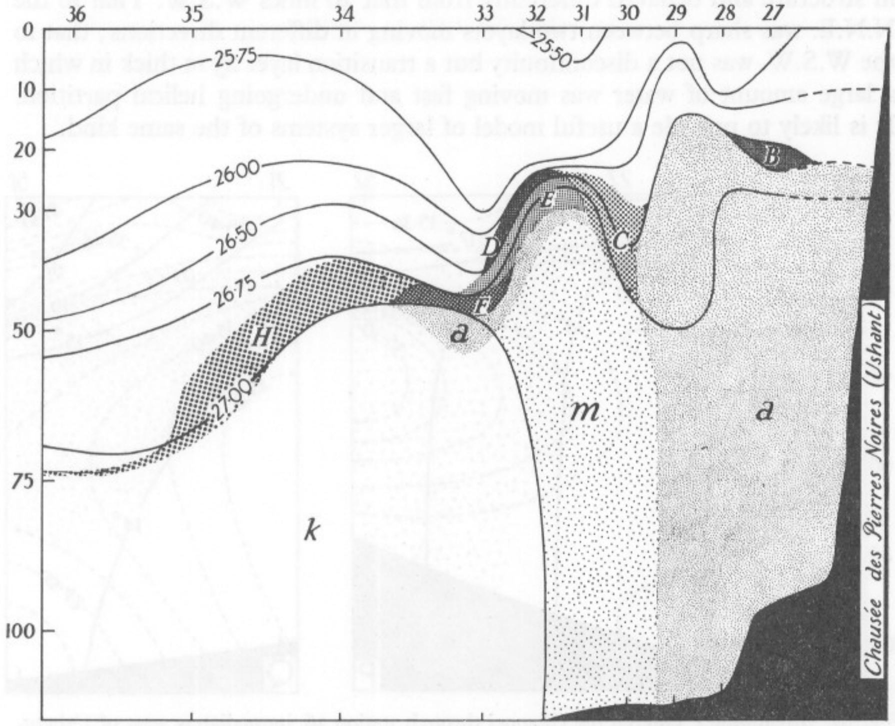

Fig. 9. Density (σ_t) section west of Ushant along lat. 48° 20′ N. on 7 August 1950 with destinations of the water in and below the thermocline. Waters which were to enter the English Channel east of a line drawn from Ushant to Scilly are denoted by capital letters, whereas lower case letters indicate waters which were not to enter the Channel.

Water masses *C*, *D*, *E* and *F*, subcomponents of one current system, were to flow along the corresponding streamlines (Fig. 12, also Figs. 4A, 5A, B, 6A) north-west of Ushant into the English Channel to occupy the whole water column between about 25 m and the bottom. Water mass *H* (Figs. 12, 6B) was to follow a similar course (streamline *H*) across the mouth of the Channel to a region south of the Wolf Rock.

The deep westerly water mass *k* was probably moving relatively slowly. Such movement as it had was towards the north. It never entered the English Channel.

Water mass *m* represents a vertical planar section of a spiral eddy. Near station 32 at about 45 m depth, the lowest water in the thermocline had a northerly spiral component. This flowed north-about station 31 and below water masses *F* to *C* to return as a slow current with a southerly component and occupying at station 30 all the water column below a depth of 50 m.

Similarly water mass *a* first lay in a vertical plane at 30–55 m between the water masses *F*–*D* which were to enter the English Channel and the water at the deep centre of the eddy (*m*). It also rotated, undercutting water mass *C* to become the deep water (below 20 m) in l'Iroise at stations 29, 28 and 27. The horizontal planar projection of the flow of water mass *a* is indicated on Fig. 12 as streamline *A*.

Apart from tidal movement water mass *a* in l'Iroise was probably almost stagnant in August. The small kernel of water marked *B*, to correspond with streamline *B* in Fig. 12, was really part of water mass *a* but in a position to be carried on the flood tide through the Passage de Fromveur to station 23 at 30–50 m depth (Fig. 4B).

Streamline *P* (Fig. 10) entered as a thin band of water immediately overlying water mass *C* in this figure; similarly the origin of streamline *Q* overlay streamline *D*. On this figure they are not easy to depict.

in structure and behaved differently from that 30 miles W.S.W. That to the N.N.E. was sharp between two layers moving in different directions; that to the W.S.W. was not a discontinuity but a transition layer 25 m thick in which a large amount of water was moving fast and undergoing helical partition. It is likely to provide a useful model of larger systems of the same kind.

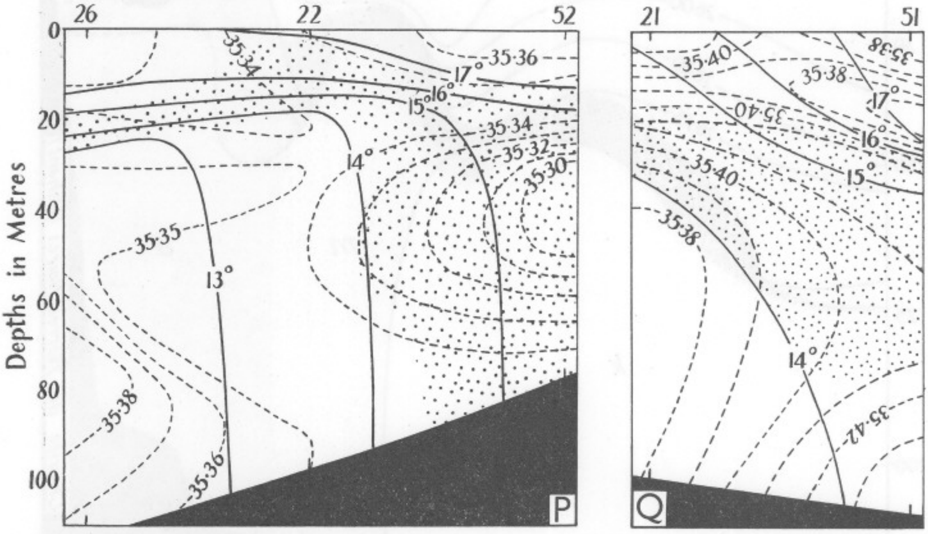

Fig. 10. Streamline *P* entered the Channel through station 26, immediately west of Ushant, between 19 and 27 m, then between station 25 and the island, to seaward of station 24 and then above the thermocline at station 22 where at depths between 3 and 19 m it crossed streamline *C*. It then sank to occupy station 52, 45 miles E.N.E., between 12 m and the bottom. Streamline *P* can be easily matched by interpolated values of temperature and salinity between stations 30 and 31 immediately above water mass *C* in Fig. 9.

Streamline *Q* also can be matched by interpolated values of temperature and salinity between stations 32 and 33 immediately above water mass *D* in Fig. 9. The elongated core of water with salinity 35·39–35·40‰ at 15–32 m depth around station 21 in Fig. 7C represents this water mass crossing over streamline *C* at an angle of intersection of +40°. It then passed up-Channel as shown here to occupy station 51 between 27 and 75 m depth.

The bottom water at station 51 gave an unsupported record of 14·29° C and 35·44‰. This is compatible with the water mass *a* which having flowed past station 33 at 50 m depth, ran north-about stations 32, 31 and 30 to proceed south-east into l'Iroise at station 29 (Fig. 9). However, no streamline can be constructed between any part of water mass *a* and station 51 without intersecting some other streamline. The result at the bottom at station 51 cannot be made to fit without unwarrantable complexity. It is more reasonable to ascribe it to an error of observation.

Two ways of presenting temperature and salinity at a depth of 50 m are shown in Fig. 11. The upper diagram shows a conventional chart where only the records from a depth of 50 m are considered and isotherms and isohalines in that plane are drawn by linear interpolation. It is grossly misleading. The lower diagram is drawn to conform with T–S diagrams, such as Figs. 4–6 and streamline drawings such as Figs. 7–9 and takes account of the changes in level of the water as it flows.

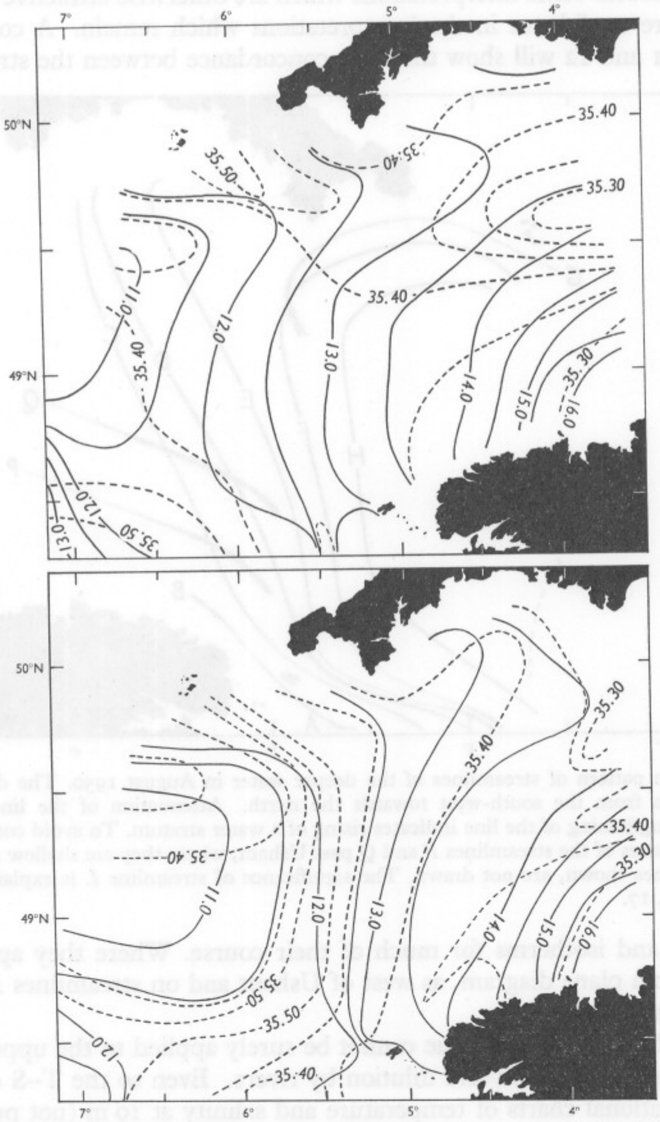

Fig. 11. Two ways of constructing isotherms and isohalines at 50 m depth from 'Sir Lancelot's' observation between 6 and 13 August 1950. The upper panel is drawn following standard conventions; the lower one is drawn to conform with the three-dimensional pattern of streamlines (see text). The position of the stations is shown in Fig. 3 (lower).

In shallow-water oceanography in summer, it would seem not merely interesting but essential to construct T–S diagrams for that part of the water column which is neither in immediate contact with the atmosphere nor subject to much absorption of radiant heat. It will be found that this approach not only forbids some interpretations which are otherwise attractive but gives much more confidence in the interpretations which remain. A comparison of Figs. 11 and 12 will show the close concordance between the streamlines, isohalines and isotherms for much of their course. Where they appear not to agree on a plane diagram, as west of Ushant and on streamlines *P* and *Q*, sinking is the cause.

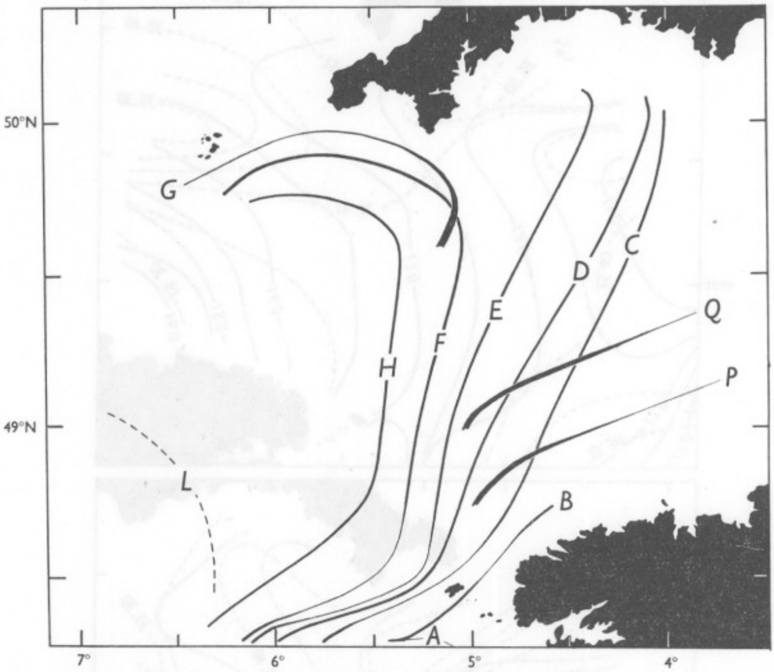

Fig. 12. The pattern of streamlines of the deeper water in August 1950. The direction of movement is from the south-west towards the north. Attenuation of the line indicates sinking, strengthening of the line indicates rising of a water stratum. To avoid confusion the southern courses of the streamlines *P* and *Q* past Ushant, where they are shallow and overlie the streamlines shown, are not drawn. The significance of streamline *L* is explained in the text and Fig. 17.

The T–S diagram technique cannot be surely applied to the upper waters subject to solar radiation and dilution by rivers. Even so the T–S diagrams and conventional charts of temperature and salinity at 10 m (not published) give no indication that there was any appreciable surface flow across the latitude 48° 20′ N. towards the English Channel. Most probably, as in May (to be discussed), it was towards the south-east.

It is remarkable that even in the upper layers some measure of conservation of properties is to be recognized. On the southern end of the line from Plymouth to Les Sept Iles at stations 50, 51 and 52 there is a surface stratum of water 20 m thick with temperatures exceeding 17° C and with salinities between 34·34‰ and 34·39‰. Very similar water was present on the Lizard–l'Ile Vierge line but only at the surface at stations 19 and 20 and nowhere else at any depth. The continuity of properties suggests a continuity of movement, i.e. that there was a thin surface current through stations 19 and 20 including water warmer than 17° C, and only a few metres thick, which fanned out to the east and south-east to become a warm surface stratum four times as thick. Moreover, the water having a temperature between 16 and 17° C at 5 to 15 or 20 m depth at stations 19 and 20, can also be followed but taking a somewhat more northerly direction.

This interpretation of surface water movements at high summer may be accepted only because it is compatible with the behaviour of the deeper streamlines.

The important conclusion is that there seems to have been a large recruitment of water into the mouth of the English Channel across the parallel 48° 20′ N. between 5° 35′ W. and 7° 00′ N. and this recruitment was from a layer at thermocline level about 20 m thick and forming part of a spiral the mirror image of that described by Ekman (1905) or, for tidal currents, by Hansen (1950).

Evidently, therefore, the spiral structure of the current is not controlled by wind but by the distribution of mass that comes into being when the summer sun shines on the Celtic Sea, on the water over the neighbouring continental slope and on the strongly tidal and shallow English, Bristol and Irish Channels.

Moreover, the recruitment of water to move into the English Channel, properly so-called, was confined between 5° 35′ and 6° 00′ W. long.

The whole argument requires and supports the hypothesis that when the change in density across the thermocline exceeds, say, one sigma-*t* unit, the temperature in the underlying water and in much of the thermocline itself may be treated as a conservative property.

The derivation from continuity of properties should be and is supported by the distribution of mass along the section 48° 20′ N. (Fig. 13). It is evident that the region between 'Sir Lancelot' stations 34 and 28 is one of strong currents or eddies, but, since there can be nothing approaching a surface of no motion and every surface slopes, it would be hazardous to deduce more than this from the geopotential topographies. They have, however, been most helpful in deciding that certain events were not possible.

This account of events associated with the month of August 1950 has had, for clarity, to be presented as though we then had an equilibrium state. Nothing is more certain than that we did not. Two points are at issue.

(*a*) We have traced streamlines between two or more points but the water in question had passed the first position some considerable time before it was observed at the later one. During this period of time the streamline may have writhed like a serpent in all three dimensions of space. Horizontal displacements may have amounted, and probably did, to many miles. Consequently

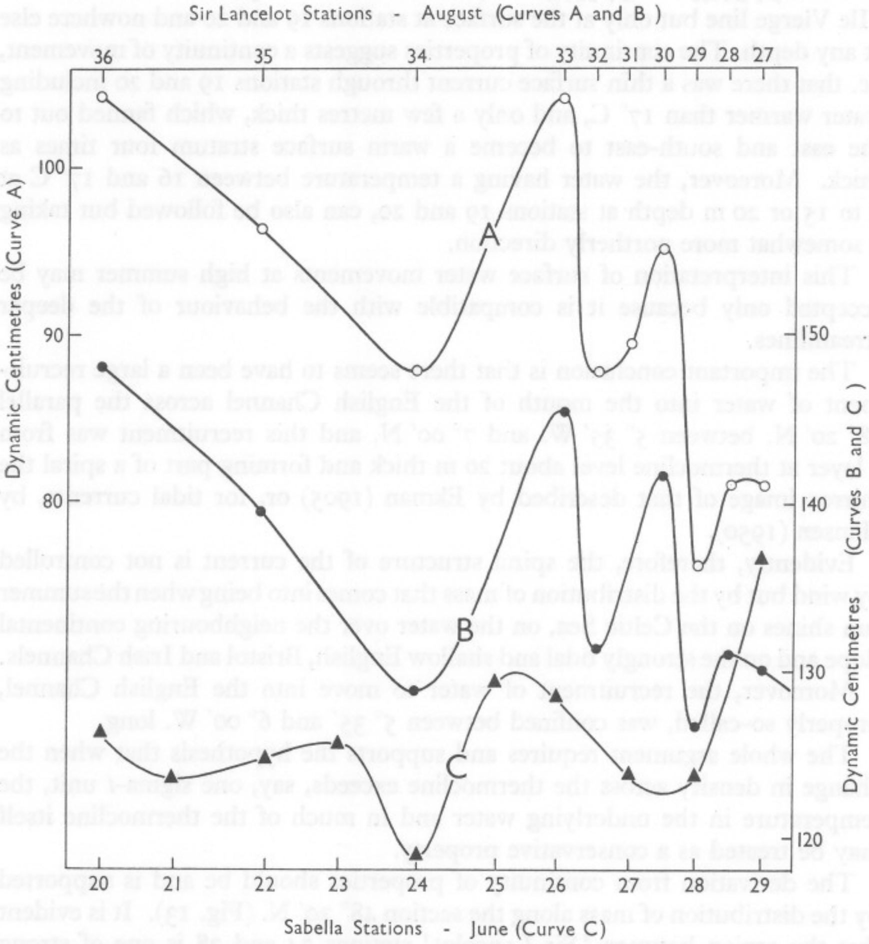

Fig. 13. Geopotential topographies: A, 'Sir Lancelot', 7 August 1950, along lat. 48° 20′ N., 0–50 db; B, the same, 0–100 db; C, 'Sabella', 13 June 1950, west of Ushant, 0–100 db. For station positions see Fig. 3.

at the time any water mass had crossed the parallel 48° 20′ N., its position may have been many miles from the position indicated in August. Streamlines have to be related to the sea water and not to the sea bed over which the water is passing.

(*b*) Smooth uniform flow at any depth in the sea seems to be rare. The bolus concept (Cooper, 1957) first developed for water cascading over a continental slope seems to be equally applicable to current systems over a continental shelf. Movement seems to proceed in surges, carrying boluses of water. Consequently the streamlines described must not be considered as bounding simple geometrical figures. When a surge of water passes, the streamlines bounding a water mass will expand to encompass a large body of water with similar properties. Between surges, the streamlines will close up, even to be nipped out altogether. Then very little of the characteristic water would be present.

In the past we have considered that the warming up during the summer of the deeper water at our station E 1 has been due to turbulent transport of heat vertically across the thermocline. This investigation suggests that this is an unnecessary hypothesis and that the rise in temperature after the thermocline is strongly developed is better explained by transport and sinking of water from the thermocline at and south of lat. 48° 20′ N. The origin of this thermocline, in its turn, now needs to be sought. Since this change of view has considerable biological significance, more work upon it would be wise before we accept it.

Density inversions in August 1950

At all 'Sir Lancelot' stations on 8 August 1950 between numbers 35 and 41 (except 35), there was an apparent density inversion around 75–100 m depth (Table 1) (cf. Spilhaus, Ehrlich & Miller, 1950). The apparent inversion

TABLE 1. DENSITY INVERSION IN SOUTHERN CELTIC SEA IN AUGUST 1950

(Minimum salinity and density in italics.)

	Station no. SL							
Depth (m)	33	34	36	37	38	39	40	41
Temperature (°C)								
50	11·63	11·62	13·66	15·57	11·32	11·02	10·98	10·82
75	11·52	11·56	11·65	11·42	11·28	11·02	11·00	10·82
100	—	11·58	11·63	11·42	11·28	11·02	10·99	—
Bottom	11·51	11·58	11·62	11·42	11·28	11·01	—	10·82
Salinity (‰)								
50	35·44	35·48	35·52	35·44	35·52	35·41	35·44	35·38
75	35·50	35·52	35·55	35·50	35·52	35·48	35·46	35·39
100	—	*35·48*	*35·53*	35·55	*35·46*	*35·44*	*35·44*	—
Bottom	*35·44*	35·50	35·55	*35·46*	35·52	*35·44*	—	*35·36*
Decrease in salinity	0·06	0·04	0·02	0·09	0·06	0·04	0·02	0·03
Density (σ_t)								
50	27·02	27·05	26·68	26·20	27·14	27·11	27·14	27·12
75	27·09	27·09	27·10	27·10	27·15	27·16	27·15	27·13
100	—	*27·06*	*27·09*	27·14	*27·10*	*27·13*	*27·14*	—
Bottom	*27·04*	27·08	27·11	*27·07*	27·15	*27·13*	—	*27·11*
Decrease in density	0·05	0·03	0·01	0·07	0·05	0·03	0·01	0·02
Bottom sample (m)	118	125	148	140	130	125	100	110
Sounding (m)	124	133·5	155·	146	137	134	108	115

is due to changes in salinity rather than temperature. Although the variations in salinity are little greater than the titration error in Knudsen's method, the coherence of the data suggests that we must consider them seriously.

For a static system, the apparent inversion can be true only if we reject the principle of constant composition of sea salt. A dynamic explanation is more probable, namely, that the fast-moving water at thermocline level was associated with considerable water movement immediately beneath. This immediately subthermocline water had the properties of a projectile and so was able to maintain itself for some time above bottom water of slightly lower density.

The 'Discovery II' section in May 1950

The section over the slope between 48° 18′ N., 7° 30′ W. and 47° 24′ N., 7° 52′ W. has already been illustrated and discussed (Cooper, 1952, fig. 14). To quote: 'Assuming only horizontal water movements, the density gradient would indicate a weak east-bound current, flowing along the edge of the slope, in agreement with the current system already deduced for the region by Helland-Hansen and Nansen; but since vertical currents and internal waves may also have played a part no firm conclusions are possible. At least it seems that the impoverished warm saline surface water is more likely to have come from the ocean to the south-west than from the Biscayan shelf to the south-east.'

TABLE 2. EVIDENCE FOR CLOCKWISE BOTTOM CURRENT IN SOUTHERN CELTIC SEA, APRIL–MAY, 1950

Station ...	'Sabella' 16			—	'Discovery' 2654		
Date ...	19 April			19 April	11 May		
Lat. ...	49° 30′ N.			48° 20′ N.	48° 20′ N.		
Long. ...	8° 30′ W.			6° 06′ W.	6° 06′ W.		
Depth ...	140 m				124 m		
Depth sampled (m)	Temp. (°C)	Sal. (‰)	Inorg. P (μg-atom/l.)	Temp. computed by applying latitude correction	Temp. (°C)	Sal. (‰)	Silicate-Si (μg-atom/l.)
50	10·48	35·44	0·39	11·05	10·87	35·44	2·11
100	—	—	—	11·05	10·85	35·43	1·97
120	10·48	35·44	0·38	—	—	—	—

The most striking feature of the section on the shelf (Figs. 3, 14) along the parallel 48° 20′ N. in May was the cold core below 50 m at station 2654 (Table 2). The mean Celtic Sea latitude temperature for 48° 20′ N. (Cooper, 1960) for 3 weeks earlier was 11·05° C. There is no question but that this water was cold for the place and date. Intrusion as a submarine eagre from the south was impossible since the silicate content was only 2·0 μg-atom/l. This cold core can have come only from the north or north-west. The 'Sir Lancelot' sections across the English Channel on 8 April show that such high salinity water could not have come from there. In the 'Sabella' line on 19 April along the parallel 49° 30′ N. (Fig. 16), similar water is recognizable only at station 16 (Table 2).

The low phosphate at the bottom at 'Sabella' station 16 is also incompatible with an 'eagre' component, but the other properties suggest none the less that it must have approached station 16 from west-south-west or south-west.

The bottom configuration severely restricts the possibilities of what a bottom current may do. It is highly probable (Fig. 16) that the movement originated in an inflow over the indentation in the shelf at about 48° 50′ N., 9° 40′ W. (not as an eagre) and that its flow was controlled between the Cockburn, Jones and associated banks on the north-west and north and the Melville Knoll on the south. The Melville Knoll formed a fulcrum around which the current was compelled to turn. Its recognition at station 16 is so explained but, if the current had been streamlined, a greater influence might have been expected at station 15.

We have seen that horizontal currents, like cascading water masses, may tend to break up into writhing boluses. When such a current system is examined by a grid of stations it is a matter of chance whether one samples the core of a bolus or the envelope of water drawn in to fill the constriction between two boluses in sequence. If the bottom current shown in Fig. 16 is accepted, then it is necessary to accept as well the bolus hypothesis for horizontal currents.

The current would seem to have passed close to the position 49° N., 7° W., turning right under the influence of the earth's rotation. Its farther southward passage had then to lie east of Parsons Bank.

The first station on this section, no. 2653, lay 20 miles west of Ushant and could give no evidence as to whether any current was flowing close into Ushant. The surface observation from line 10 (Figs. 2, 3) on the following day at 48° 26′ N., 5° 16′ W., showed such a current at least weakly. The surface water had a density (σ_t) 26·84.

Combining the evidence from the distribution of salinity between 'Discovery' stations 2657 and 2659 and the evidence from the bottom water at station 2654, we have a picture of a current of saline water setting parallel with the break of slope, i.e. towards east-south-east. That none of this water was entering the English Channel in May is confirmed by the total absence of high salinity water ($> 35{\cdot}5‰$) on 'Sabella's' June section a few miles farther north.

An application of this deduction may be to the spawning habits of the hake. The Melville Knoll, according to Hickling (1935), is one of its largest spawning centres. He believes that the success of the spawning depends on the prevailing winds setting the young fish towards the east into shallower water.

The probable set of the bottom current in 1950 suggests something rather different—a drift towards La Chapelle Bank where in June a rich and very characteristic euphausian type of plankton may occur in a narrow band parallel with the slope. The lead, slim though it is, seems worth further study.

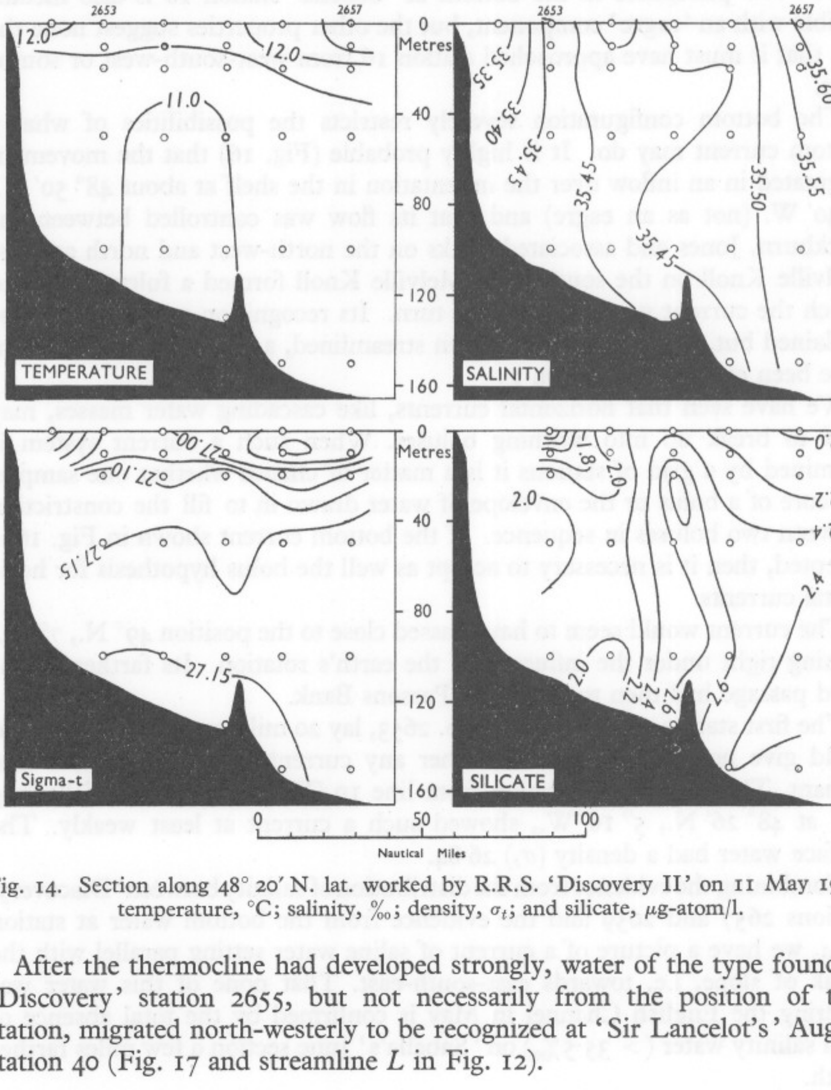

Fig. 14. Section along 48° 20′ N. lat. worked by R.R.S. 'Discovery II' on 11 May 1950; temperature, °C; salinity, ‰; density, σ_t; and silicate, μg-atom/l.

After the thermocline had developed strongly, water of the type found at 'Discovery' station 2655, but not necessarily from the position of that station, migrated north-westerly to be recognized at 'Sir Lancelot's' August station 40 (Fig. 17 and streamline *L* in Fig. 12).

The 'Sabella' section in June 1950

The course west of Ushant on 13 June 1950 is shown in Fig. 3 (p. 179), and the temperature, salinity and density in Fig. 15 (left-hand panels).

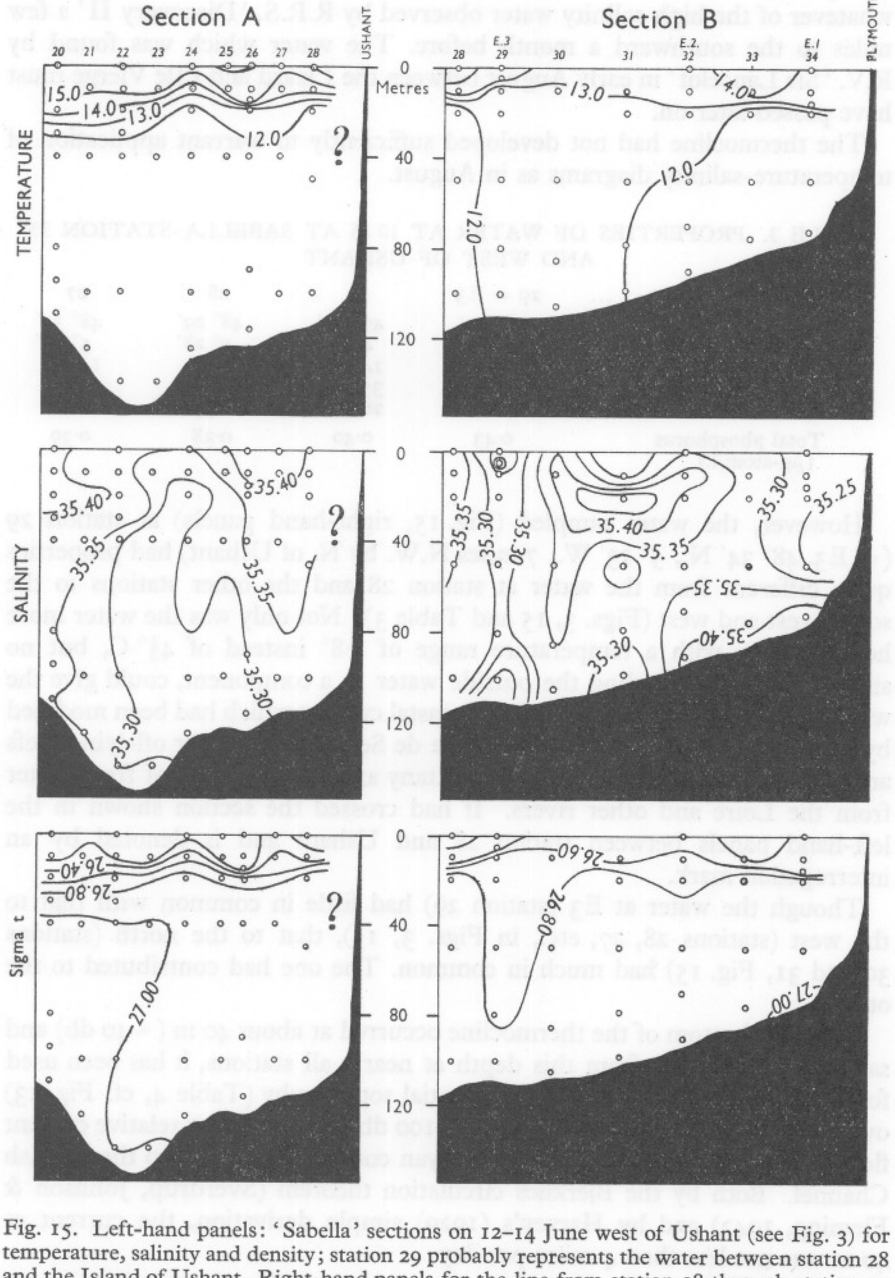

Fig. 15. Left-hand panels: 'Sabella' sections on 12–14 June west of Ushant (see Fig. 3) for temperature, salinity and density; station 29 probably represents the water between station 28 and the Island of Ushant. Right-hand panels for the line from station 28 through station 29 (E 3) to Plymouth.

Except near Ushant the section is rather featureless. There is no evidence whatever of the high-salinity water observed by R.R.S. 'Discovery II' a few miles to the southward a month before. The water which was found by R.V. 'Sir Lancelot' in early August between the Lizard and l'Ile Vierge must have passed later on.

The thermocline had not developed sufficiently to warrant application of temperature-salinity diagrams as in August.

TABLE 3. PROPERTIES OF WATER AT 10 M AT SABELLA STATION 33 AND WEST OF USHANT

Station ...	29 = E3	33	28	27
Latitude N.	48° 34′	49° 45′	48° 29′	48° 31′
Longitude W.	5° 13′	4° 32′	5° 28′	5° 42′
Temperature (°C)	12·74	14·31	14·69	14·59
Salinity (‰)	35·26	35·34	35·38	35·44
σ_t	26·66	26·40	26·35	26·42
Total phosphorus (μg-atom/l.)	0·43	0·40	0·38	0·39

However, the water sampled (Fig. 15, right-hand panels) at station 29 (= E3, 48° 34′ N., 5° 13′ W., 7 miles N.W. by N. of Ushant) had properties quite different from the water at station 28 and the other stations to the south-west and west (Figs. 3, 15 and Table 3). Not only was the water more homogeneous with a temperature range of 1·8° instead of 4½° C, but no simple mixture, including the outside water as a component, could give the water found at E3. This was part of a coastal current which had been modified by turbulent passage over the Chaussée de Sein and the other off-lying reefs and islands along the west coast of Brittany and by admixture of fresh water from the Loire and other rivers. It had crossed the section shown in the left-hand panels between station 28 and Ushant and is denoted by an interrogation mark.

Though the water at E3 (station 29) had little in common with that to the west (stations 28, 27, etc., in Figs. 3, 15), that to the north (stations 30 and 31, Fig. 15) had much in common. The one had contributed to the other.

Since the bottom of the thermocline occurred at about 40 m (~40 db) and samples were drawn from this depth at nearly all stations, it has been used for drawing charts of relative geopotential topography (Table 4, cf. Fig. 13) over the whole area. That for 40 against 100 db shows a strong relative current flowing close to Ushant from the Biscayan coast of Brittany into the English Channel. Both by the Bjerknes circulation theorem (Sverdrup, Johnson & Fleming, 1942) and by Harvey's (1929) simple derivation, the current at 40 m was not less than 4 miles per day.

There is little doubt that this represents a northward moving coastal mid-water current, strongest at 40 m, and not a reverse current strongest at the bottom. The chart for the current at the surface relative to that at 40 m indicates either a surface current towards the south or a current at 40 m towards the north. Here, to reconcile the two charts, the second explanation must be true.

Dissection of geopotential anomalies at stations 29 to 26 (Table 4) shows that the components of relative current were small within the 20–40 m layer and were largely confined to the layers above 20 m and below 40 m, as required by the theory. The maximum strength of the north-flowing current therefore lay somewhere in the 20–40 m stratum.

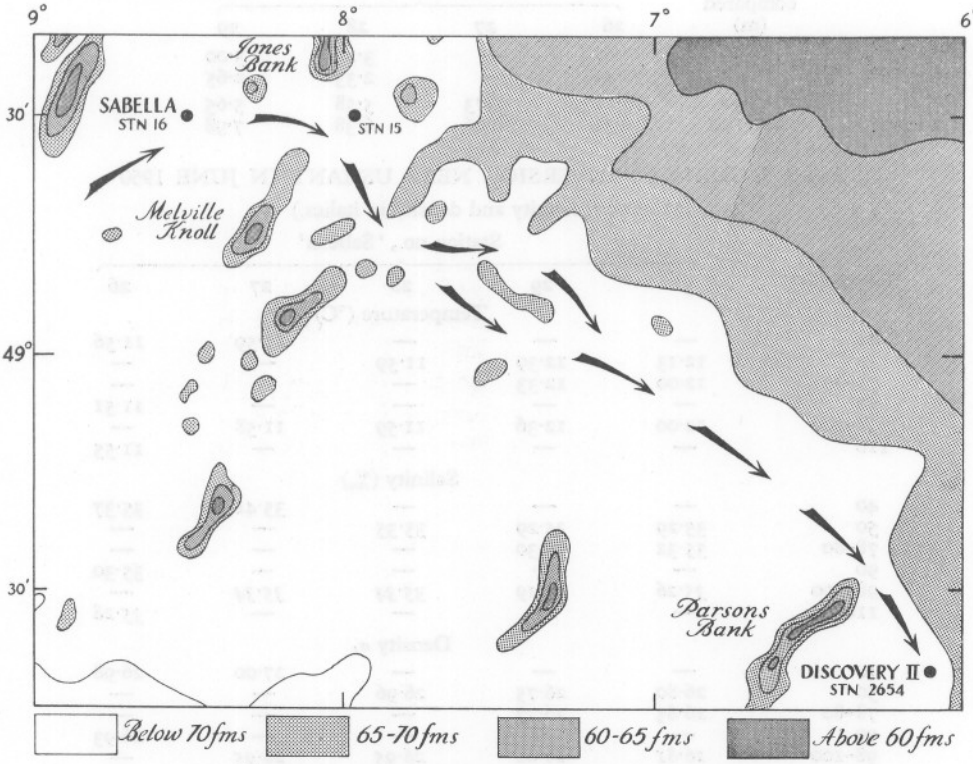

Fig. 16. Probable course of a bottom current in April–May 1950.

Much of the water entering the English Channel at the time had temperature between 12·3 and 12·5° C, salinity about 35·3‰, density (σ_t) about 26·7–26·8, total phosphorus 0·45 μg-atom/l. This warm, nutrient-poor bottom water was found north of Ushant for more than 30 miles. The situation was closely similar to that found north of west Cornwall.

The inflexion in geopotential farther west at station 24 in all curves involving the surface was not shown in the curve for 40 against 100 db. It was due to a shallow (0–20 m depth) current of cold, relatively low-salinity water, but whether this was an eddy from the Ushant corner current or whether it came from the north cannot be decided.

This picture is relative. The whole of the water as far west as 7° 45′ W. was moving slowly northward, a movement which needs to be superimposed upon the relative corner currents at Ushant.

TABLE 4. ANOMALIES OF GEOPOTENTIAL WEST OF USHANT, JUNE 1950, DYNAMIC CENTIMETRES

Depths compared (m)	Station: West			East
	26	27	28	29
0–20	3·67	—	3·25	3·00
20–40	2·45	—	2·33	2·65
0–40	6·12	5·73	5·58	5·65
40–100	6·71	6·66	6·38	7·98

TABLE 5. DENSITY INVERSION NEAR USHANT IN JUNE 1950

(Minimum salinity and density in italics.)

Depth (m)	Station no., 'Sabella' 31	29	28	27	26
	Temperature (°C)				
40	—	—	—	11·59	11·56
50	12·13	12·39	11·59	—	—
78–80	12·00	12·33	—	—	—
90	—	—	—	—	11·51
98–100	12·00	12·36	11·59	11·58	—
116	—	—	—	—	11·55
	Salinity (‰)				
40	—	—	—	35·41	35·37
50	35·29	35·29	35·35	—	—
78–80	35·32	35·30	—	—	—
90	—	—	—	—	35·30
98–100	*35·26*	*35·19*	*35·34*	*35·34*	—
116	—	—	—	—	*35·28*
	Density σ_t				
40	—	—	—	27·00	26·98
50	26·80	26·75	26·96	—	—
78–80	26·85	26·77	—	—	—
90	—	—	—	—	26·93
98–100	*26·81*	*26·68*	*26·95*	*26·95*	—
116	—	—	—	—	*26·91*
Sounding	103	110	115	119	124

No water from westward of the meridian 5° 30′ W., and below 30 m in depth had entered the English Channel. There is some evidence that a little of the surface water of the kind found in the water westward of Ushant (stations 28–26) had reached station 33 (Figs. 3, 15) (Lizard Point 29 miles 209°) on the English side of the Channel. Apart from this no water from west of 5° 30′ W. crossed the Plymouth–Ushant line, a situation very different from that found in August.

In August we had evidence for a density inversion beneath the water moving fastest, so also have we in June (Table 5). On this occasion the fast-moving water and apparent density inversions were both grouped around Ushant. A similar explanation, no doubt, applies.

The sequence of events in the summer of 1950

The prevailing winds of this sea area are from the south-west and west. Such winds will tend to initiate surface currents towards the east and south-east. Wind-induced currents, at greater depths will tend, according to the theory of the Ekman spiral, to set still farther to the south.

Under these conditions there will be no tendency for the wind to set homogeneous water from south of 48° 20′ N. into the English Channel. This agrees with the findings by R.R.S. 'Discovery II' in May.

The same prevailing winds will tend to initiate the same kind of currents in homogeneous water at any time of year, whatever the water temperature, so that these winds should never set water from west of Ushant into the English Channel (cf. Cooper, 1960). Under these conditions recruitment of water into the Channel from the west should be from north of 49° N. lat.

As soon as the thermocline begins to form, the wind will cease to influence the direction of movement of the deeper water. This will tend to move solely in accordance with the distribution of mass over the whole of the Celtic Sea, its bounding continental slope and the English, Bristol and Irish Channels.

As an empirical finding we can say that as the summer advanced the direction of movement of the deeper water in 1950 changed. The north-easterly movement first appeared in June as a coastal current around Ushant from the west coast to the north coast of Brittany.

As the thermocline strengthened, the site of the current entering the English Channel moved westwards. Water bound towards the English Channel was then confined to a thermocline layer about 20 m thick and crossing the parallel of latitude 48° 20′ N. between 5° 35′ W. and 7° 00′ W. That part bound for the English Channel east of the Lizard headland was restricted to the range of longitude 5° 35′–6° 00′ W. This current impinged on the north-western corner of Ushant.

At any time of year, heavy rainfall over western France and consequent river outflow to the sea will lead to a strong coastal current around Ushant. This will over-ride or supplement the circulation arising from the heat balance in the water to the westward and northward.

This reconstruction needs confirmation. It will be difficult to extract from our earlier records since our standard stations are too far apart. It would not have been possible to deduce this account if we had had data only from 'Sir Lancelot' August stations no. 25 and 34 and from 'Sabella' June stations 29 and 23, equivalent to international stations E3 and E4.

The influence of these events on the English Channel as a whole and comparison with other years (Matthews, Lumby and Harvey) will be deferred. Preliminary comparison with the work of Dietrich (1950) has already been made. Further comparison is best achieved not by argument here but by seeking more measurements.

A comparison with the distribution of biological indicators is also deferred but mention may be made of the close parallel with Russell's (1935) findings. In his fig. 4 he sets out the arrival of south-western water off Plymouth in mid-August, 1930, 1931, 1932, in July 1933 and September 1934.

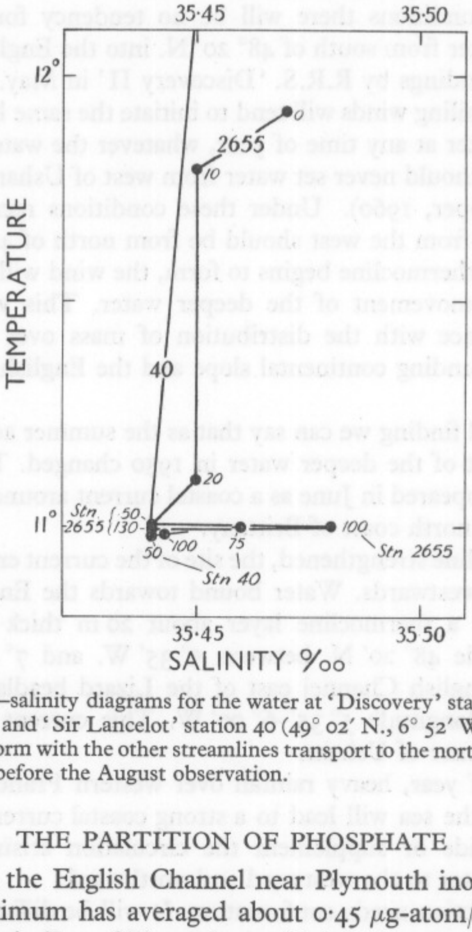

Fig. 17. Temperature–salinity diagrams for the water at 'Discovery' station 2655 (48° 20′ N., 6° 34′ W. on 11 May) and 'Sir Lancelot' station 40 (49° 02′ N., 6° 52′ W. on 8 August 1950); streamline *L*. To conform with the other streamlines transport to the north must have occurred mostly in the month before the August observation.

THE PARTITION OF PHOSPHATE

For many years in the English Channel near Plymouth inorganic phosphate at the winter maximum has averaged about 0·45 μg-atom/l., three-quarters of that available in the Bay of Biscay from which by a more or less direct route the water of the English Channel is recruited. It has long been a problem as to how 0·15 μg-atom/l. of inorganic phosphate or so is permanently removed from the water.

The present study provides the answer for about half of this. In 1950 we hoped that total phosphorus would prove a more nearly conservative property than inorganic phosphate; it also has the advantage of not requiring analyses to be made at sea. It has not proved conservative, so that analysis of total phosphorus has lost favour. Samples from 10, 20 and 50 m and greater depths were sampled by R.V. 'Sir Lancelot' on the cruise of August 1950 and analysed at the Plymouth Laboratory by Harvey's methods by Mr F. A. J. Armstrong.

Due to the problems of particulate distribution of phosphorus in living organisms and in detritus (seston) (cf. Cooper, 1948, for the parallel problem with iron), analyses of total phosphorus are less reproducible than those of inorganic phosphate. None the less, the August 1950 analyses are sufficiently precise to make my point.

First, let us consider all the analyses of total phosphorus at stations 30–34 between which at thermocline level water was entering the western English Channel. The mean of the eighteen analyses of bottom water below the thermocline is at 11·67 ± (S.D.) 0·09° C and 0·62 ± (S.D.) 0·04 μg-atom/l. of total phosphorus. This is taken as a measure of the winter stock of total phosphorus available to enter the Channel. It may be somewhat lower than the average.

There is another cluster of nine analyses on the warm upper water with mean at 17·75 ± (S.D.) 0·20° C and 0·305 ± 0·02 μg-atom/l. total phosphorus. The straight line which joins the two centres of gravity leaves three analyses within the thermocline about 0·02 μg-atom/l. to the right.

This straight line has been used to estimate what the total phosphorus content in the deeper water at stations 25–18 and 45–43 should have been if it had suffered no change during passage from the thermocline at latitude 48° 20′ N. to the observed position (Table 6, col. 3). In the next column (col. 4) is given the content of total phosphorus observed. Column 5, representing the loss by thermocline partition, is the difference between 0·62 μg-atom/l. and the computed value in col. 3.

At the stations near Ushant (25–23) where the time of travel was short and there was no opportunity for further partition, the computed and observed values agree well. The loss unaccounted for is small. As, however, we go northward and the travel time of the water becomes greater, the loss in total phosphorus unaccounted for becomes greater. A calculation in terms of density instead of temperature gives a similar result.

The physical partition occurring at the thermocline at 48° 20′ N. therefore accounts for about one-half of the loss regularly observed off Plymouth. The fate of the other half will be considered when the physical and chemical oceanography of the English Channel in 1950 comes to be published.

TABLE 6. LOSS OF TOTAL PHOSPHORUS ON PASSAGE BETWEEN THE BAY OF BISCAY AND THE WESTERN ENGLISH CHANNEL

Station, 'Sir Lancelot'	Depth (m)	Total phosphorus (μg-atom/l.)			
				Loss of ΣP	
		Computed graphically	Observed	By thermocline partition	Unaccounted for
25	50	0·55	0·53	0·07	0·02
	75	0·57	0·54	0·05	0·03
	100	0·59	0·56	0·03	0·03
24	50	0·52	0·57	0·10	−0·05
	90	0·53	0·53	0·09	Nil
23	50	0·49	0·47	0·13	0·02
	88	0·50	0·50	0·12	Nil
22	50	0·51	0·46	0·11	0·05
	92	0·53	0·51	0·09	0·02
21	50	0·51	0·46	0·11	0·05
	94	0·53	0·50	0·09	0·03
20	50	0·53	0·46	0·09	0·07
	87	0·54	0·50	0·08	0·04
19	50	0·56	0·43	0·06	0·13
	80	0·56	0·47	0·06	0·09
18	50	0·58	0·48	0·04	0·10
	73	0·58	0·49	0·04	0·09
46	—	—	No analyses	—	—
45	50	0·60	0·52	0·02	0·08
	70	0·60	0·54	0·02	0·06
44	50	0·59	0·49	0·03	0·10
	80	0·60	0·54	0·02	0·06
43	85	0·59	0·52	0·03	0·07

ON PRESENTATION

This paper has been difficult to write and may prove even more difficult to read. None the less it is a foretaste of what may come apace when the increasing application of the salinometer makes it possible to unravel certain movements of stratified waters in great detail. Biologists need such information but, confronted with it, may recoil in horror. Physical oceanographers may therefore need to consider how they can systematize the extraction and presentation of the desired information. Probably diagrams, such as Figs. 4–7 presented here solely to illustrate a worked example, should be pigeon-holed when they have served their turn and publication restricted to diagrams such as Figs. 9 and 12 and the minimum of textual description. It may be necessary to develop a block diagram form of presentation on the lines of Fig. 8. The possibility of criticism should have vanished so that conclusions would need to be taken on trust. Comment will be appreciated.

The author is greatly indebted to Mr G. A. W. Battin for his excellent illustrations. Without these the paper would have been even more turgid.

He is also grateful to Lt.-Cdr. C. A. Hoodless, D.S.C., R.N.R., then master of R.V. 'Sabella', and his crew for much help in 1950; also to Mr David Vaux of the Lowestoft Laboratory for making data and diagrams of 'Sir Lancelot's' cruises quickly available.

SUMMARY

The currents around a prominent headland, the island of Ushant between the Bay of Biscay and the English Channel, are discussed.

The flow in the spring of 1928 has been re-examined. Run off from the Loire watershed reached Ushant in March. North of Ushant it spread out before passing up the English Channel on the French side. Some of this water spread northwards from Guernsey towards England and reached the neighbourhood of Plymouth by mid-April and the Seven Stones Light Vessel a fortnight later, i.e. the flow was cyclonic within the western bight of the Channel and took about 10 weeks to travel from Ushant to Land's End at a rate over the ground of 3 miles a day.

In May 1950 currents in the southern Celtic Sea were setting east-south-east parallel with the slope. No water there was moving towards the English Channel in May and June. The bearing of this result on successful hake spawning is briefly discussed.

In June 1950 a narrow coastal current, strongest at about 40 m depth, was setting round Ushant and fanning out in the English Channel north of Brittany; however, no water from west of 5° 30′ W. long. was then entering the Channel near Ushant.

Once the thermocline had become well established the pattern of currents changed completely, as shown by closely spaced stations worked by R.V. 'Sir Lancelot' in August. The salinities have the greatest precision attainable by the Knudsen technique and have made possible a detailed study of current streamlines. It is assumed that properties beneath the thermocline were conservative. Using temperature–salinity diagrams, a sheaf of streamlines has been constructed which, except for 1 salinity out of about 120 which are relevant, form a completely coherent pattern. There was a large recruitment of water into the mouth of the English Channel across the parallel 48° 20′ N. between 5° 35′ W. and 7° 00′ W., and this recruitment was from a layer at thermocline level about 20 m thick. The deeper water followed the streamlines, *A–F* and *H* in Fig. 12. These thermocline waters were undergoing a partition, the shallower waters setting to the right of the deeper and sinking while so doing (streamlines *G*, *P* and *Q*). This mechanism explains in part the excessive warming up of the south-western English Channel to which Dietrich drew attention. There is an apparent conflict with some of the German conclusions which will need further sea work to resolve.

This mechanism accounts for about one-half of the impoverishment in

phosphate observed as between the Bay of Biscay and the winter maximum in the English Channel.

Slight density inversions occurred in June and August.

In order that the conclusions may be fairly criticized much intricate scaffolding has had to be presented. This may have obscured the results of interest to biologists.

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Printed in Great Britain

MASSIVE UPWARD DISPLACEMENT IN THE DEEP OCEAN

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The Plymouth Laboratory

(Text-figs. 1 and 2)

For a third of a century many and varied studies on sea water have been concentrated upon a single accessible shallow-water station in the English Channel, E1, supplemented by more extensive excursions usually designed to test working hypotheses. This concentration of effort has been richly rewarded. In deep-water oceanography a similar approach is appropriate; a standard station, 'Cavall' has therefore been selected in the north-eastern Bay of Biscay in 4700 m of water at lat. 46° 30′ N., long. 8° 00′ W., nominal, a position worked by the Danish Research Vessel 'Dana' in 1922 and 1930. It is not only the nearest deep water position to Plymouth but it has best possible coverage by the Decca Navigator system. For our experimental programme it is essential that the station positions be maintained and repeated precisely. To achieve this a working Decca chartlet (Fig. 1) on a scale of 1:20,000 has been prepared for each station from a portion of the Admiralty Decca Lattice chart no. L 1104. On this a circle of radius one mile is inscribed. Throughout operations the ship is maintained within this circle by stopping work when necessary and steaming back on Decca co-ordinates towards the centre, or beyond to pre-compensate expected drift.

On a number of occasions the deep-water station Cavall has been fixed astronomically. The position found is 6 km from the nominal. The discrepancy may arise from error in the 50-fold expansion of the small scale chart or from distortion of the Decca Lattice over the sea area. It is of no practical consequence so that, although a correction could now be made, to do so would lead only to confusion. In station lists and precision statements the astronomical fix, 46° 27′ N., 8° 02′ W., will need to be reported but in descriptive statements the easily remembered nominal position will continue to be used. In both cases the over-riding definition is by Decca co-ordinates: Red G 21.55, Green D 44.90, which alone matter for navigation.

Two more standard stations (Table 1) have been established on course from Plymouth over the continental slope of La Chapelle Bank and one precisely at the break of slope which is very sharp (Cartwright, 1959, Fig. 2, upper). A further shallow water station over the Bank is sometimes worked 9 miles within the break of slope.

It has become essential to have convenient names for these stations and I have selected some from Celtic mythology.

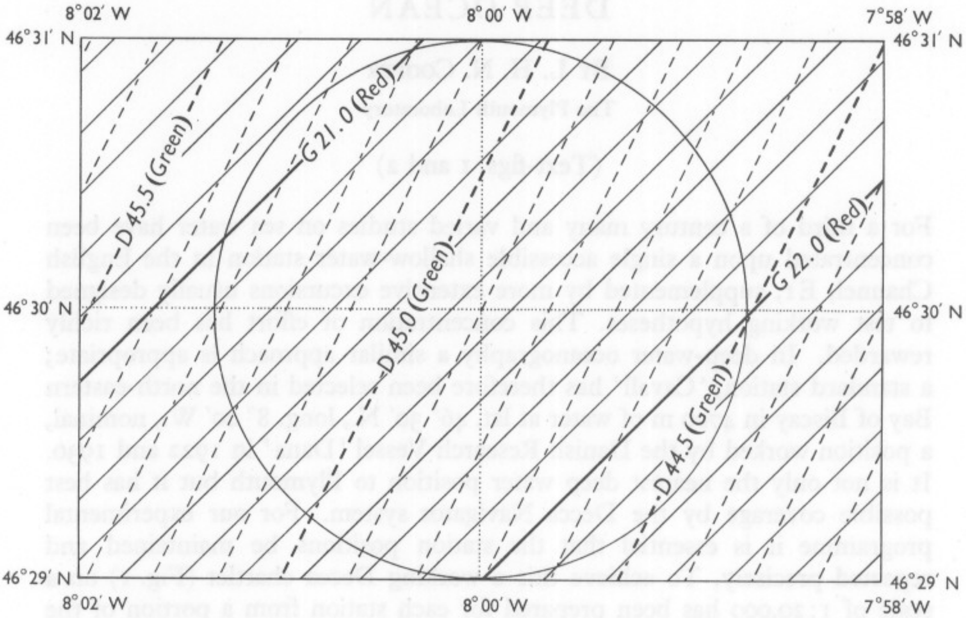

Fig. 1. Working chartlet (scaled 1:20,000) used for maintaining station Cavall within a circle of radius 1 mile using the Decca Navigator system.

TABLE 1. POSITION OF STANDARD STATIONS, BAY OF BISCAY AND LA CHAPELLE BANK

	Nominal position		Astronomical position		Decca Co-ordinates		
Station	Lat. N.	Long. W.	Lat. N.	Long. W.	Red	Green	Depth (m)
Geraint	47° 45′	7° 05′	Not known		F 22.20	D 45.00	—
Ysolde	47° 35′	7° 12′	Not known		G 02.50	D 44.60	175–185
Arthur	47° 30′	7° 18′	Not known		G 03.69	D 45.57	Variable 800–1400
Bedivere	47° 20′	7° 22′	Not known		G 08.46	D 44.28	Variable 3100–3800
Cavall	46° 30′	8° 00′	46° 27′	8° 02′	G 21.55	D 44.90	4710

UPWARD DISPLACEMENT

Views already published (Cooper, 1955*a*, *b*, 1956; cf. Dietrich, 1956) require that room for the water sinking into the eastern North Atlantic from the Iceland–Faroe Ridge may be found only by upward displacement somewhere or other of water already there. In any one year it was envisaged that this effect would not exceed 7–10 m and that northern water was most unlikely to intrude at the very bottom of the ocean. The 1956 programme was designed

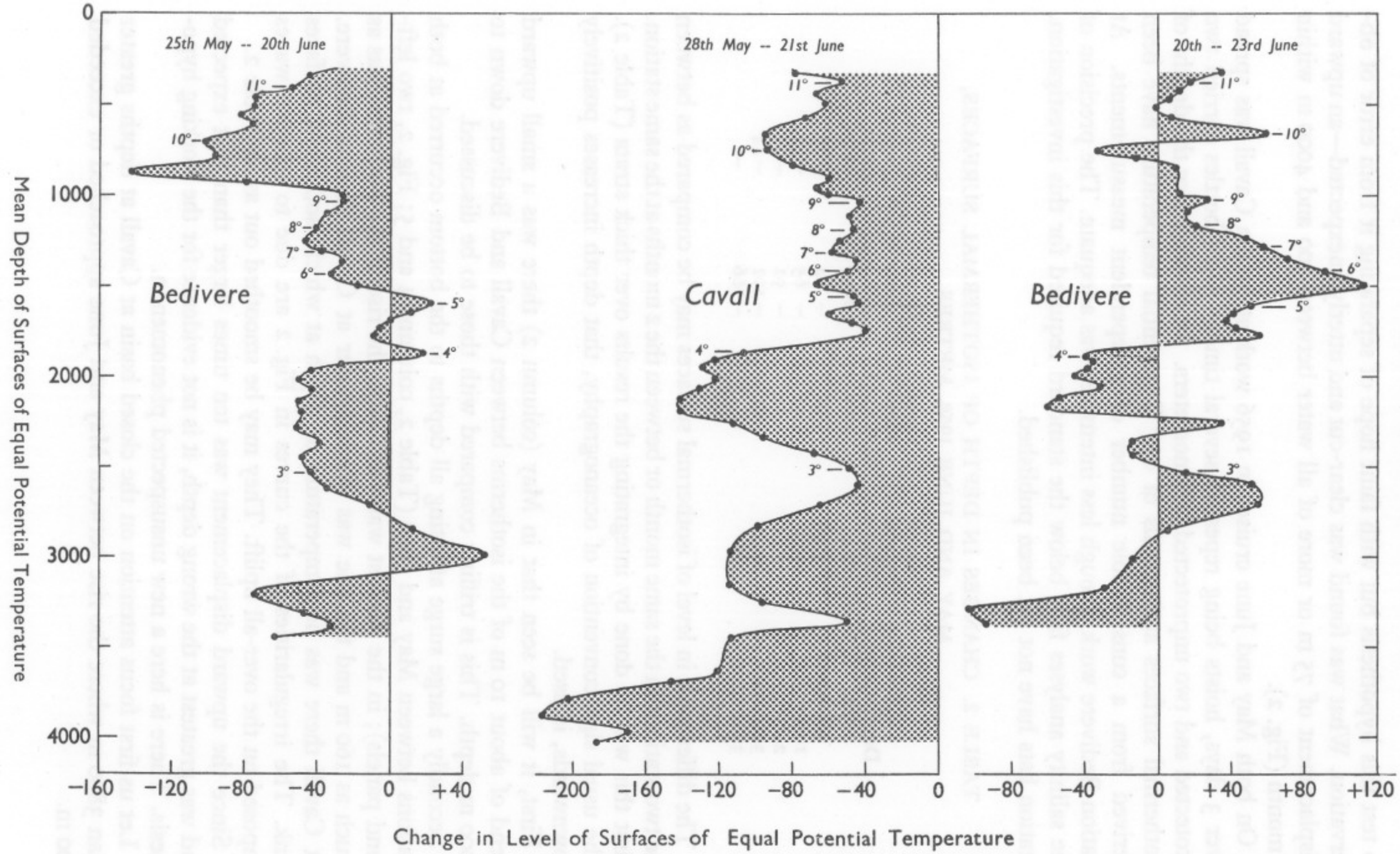

Fig. 2. Changes in level of surfaces of equal potential temperature in the Bay of Biscay, May and June 1956, plotted against weighted mean depths of the surfaces. All depths and levels in metres.

to test this hypothesis but with faint hope of separating it from error of observation. What was found was clear-cut and utterly unexpected—an upward displacement of 75 m or more of all water between 300 and 4000 m within a month (Fig. 2).

On both May and June cruises in 1956 work at station Cavall was spread over 3 days, hoists being repeated several times. Most bottles carried two protected and two unprotected thermometers. In consequence the depths of isothermal surfaces at intervals of 0·1° C potential temperature have been derived from a considerable number of independent measurements. At station Bedivere work, though less intensive, was adequate. The precision of the salinity analyses falls below the standard required for this investigation. Station lists have not yet been published.

TABLE 2. CHANGES IN DEPTH OF ISOTHERMAL SURFACES, MAY AND JUNE 1956, METRES

Depth range (m)	Cavall minus Bedivere: May	Cavall minus Bedivere: June	Cavall: June minus May	Bedivere: June minus May
300–1000	+13	+18	− 74	−79
1000–2000	+ 6	−42	− 65	−17
2000–3000	+12	−52	− 91	−27
3000–3500	− 4	−61	−101	−44
3500–4000	—	—	−166	—

The differences in level of isothermal surfaces may be compared as between the two stations in the same month or between the 2 months at the same station. First this will be done by integrating the results over thick strata (Table 2). The usual sign convention of oceanography, that depth increases positively downwards, is used.

First, it will be seen that in May (column 2) there was a small upward trend of about 10 m of the isotherms between Cavall and Bedivere down to 3000 m depth. This is trifling compared with those to be discussed.

Secondly a large surge affecting all depths to the bottom occurred at both stations between May and June (Table 2, columns 4 and 5; Fig. 2, two left-hand panels); in the deepest water at Cavall the rise in the isotherms was as much as 160 m and the rise was much greater at Cavall than at Bedivere. At Cavall there was no temperature or depth at which isothermal surfaces sank. The irregularities of the curves in Fig. 2 are due to internal waves imposed on the over-all uplift. They may be smoothed out as in Table 2.

Since the upward displacement was ten times larger than that expected and was greatest at the wrong depth, it is not evidence for the working hypothesis. There is here a new unsuspected phenomenon.

Let us first focus attention on the closed basin at Cavall at depths greater than 3800 m where the rise between May and June approached or exceeded 200 m.

First, let us assume that some kind of abyssal surge, internal wave or seiche occurred within the basin. If so the isotherms on the south-western side of the basin should have been falling while those on the north-eastern were rising. The event occurred where small changes in temperature and of salinity so nearly compensate each other that the abyssal water within very narrow limits is in neutral dynamic equilibrium. In such water it is difficult to visualize any kind of wave or seiche. Oscillations would seem to involve large changes in momentum though the energy involved must be very small, much too small to lift an overlying body of water, 3500 m thick through 70–100 m. This first assumption therefore is highly improbable.

Secondly, let us assume that a new supply of very heavy water entered the basin upwardly displacing the water already there. On this explanation, the maximum upward displacement at a mean depth of about 3900 m was about 210 m. This explanation requires rapid transport of a very large volume of water from an unknown source. It could provide the means of uplifting all the overlying water. The content of silicate does not agree with recruitment of much water from the north. The existence of the Mid-Atlantic and Walvis Ridges would make it difficult for a large scale flow of water to have come from the far south. The second assumption, in this form, is as improbable as the first. It can be modified to yield a third assumption.

Thus, thirdly, let us assume that the basin of the eastern North Atlantic may exhibit large-scale oscillations and displacements of water which affect all of it at once. The oscillations of the deepest waters would then be not a cause but a consequence of the massive displacements of the overlying more strongly stratified waters.

The least controversial explanation of the observations is therefore that within the 3 weeks between the May and June cruises we witnessed a massive oscillation of the whole of the eastern North Atlantic with a displacement of water at all depths between about 300 m and the bottom, reminiscent of the internal tide waves discussed by Defant (1950). On this view the massive oscillation was part of an equilibrium long-period tide, probably the lunar fortnightly or lunar monthly constituent (Doodson & Warburg, 1941, p. 49). In the 3 days between 20 and 23 June at station Bedivere, the movement of isothermal surfaces was predominantly downwards (Fig. 2, right-hand panel); this phasing rather favours the lunar fortnightly tide. As Defant pointed out, internal tide waves gravely interfere with the design of experiment in the deep ocean since the amplitudes of motions due to internal tides may be larger than those of the displacement phenomena we wish to study.

My hypotheses to explain the enrichment in the 1920's of the English Channel with nutrients require first that there should have been a long-period upward displacement of nutrient levels in the eastern North Atlantic, and that secondly there should have been an intensification of the internal waves beating against the continental slope. On a first appreciation the upward displacement of about 75 m in May–June 1956 provided very strong evidence. But as time passed, no consequent enrichment of the waters of the English Channel followed so that, it would seem, such massive upward displacements may be commonplace and may not provide an explanation of the enrichment of the English Channel in the 1920's.

Again, since the sea surface cannot be displaced upwards by more than a few centimetres, the upwardly displaced water had to escape as horizontal currents at depths between the surface and 300 m, so influencing the pattern of surface currents in the Bay of Biscay. If the deep oscillation was tidal, the consequent pattern of surface currents was also tidal and should be identifiable with a harmonic component in tidal analyses around southwestern Britain.

TABLE 3. CHANGE IN POTENTIAL TEMPERATURE WITH TIME

Depth	Caribbean, March 1933 to December 1954	Bay of Biscay, 28 May to 21 June 1956	Ratio: Biscay/ Caribbean
1500	+0·047	−0·45	− 9·6
1600	+0·036	−0·21	− 5·8
1750	+0·024	−0·15	− 6·3
2000	+0·015	−0·13	− 8·7
2500	+0·008	−0·08	−10
3000	+0·005	−0·08	−16

If we were dealing solely with upward displacement the concentration of oxygen, phosphate and silicate would have moved precisely with temperature. This was not so at any depth. Consequently upward displacement must have been accompanied by considerable horizontal displacement.

Worthington (1955) published observations to suggest that the deep water of the Caribbean is warming up (Table 3). By the same argument the Bay of Biscay would be cooling down very fast. The fall in temperature within 24 days in the summer of 1956 was ten times larger that the rise within 21 years in the Caribbean. Table 3 points the need for great caution in assessing long-term changes in the deep ocean from the scanty data we have.

SUMMARY

A set of 'standard' stations has been established in the Bay of Biscay and related to the grid of the Decca Navigator system. Whilst on station the ship is maintained within a circle of radius 1 mile.

In May and June 1956 repetitive hoists were made to the bottom at station Cavall (4700 m deep) and Bedivere at the foot of the continental slope. In 3 weeks there was a large upward displacement of all isotherms, averaging about 40 m at Bedivere and 80 m at Cavall, over all depths between 300 and 3500 m. The upward displacement was even greater at 3500–4000 m depth.

Oscillations in the ocean abyss and inflows at the bottom of Arctic and Antarctic waters are examined and dismissed as likely explanations. The least

controversial explanation is that a massive oscillation of the whole of the eastern North Atlantic occurred in June 1956. This may have been a long period tidal phenomenon.

At standard depths the fall in temperature in 24 days was ten times greater than changes in the Caribbean reported as evidence for long-term warming-up of the ocean.

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Printed in Great Britain

THE VERTICAL DISTRIBUTION OF CHLOROPHYLL[1]

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(Text-figs. 1–7)

The vertical distribution of chlorophyll in the sea generally shows a maximum concentration at a depth which may vary from at or just below the surface, to near or below the bottom of the euphotic zone. The easiest distributions to explain are those where the maximum chlorophyll concentration is at or very near the surface. These are found when a population is photosynthesizing actively during the first stages of an outburst, and the distribution corresponds roughly with the change with depth of the photosynthetic rate (Steele, 1957). However, these form a small proportion of observations, probably because outbursts are usually restricted to comparatively short periods of time. The more usual distributions show a maximum in the chlorophyll concentrations well below the surface and below the depth of maximum photosynthesis.

Such features are normally explained by the sinking of plants and a sinking rate constant with depth is used in the mathematical models of Riley, Stommel & Bumpus (1949) to explain some observed patterns of vertical distribution. However, on the basis of their model, the chlorophyll maximum must occur above the compensation depth. Although many of the maxima are of this type, there are as many which occur below or just at the compensation point and so are not explicable by a constant sinking rate. In particular, this feature is the dominant one in the distributions found during summer by the Woods Hole Oceanographic Institution in waters off New York (Ketchum, Ryther, Yentsch & Corwin, 1957; Ryther & Yentsch, 1958; Yentsh & Vaccaro, 1958). This work is concerned with a possible explanation for such distributions.

THE OBSERVED DISTRIBUTIONS

Two examples of chlorophyll distribution in which the maximum concentration was found near the compensation depth are given in Table 1, which includes simultaneous observations of the ^{14}C *in situ* rate of photosynthesis, and the concentrations of nitrate and phosphate in water. Crawford station

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[1] Contribution no. 1078 from the Woods Hole Oceanographic Institution. This work was supported in part by A.E.C. Contract AT (30–1) 1918.

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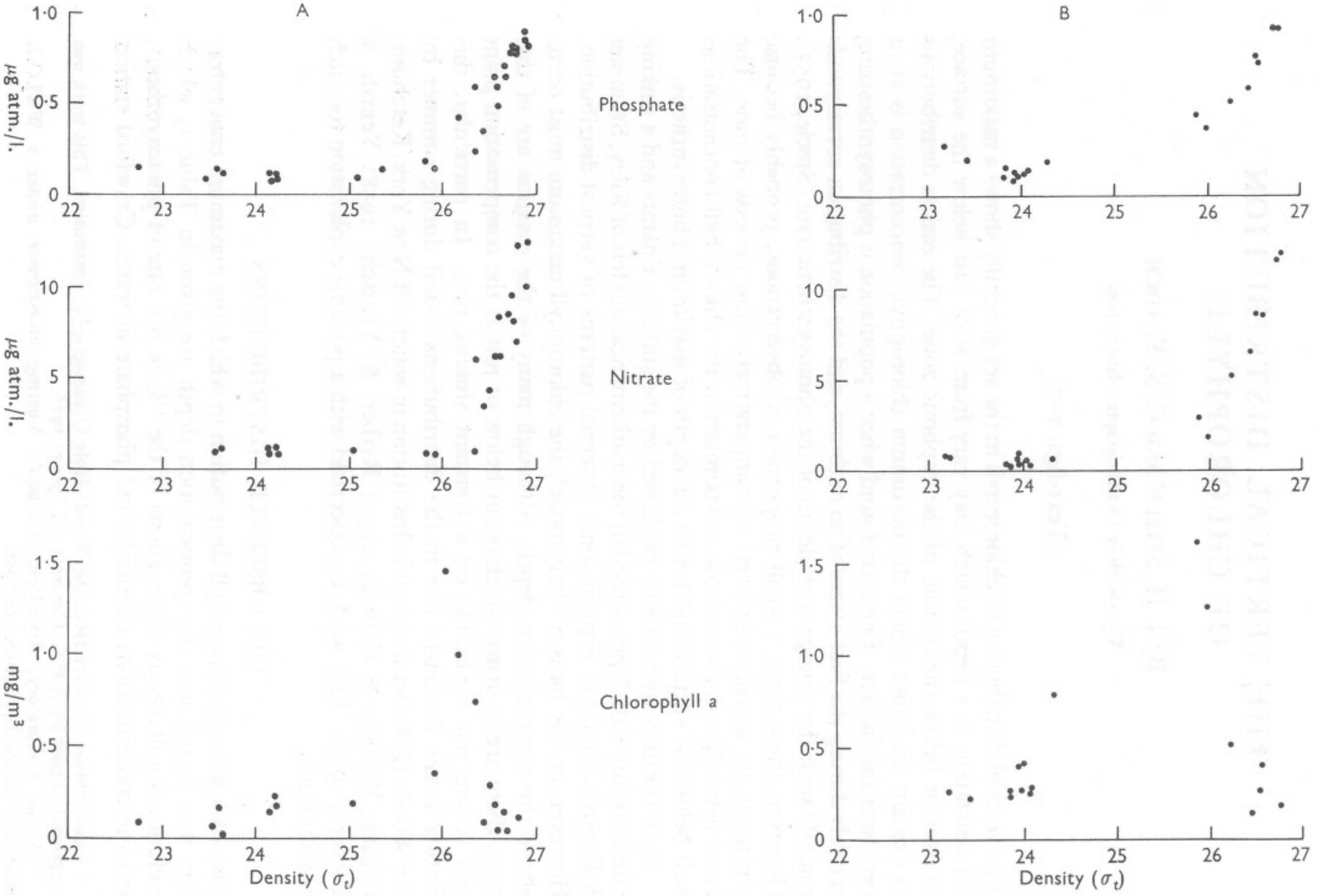

Fig. 1. Observed conditions in July (A) and September (B) 1957.

no. 194 was occupied where the total depth was 3000 m and the other station (Crawford no. 209) was in water with a depth of 40 m.

For four offshore stations in depths greater than 1000 m the relations between nitrate, phosphate and chlorophyll in July and September 1957 are shown in Fig. 1 by plotting these against density. The July chlorophyll values suggest a very sharp peak at $\sigma_t = 26$, but the September values do not have enough observations in the middle range of density to determine the sharpness. In all cases the high values are found at 50 m, although there are some stations at which no pronounced peak is found; this is probably due to the wide spacing of the sampling depths and the comparative sharpness of the peak. The occurrence of the peak in both July and September and the similarity of the nutrient distributions suggest that conditions during this interval can be considered to approximate a steady state. Perhaps the most convincing evidence that the depth of the mean daily euphotic zone is near these peaks is shown by the concentrations of nutrients which increase sharply at about the same depth. The ^{14}C data can be used to define the depth distribution of production. It appears that the compensation point at station 194 must be just below 50 m and the 1 % light level was found at 58 m. At the shallower station the compensation depth was between 20 and 30 m and the 1 % level was at 19 m.

THEORETICAL DISTRIBUTIONS

The purpose of these theoretical considerations is to show how the sinking rate interacts with other factors affecting vertical distribution of plants, and how a variable sinking rate can produce idealized distributions similar to those described above. These concepts do not explain how this decreasing sinking rate could be brought about and since the main possible explanation is in terms of the effect of density, the theoretical relations between size, shape and density will be considered.

Since sinking is only one factor which can affect the vertical distributions of plants, the effects of variations in this rate must be linked with other factors —photosynthesis and respiration of the plants, grazing by herbivores and vertical mixing of the water. These five variables have been combined in a mathematical form by Riley *et al.* (1949). Assuming a sinking rate that is constant with depth, z, the equation for a steady state is

$$A\frac{\partial^2 p}{\partial z^2} - v\frac{\partial p}{\partial z} + (w-h)\,p = 0, \qquad (1)$$

where p is the plant concentration, A is the coefficient of eddy diffusivity, v is the sinking rate, w is the photosynthetic rate and h is the combined effect of grazing and plant respiration. For a maximum concentration of plants, p

$$\frac{\partial p}{\partial z} = 0 \quad \text{and} \quad \frac{\partial^2 p}{\partial z^2} = \left(\frac{h-w}{A}\right) p < 0.$$

The latter holds only for $w > h$, that is when the photosynthetic rate exceeds the combined loss due to respiration and grazing. Thus for a constant sinking rate the maximum must occur above the mean daily compensation depth. This conclusion is independent of variations with depth in grazing or mixing. (Although it can be seen from this how decreased mixing tends to increase the sharpness of the maximum.)

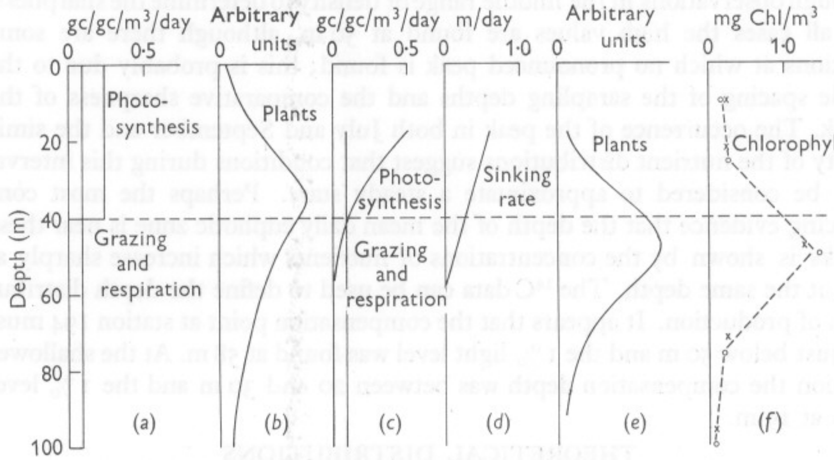

Fig. 2. (*a* and *b*) Conditions from the theory of Riley *et al.* (1949), using a constant sinking rate. (*c*, *d*, *e*) Conditions with a variable sinking rate. (*f*) Data from Station 194.

On this basis, Riley *et al.* (1949) constructed profiles of vertical plant distributions. With their solution, the deepest possible maximum will be given when a constant photosynthetic rate throughout the euphotic zone is assumed, Fig. 2(*a*). Constant sinking, grazing and respiration rates throughout the water column are assigned. With a sinking rate of 3 m/day and numerical values for the other factors corresponding roughly to the offshore conditions, the example in Fig. 2(*b*) is obtained. Its disadvantage is that the form of the photosynthetic coefficient is unrealistic and biases the plant maximum downwards.

If a variable sinking rate is introduced, (1) takes the form

$$A\frac{\partial^2 p}{\partial z^2}-v\frac{\partial p}{\partial z}+(w-h-v^1)\,p = 0, \tag{2}$$

where v^1 is the rate of change of the sinking rate. Then a maximum occurs when

$$\frac{\partial p}{\partial z}=0 \text{ and } \frac{\partial^2 p}{\partial z^2}=\left(\frac{h+v^1-w}{A}\right)p<0,$$

i.e. when $-v^1 > h-w$. This permits a maximum below the foot of the euphotic zone.

Thus a decreasing sinking rate is not only a possible means of securing a maximum at or below the compensation depth, which is fairly obvious; it is also the only way it can be achieved in terms of the variables considered here.

As an example of the kind of profile that can be obtained in the thermocline region offshore, a solution of (2) was constructed with a linearly decreasing sinking rate and a more realistic photosynthetic rate as shown in Fig. 2(*c*) and (*d*). The zero sinking rate has been set at 58 m so that the balance between photosynthesis and grazing plus respiration, the compensation depth of the community, occurs at nearly the same depth as in Fig. 2(*a*) and is indicated by a dashed line. This leads to the profile given in Fig. 2(*e*). The data from station 194 are shown for comparison in Fig. 2(*f*). This example shows how a decreasing sinking rate depresses the chlorophyll maximum to below the compensation depth of the community. It also provides a value for the decrease in sinking rate that is required to give a profile similar to those observed.

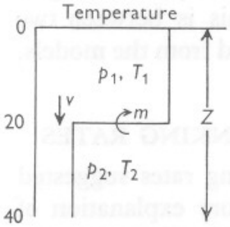

Fig. 3

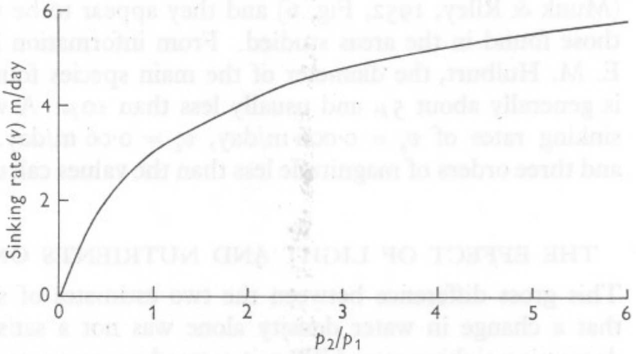

Fig. 4

Fig. 3. Idealized inshore distribution of temperature (T_1, T_2), plants (p_1, p_2), zooplankton (Z) with mixing (m) and sinking (v) between the layers.

Fig. 4. Relation between sinking rate and ratio of plant concentrations in lower and upper layers.

A second theoretical example corresponding to inshore conditions can be constructed by considering a sea 40 m deep divided into two equal layers, Fig. 3, with a positive sinking rate v in the upper layer and zero rate in the lower; this gives the relation between v and the ratio p_2/p_1 shown in Fig. 4. It can be seen that ratios of three to six which is around the observed range are obtained for a sinking rate of 5–6 m/day which is about the same value as that deduced for the upper layers in the offshore example. These values are realistic in terms of previously calculated sinking rates (Riley *et al.* 1949; Steele, 1956, 1957; Steemann-Nielsen & Jensen, 1957).

In both areas the density increase across the thermocline is in the range

0·002–0·003. From Munk & Riley (1952) the relations between the sinking rates, size of the plants, and the density difference between the plants and the water, for the simple shapes, spheres and cylinders, can be expressed approximately as

$$v_s = \frac{\Delta p d_s^2}{10} \quad \text{for a sphere (Stokes Law),}$$

$$v_c = \Delta p d_c^2 \quad \text{for a cylinder,}$$

where v_s, v_c are the sinking rates (m/day) and d_s, d_c are the diameters (μ) of spheres and cylinders, respectively; Δp is the density difference between the cell and the water.

Assuming the extreme case considered earlier, when the cells are neutrally buoyant in the lower layers, then the approximate sinking rates are obtained by putting $\Delta p = 0{\cdot}0025$. For a sinking rate of 5 m/day the required diameters are $d_s = 140\ \mu$, $d_c = 45\ \mu$. These values are high for generally observed sizes (Munk & Riley, 1952, Fig. 6) and they appear to be very much higher than those found in the areas studied. From information kindly provided by Dr E. M. Hulburt, the diameter of the main species found during the summer is generally about $5\,\mu$ and usually less than $10\,\mu$. A value of $5\,\mu$ would give sinking rates of $v_s = 0{\cdot}006$ m/day, $v_c = 0{\cdot}06$ m/day. This is between two and three orders of magnitude less than the values calculated from the models.

THE EFFECT OF LIGHT AND NUTRIENTS ON SINKING RATES

This gross difference between the two estimates of sinking rates suggested that a change in water density alone was not a satisfactory explanation of decreasing sinking rates.[1] Thus it seemed necessary to look for changes in the density of the cells themselves as a possible explanation. It seemed probable that a decrease in sinking rate could be produced as a result of recovery of the plant cells from nutrient deficiencies. The depth at which maximum chlorophyll is observed is frequently within the thermocline, where nutrient concentrations increase with increasing depth. Gross & Zeuthen (1948) have observed variations in the sinking rates of diatoms under different culture conditions. It is a common phenomenon for the algal culturist to observe that old cultures settle out more rapidly than do young actively growing cultures.

To examine the effects of light and nutrients on the sinking rate we have conducted the following experiments. Cultures of the diatom *Skeletonema costatum* (Grev.) were grown in 4B media (Yentsch & Vaccaro, 1958) at 18° C in constant optimal light intensity. Periodically this culture was

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[1] Jerlov (1959) by the same reasoning given earlier noted the necessity of decreasing sinking rates to explain deep particle maxima. However, he had no information on the particle sizes and accepted density changes in the water as sufficient explanation.

sampled and the sinking rate of the cells measured. Approximately 30 c.c. of well-agitated culture were placed in a 5 cm, large volume, optical cuvette. In the first experiment clumping was removed with a Potter–Eluehjehm homogenizer using a Teflon pestle. Optical density measurements were made in a Beckman DU spectrophotometer at a wave-length of 750 mμ. Decreases in the optical density at this wave-length, resulting from cells settling out of the light path, were measured at regular intervals over a period of 1 h (Fig. 5). The percentage decrease of the optical density during the hour is used as a measure of relative sinking rate.

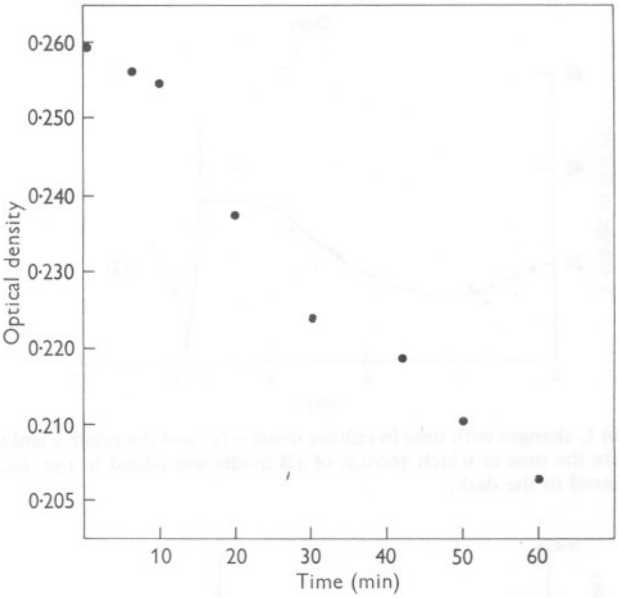

Fig. 5. Changes in optical density of a culture in a cuvette, resulting from cells settling.

The results of two experiments show that the settling rate of actively dividing cells was approximately one-half the rate of slowly dividing, senescent cells. In the first experiment, Fig. 6, an aliquot of the culture was removed between the seventh and eighth day, enriched with nutrients, and placed in the dark. During the first half day the cells in the dark settled more slowly than the illuminated cells, after which the settling rate increased.

In the second experiment three aliquots of the illuminated culture were removed between the third and fourth day of growth. Two of these were enriched, one was darkened, the other illuminated. The third aliquot was not enriched but was placed in the dark. In all three aliquots the settling rate of cells was decreased relative to that of the original culture. The lowest settling

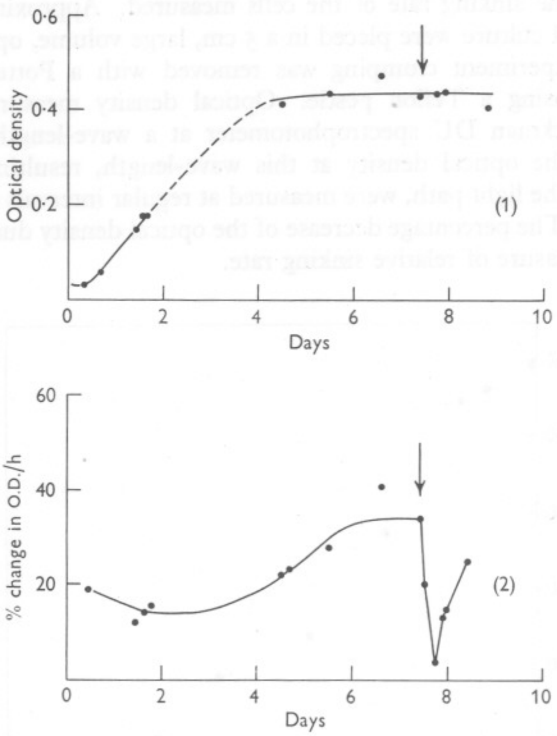

Fig. 6. Experiment I, changes with time in culture density (1) and the relative sinking rate (2). The arrows indicate the time at which 300 c.c. of 4B media was added to 150 c.c. aliquot of the culture and placed in the dark.

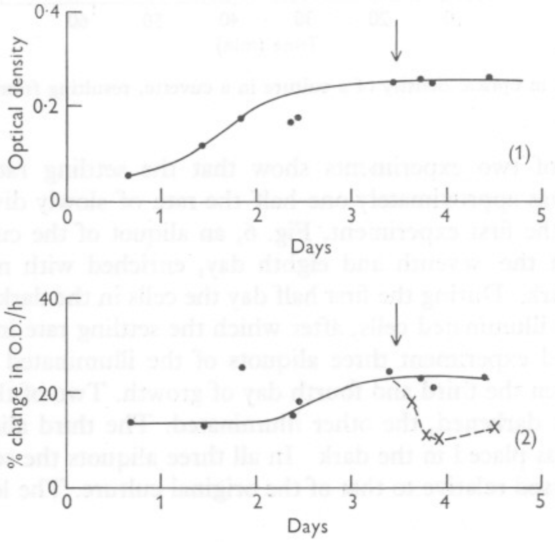

Fig. 7. Experiment II, changes with time in culture density (1) and relative sinking rate (2). The arrows indicate the time at which 300 c.c. of 4B media was added to 150 c.c. aliquot of the culture and placed in the dark.

rate occurred in the enriched darkened aliquot, Fig. 7, broken line, with the others intermediate between this and the control.

The results of these experiments show that older cells settle faster than do rapidly growing cells. Furthermore, when old cells are enriched in the dark, the settling rate is considerably reduced.

DISCUSSION

From a mathematical model which used as parameters of the phytoplankton environment, photosynthesis, respiration, grazing and eddy diffusion, we have concluded that a decreased sinking rate is needed to produce chlorophyll maxima at or below the base of the euphotic zone. Density differences observed throughout the water column appeared unable to explain these vertical distributions, and so we postulated the concept that the chlorophyll maxima are due to a decrease in sinking rate of the plants themselves caused by their entry into the dark, nutrient-rich waters found at the foot of the euphotic zone. The justification of this rather tentative hypothesis is that it predicted an experimental result.

Our experimental results show that as growth slows down, the cells sink more rapidly. When the deficient cells are re-enriched and placed in the dark, their sinking rate decreases rapidly. The picture that emerges is one where the general physiological condition of the cell and its buoyancy are closely related, as Gross & Zeuthen (1948) have also suggested. On this basis, seasonal variations in the vertical distribution of chlorophyll can be explained. For example, during early spring when nutrients are sufficient, phytoplankton cells would tend to have a low sinking rate, and populations undergoing rapid growth would tend to accumulate near the surface. In late summer when nutrients are depleted in the surface waters, phytoplankton would sink and accumulate in the nutrient rich water at the base of the euphotic zone. Here the assimilation of nutrients which can proceed in the dark (Ketchum, 1939) would, as our experiments show, decrease the sinking rate of the phytoplankton cells.

SUMMARY

Theoretical considerations of the occurrence of chlorophyll maxima at the foot of the euphotic zone show that a decreasing sinking rate is necessary to explain this feature but that the required decrease could not be obtained from density changes in the water alone. It is thought that the cells themselves might increase their buoyancy when they reach dark, nutrient-rich waters, and this has been confirmed by two experiments in which deficient laboratory cultures of *Skeletonema costatum* were re-enriched in the dark and decreased their sinking rate considerably.

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TABLE 1. EXAMPLES OF THE VERTICAL DISTRIBUTION OF CHLOROPHYLL, OF THE RATE OF PHOTOSYNTHESIS AND CONCENTRATION OF NUTRIENTS AT STATIONS WHERE THE MAXIMUM CHLOROPHYLL CONCENTRATIONS OCCURRED AT OR NEAR THE COMPENSATION DEPTH

Depth (m)	Chl *a* mg/m^3	^{14}C *in situ* measurements mg C/m^3/day	NO$_3$—N μg atm./l.	PO$_4$—P μg atm./l.
Crawford station 194, July 1957				
10	0·18	1·8	0·53	0·09
25	0 24	5·2	0·39	0·11
50	1·46	5·6	0·43	0·19
75	0·19	0	6·00	0·59
100	0·09	0	6·20	0·66
Crawford station 209, July 1957				
0	0·40	24·0	0·96	0·48
10	0·57	9·3	0·50	0·36
20	1·62	8·7	1 17	0·54
30	0·25	0	4·50	0·41

J. mar. biol. Ass. U.K. (1960) 39, 227–238
Printed in Great Britain

UNDERWATER DAYLIGHT MEASUREMENTS IN THE BAY OF BISCAY

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(With Plate I and Text-figs. 1–8)

As modern instrumentation improves the precision of the measurements of underwater light, particularly of monochromatic light, both biological and physical oceanographers are becoming increasingly interested in such measurements in deep water.

Two sets of observations of ambient light to depths of 400 m are presented here. It is suggested that the results were affected by both biological and physical factors.

MATERIALS AND METHOD

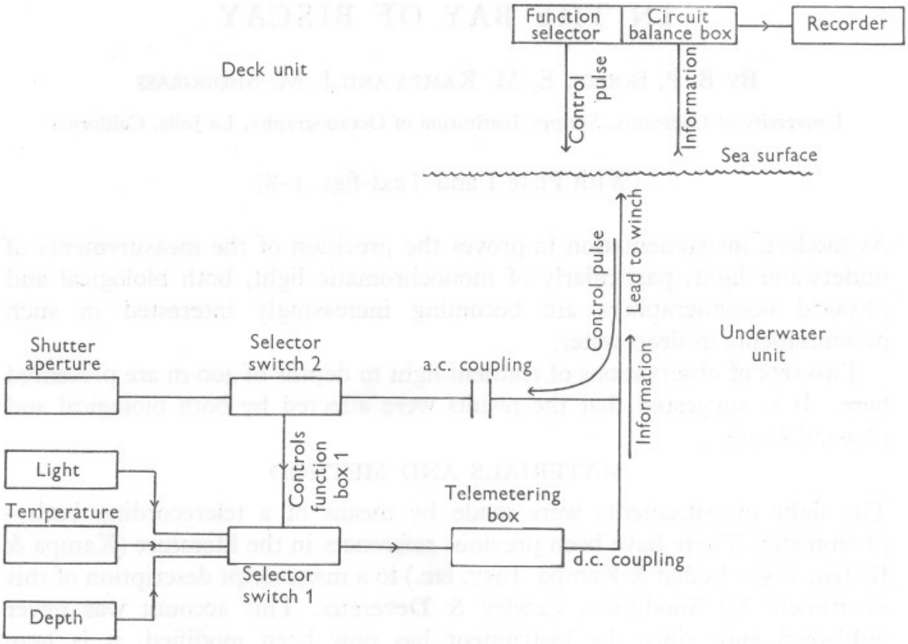
The light measurements were made by means of a telerecording bathyphotometer. There have been previous references in the literature (Kampa & Boden, 1956; Boden & Kampa, 1957, etc.) to a manuscript description of this instrument by Snodgrass, Cawley & Devereux. This account was never published and, since the instrument has now been modified, it is here described. This instrument comprises two units—an underwater unit and a deck unit.

The underwater unit (Pl. 1 A, B) is housed in a stainless-steel tube with walls $\frac{1}{2}$ in. thick and consists of a photosensor (RCA 931-A multiplier phototube) with a shutter, a depth sensor, a temperature sensor, control circuits and power supply, and the telemetering circuit by which light, depth, and temperature information are transmitted. It is supported by an insulated, single-conductor cable along which the data are telemetered. There are several advantages to the use of this type of cable. It is extremely strong (breaking strain 2800 lb.) and can be wrapped on a relatively small winch (800 lb. total weight). Due to the buoyancy of the polythene insulation the weight of this cable in water is only 16 lb./1000 ft. In multi-channel cable there is always a danger of short-circuits between the conductors due to mechanical stresses on the winch or block. This is eliminated here. The system uses a sea return.

Signals from the cable are transmitted via slip-rings on the winch to the deck unit.

The deck unit (Pl. 1 C) includes the circuitry that enables the operator to select the function (light, depth or temperature) to be recorded, a number of bias circuits for zeroing the instrument, and a recorder (Pl. 1 D) to which the information is relayed.

The connexions are summarized in Text-fig. 1.



Text-fig. 1

Circuits

Circuit diagrams for the entire instrument are shown in Text-figs. 2–4. The photometric circuitry (modified from Sweet, 1946) gives a logarithmic response over seven decades of light intensity.

The use of a pentode tube as a telemetering coupler (Valley & Wallman, 1948) obviates the interference of various potentials in the earth circuit, such as potentials between the steel hull of the ship and bronze propellor shafts and the water.

Depth

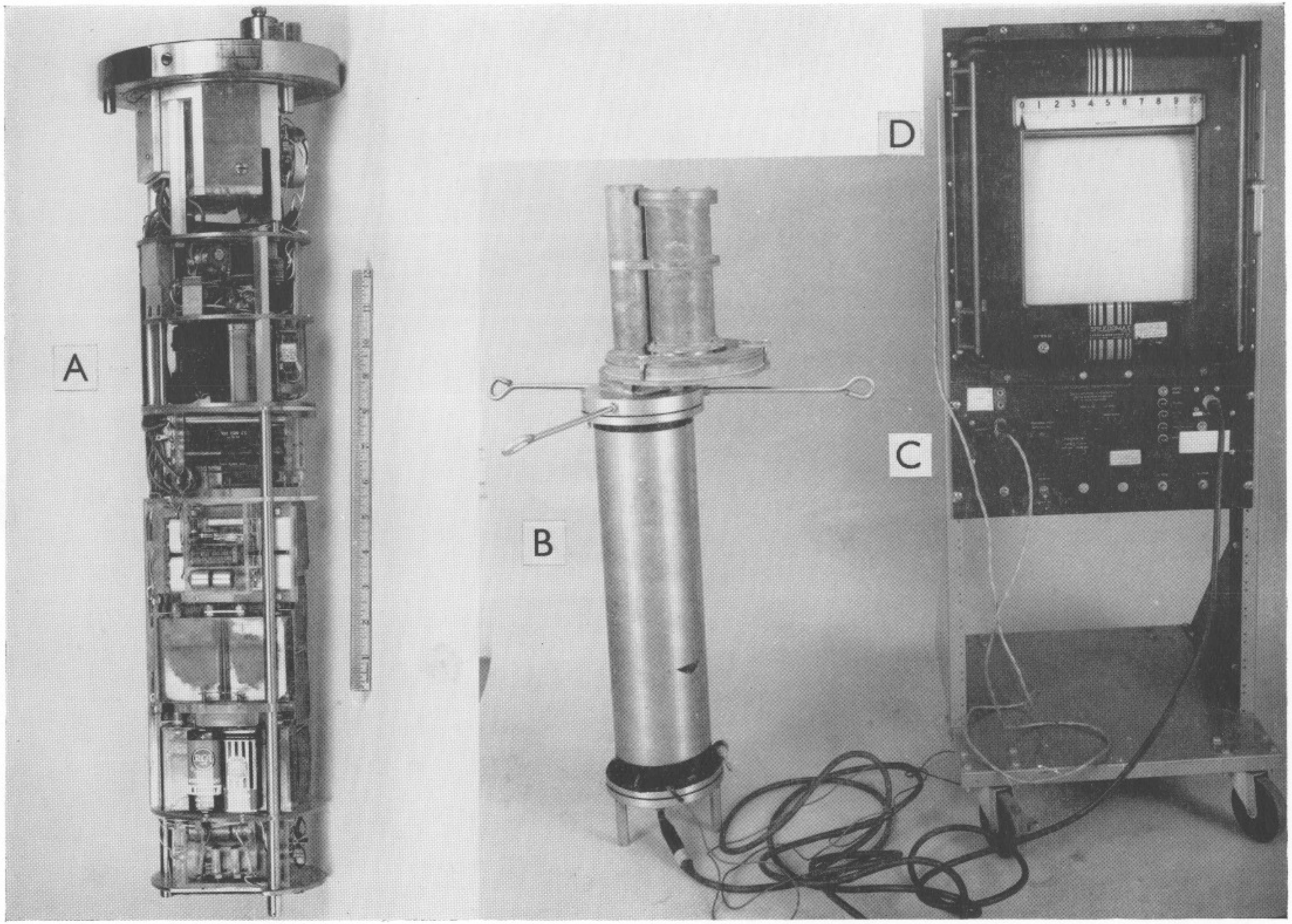
This element is a Bourdon tube coupled to a slide-wire potentiometer. It has been described elsewhere (Boden, Kampa, Snodgrass & Devereux, 1955).

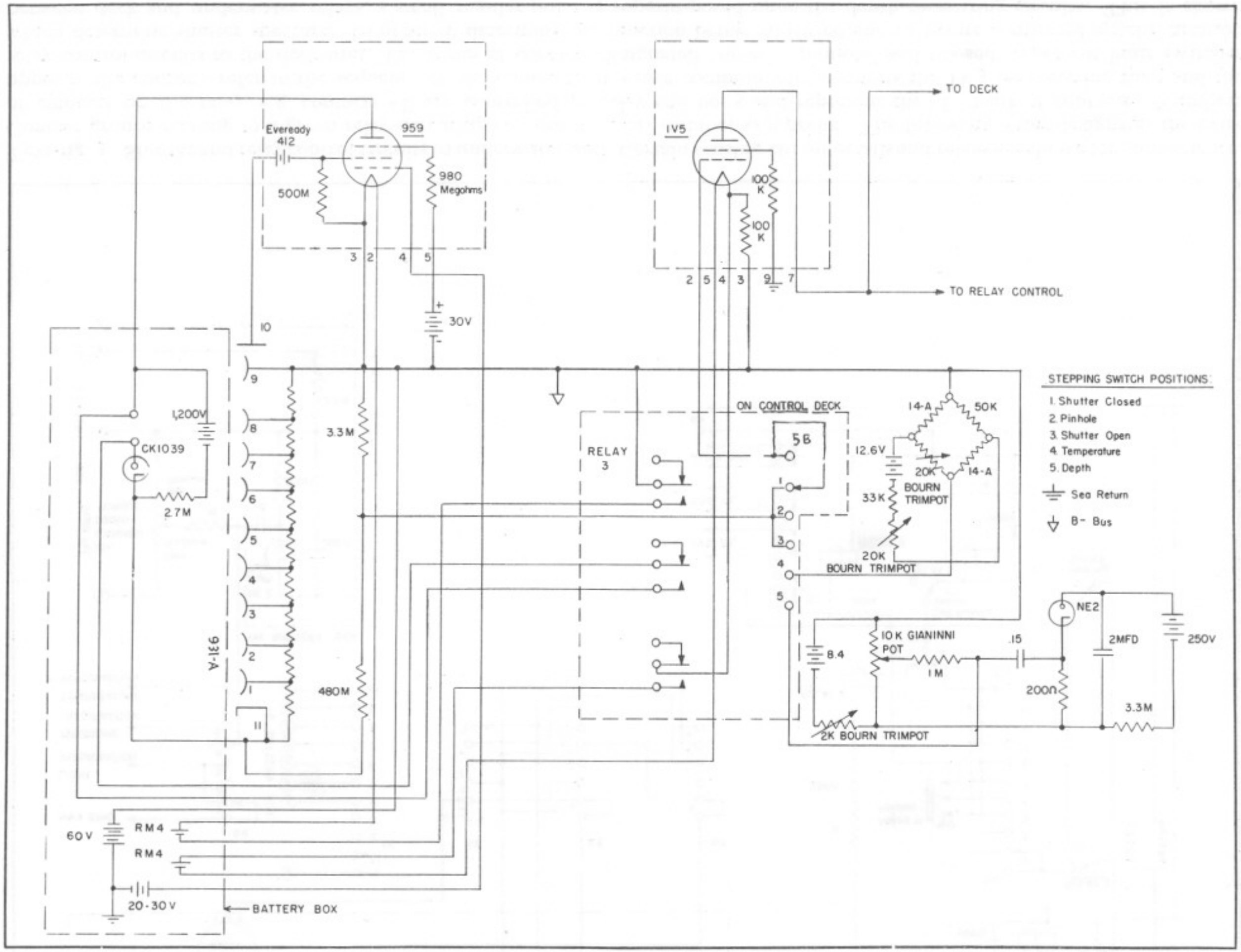
Temperature

Water temperature is measured by a matched pair of 14-A thermistors, which operate in opposite arms of a full-resistance bridge. The bridge unbalance potential is applied directly to the grid of the IV 5 telemetering tube through a stepping switch.

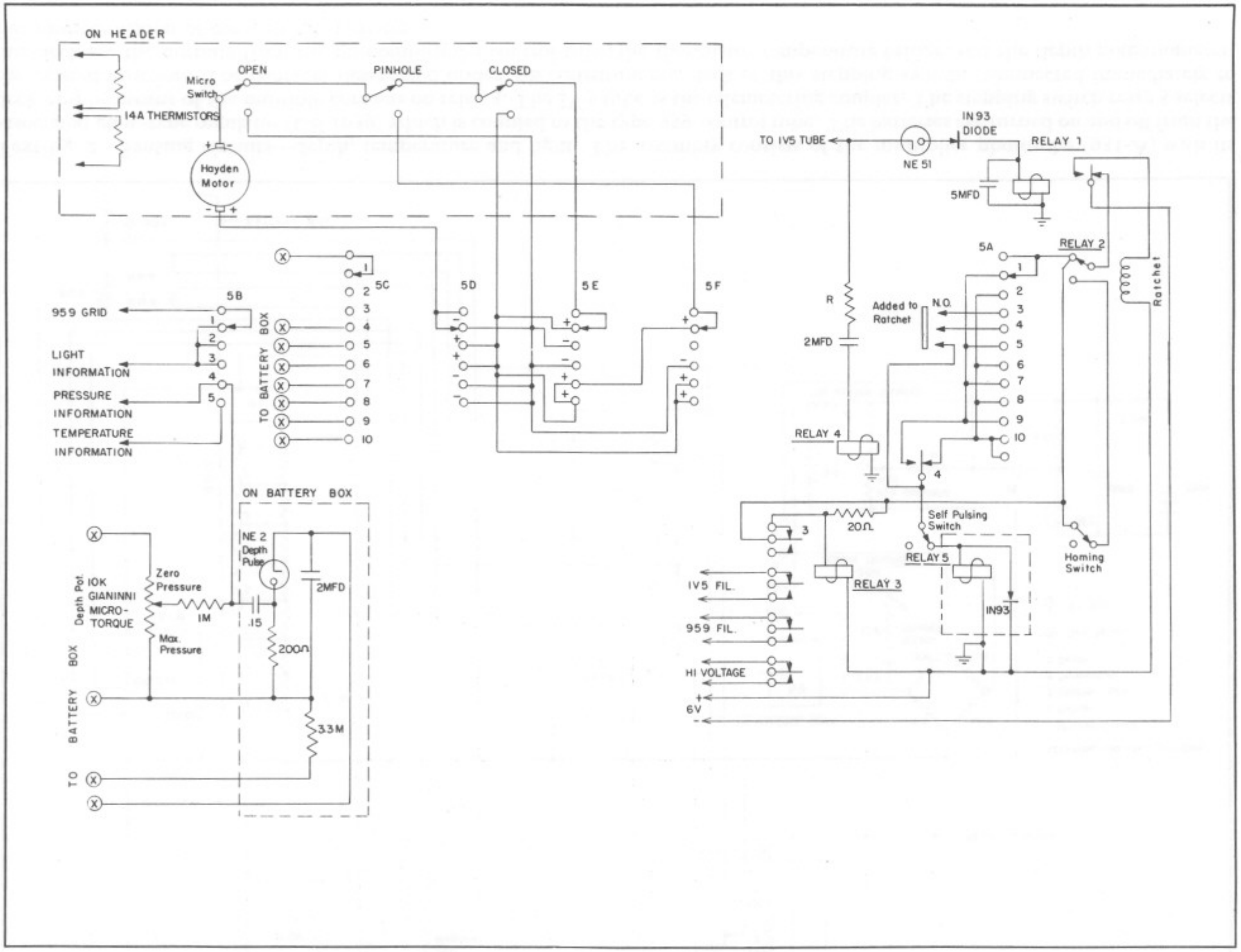
EXPLANATION OF PLATE 1

A, underwater unit of photometer without case. B, underwater unit in case with collimating tube and automatic filter changer in position. The unit is connected by a test lead to C, the deck control unit, which is connected to D, a Leeds and Northrup Speedomax recorder.

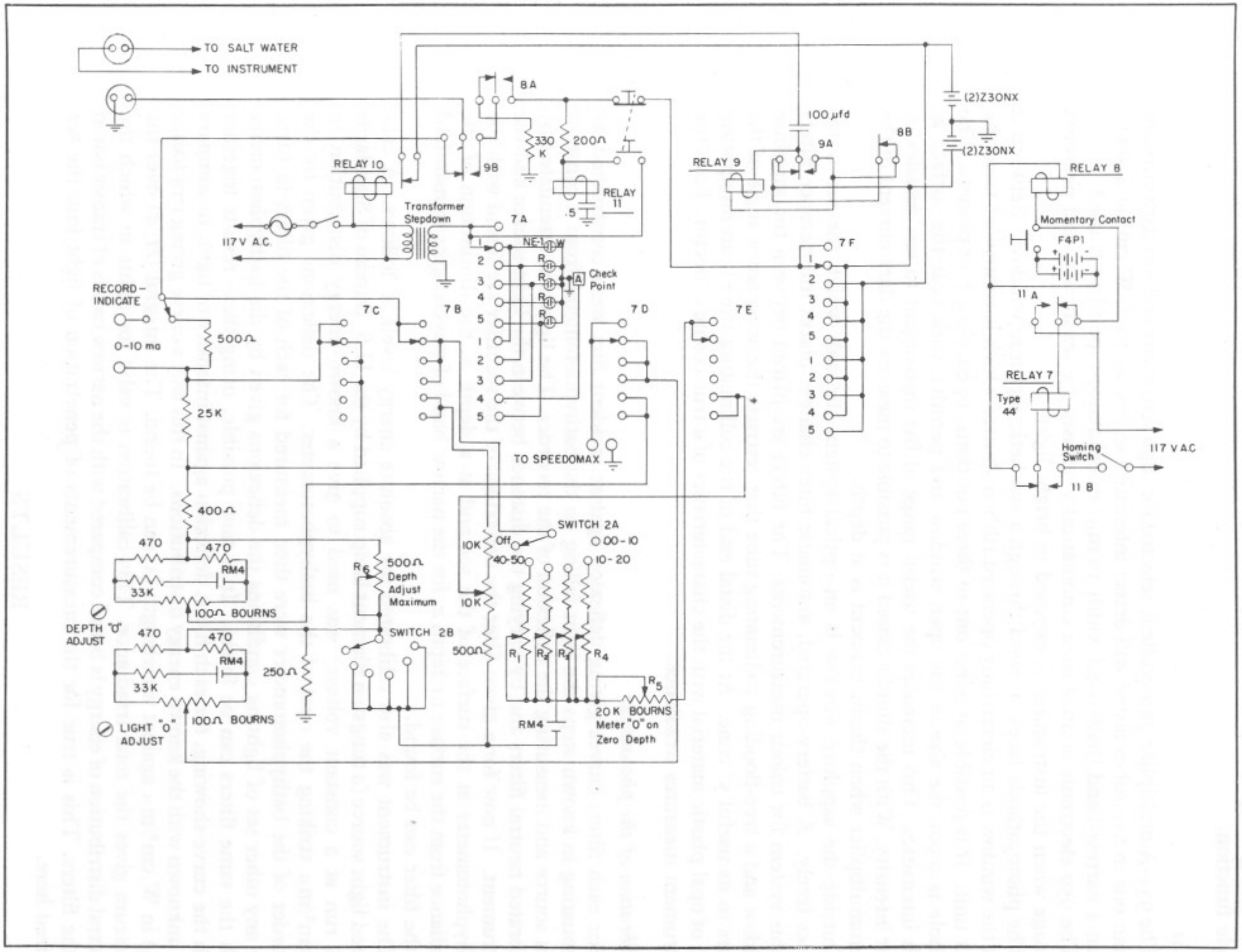

A
B
C
D



Text-fig. 2. Sensing circuits—depth, temperature and light. The assembly consists of the multiplier phototube (931-A) with its associated glow-type regulator (CK 1039) which is coupled to the type 959 control tube. The batteries are turned on and off from the deck unit by means of the multiple contacts on relay 3. The IV 5 tube is the telemetering coupler. The stepping switch relay 5 selects the desired function. The contacts designated under 5 B constitute one deck of this stepping switch. Connected immediately to this deck are the outputs from the photomultiplier control tube, the thermistor temperature bridge, and the depth potentiometer. For interconnexion of controls see Text-fig. 3.



Text-fig. 3. Shutter and relay control circuits in underwater unit. Certain sensing circuit details and relays are shown for convenience. Contact groups relating to a given relay-actuating coil use the relay number as a prefix. The following letter designates the bank of contacts on the relay, e.g. contacts 5E are controlled by relay coil no. 5 and represent the 'E' bank of contacts. Numbers opposite the contacts refer to the sequence of the contacts. A single common wire connects the IV5 telemetering tube and the relay control circuits to the deck unit. The series of contacts designated 'open', 'pinhole' and 'closed' represent limit switches which determine shutter aperture. In order to determine the function being measured and to insure continued synchronization between deck and underwater relays, a small regular pulse is superimposed upon the depth-measuring circuits. This is shown as a simple relaxation oscillator.



Text-fig. 4. Deck control unit. The same designations are followed as in Text-fig. 3. In order to indicate the function being measured and to insure synchronization between deck and underwater units, two identical stepping switches are pulsed in series. These are relays 5 (in the underwater unit) and 7 (in the deck unit). To insure the operator's safety an isolating step-down transformer is used between the circuits and the 117 V a.c. power supply. Numerous range-adjusting and balancing networks are incorporated for convenience of read-out. A ground symbol indicates a good sea-water contact. The string of neon lamps connected to contacts 7A indicate the function being measured.

The stepping switch controls shutter position and also permits programmed telemetering of light, depth and temperature, or continuous recording of any selected single function.

Light

The 931-A multiplier phototube is selected for high sensitivity and low dark current. About one in five tubes tested will detect intensities as low as $10^{-5}\mu$W/cm^2 at 420 mμ when a narrow band (half-band width 10 mμ) interference-type filter is used.

The 959 electronic control tube automatically adjusts the sensitivity, and prevents damage when the instrument is exposed to bright light.

The photocathode faces outward through a synthetic sapphire window. Between it and the window is an electrically operated ribbon shutter which is controlled from the deck unit. It is possible to select one of three positions: open, closed, or pinhole. The pinhole is 0·001 the size of the open window and permits work near the surface at high intensities. This increases the useful range of the instrument to ten decades of light intensity. With the shutter closed it is possible to measure the dark current of the photomultiplier when the instrument is at depth.

Outside the sapphire window is an optical system through which the sea water passes freely. A battery-operated, automatic filter-changer places interference filters in this system for colour measurements. The filters are placed between the sapphire window and a free-flooding collimating tube that restricts the acceptance angle of the filters to its useful 5° cone. At the distal end of the collimating tube is an integrating disc of opal plastic material with the characteristics of a true cosine collector. Thus the instrument measures irradiance.

Calibration of the photometer

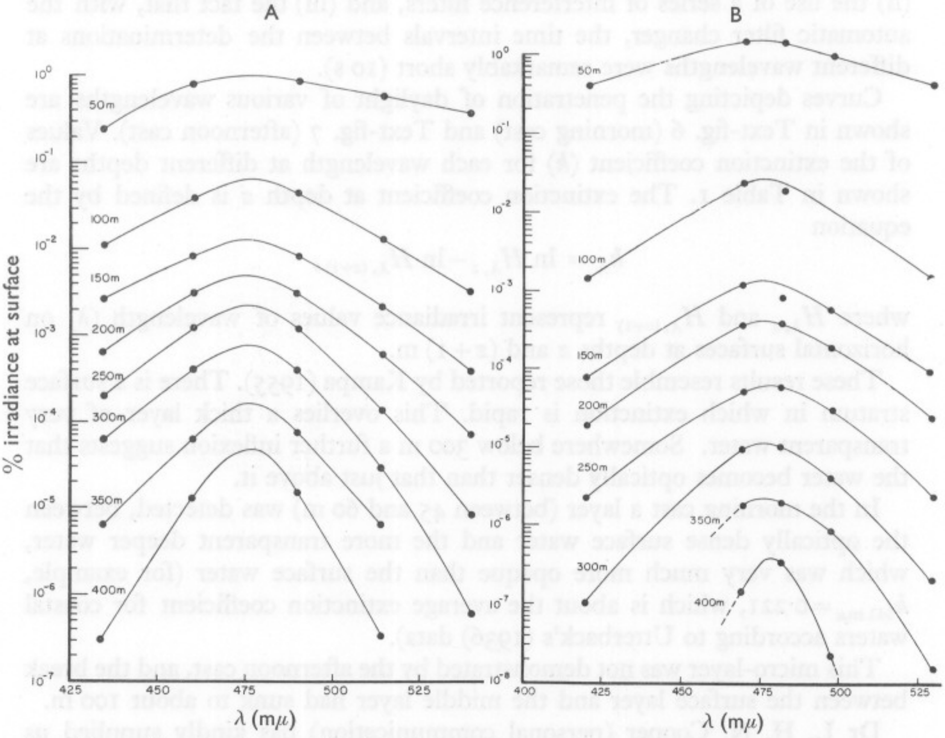
For each filter, curves giving deflexion against incident flux were constructed by attenuating in known steps the light falling on the bathyphotometer from a constant light source and measuring the deflexion of the recorder. The light was attenuated by calibrated neutral filters and by varying the distance between the light source and the instrument. If now for a given filter the deflexions of the recorder are found with the bathyphotometer at the surface of the sea and at a depth z, the diminution of the irradiance from the surface to depth z, for the narrow band of wavelengths transmitted by the filter can be found.

The instrument was also calibrated for absolute energy levels as follows. A calibrated light source (a tungsten filament lamp supplied by the U.S. Bureau of Standards and run at a constant voltage) was used to give a known energy distribution in W/cm^2/mμ striking the opal of the bathyphotometer. The deflexions given by the recorder of the bathyphotometer were then measured for each of the filters in turn. For any other set of lighting conditions the deflexions given by the bathyphotometer with the same filters can be found. It is now possible, using these results together with the curve showing, for each filter, deflexion against intensity of light, to compare the unknown with the known energy distributions. In this way a curve giving irradiance (H_λ) in W/cm^2/mμ against wavelength (λ) can be found. The integral $\int H_\lambda d\lambda$ over the spectrum gives the total irradiance. This calibration is valid for lights in which the spectral distribution of energy is broad compared with the narrow bands of transmission of the filters. This is true for the measurements of penetration of light into the sea desired here.

RESULTS

The results reported here were obtained at Station Cavall in the Bay of Biscay (lat. 46° 29′ N., long. 7° 59′ W.) on 25 September 1958, from the Plymouth laboratory R.V. 'Sarsia'. Station Cavall is one of several hydrographic stations established by Dr L. H. N. Cooper during his investigation of this area, and it was occupied for several days at this time.

The bathyphotometer was lowered twice during the day. The morning cast was made between 10.30 and 11.30 h and the afternoon cast between 13.25 and 14.10 h. The interference filters used in the morning cast had pass bands with peaks at 434, 460, 491, 514 and 540 mμ. Those used in the afternoon transmitted maximally at 421, 470, 482, 498 and 528 mμ.



Text-fig. 5. Spectra of transmitted sunlight at 50 m intervals of depth in the Bay of Biscay (lat. 46° 29′ N., long. 7° 59′ W.) on 25 September 1958. A, 10.30–11.30 h G.M.T.; B, 13.25–14.10 h G.M.T.

At this latitude, at this time of the year, differences in degree of underwater irradiance due to differences in the sun's altitude at periods as closely spaced as these during the middle of the day are less than 5%. However, sky conditions changed between the two casts. In the afternoon a light, high haze caused some forward scattering. The afternoon irradiance values are higher than those obtained in the morning, but this is not a matter of importance, since the values have been equated to 1 at the surface, and only relative values are considered.

The spectral composition of the light at 50 m intervals to a depth of 400 m is shown in Text-figs. 5 A, B. The distribution obtained in the morning is very similar to that obtained in the afternoon, although different sets of filters were used. The light becomes steadily bluer with depth until at 400 m the spectrum peaks sharply between 475 and 480 mμ. This is an excellent illustration of the ocean acting as a monochromator as described by Tyler (1959). These results agree closely with those obtained by Jerlov (1951) and the main interest attached to them is: (i) the relatively great depth attained, (ii) the use of a series of interference filters, and (iii) the fact that, with the automatic filter changer, the time intervals between the determinations at different wavelengths were remarkably short (10 s).

Curves depicting the penetration of daylight of various wavelengths are shown in Text-fig. 6 (morning cast) and Text-fig. 7 (afternoon cast). Values of the extinction coefficient (k) for each wavelength at different depths are shown in Table 1. The extinction coefficient at depth z is defined by the equation

$$k_{\lambda} = \ln H_{\lambda, z} - \ln H_{\lambda, (z+1)},$$

where $H_{\lambda, z}$ and $H_{\lambda, (z+1)}$ represent irradiance values of wavelength (λ) on horizontal surfaces at depths z and $(z+1)$ m.

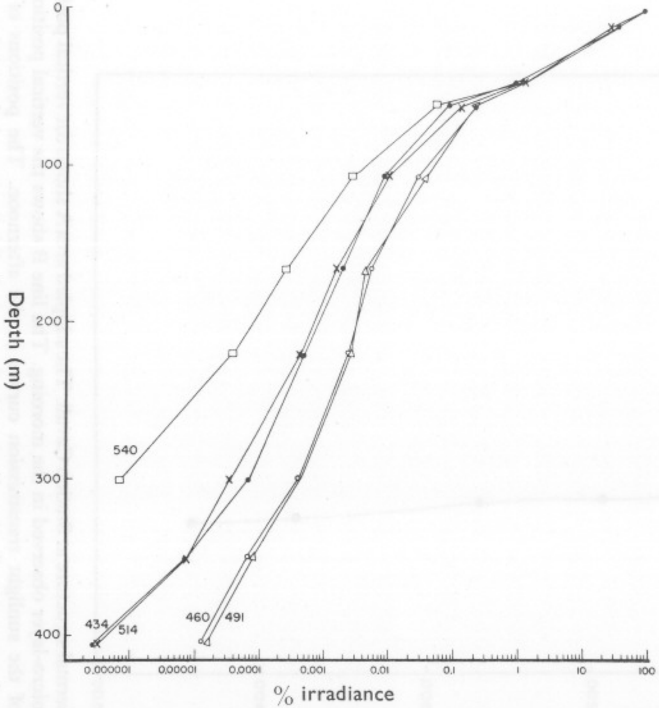
These results resemble those reported by Kampa (1955). There is a surface stratum in which extinction is rapid. This overlies a thick layer of very transparent water. Somewhere below 300 m a further inflexion suggests that the water becomes optically denser than that just above it.

In the morning cast a layer (between 45 and 60 m) was detected, between the optically dense surface water and the more transparent deeper water, which was very much more opaque than the surface water (for example, $k_{541\,\mathrm{m}\mu} = 0{\cdot}221$, which is about the average extinction coefficient for coastal waters according to Utterback's (1936) data).

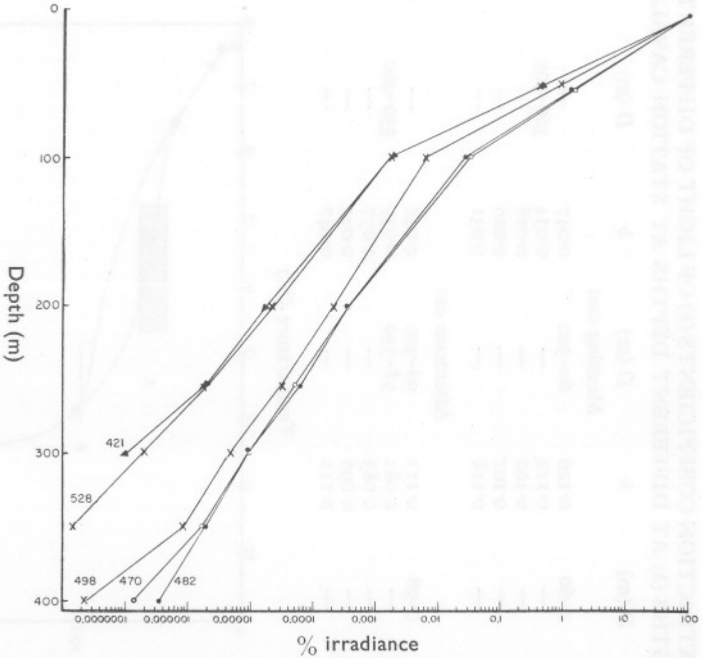
This micro-layer was not demonstrated by the afternoon cast, and the break between the surface layer and the middle layer had sunk to about 100 m.

Dr L. H. N. Cooper (personal communication) has kindly supplied us with the data showing the vertical thermal structure (Text-fig. 8) at the time of the casts. Our thermistor circuit failed during the operation, and we did not record temperature. It can be seen that there was a very strong thermocline somewhere between 40 and 97 m. Correlations between attenuation coefficients and thermoclines in the north Pacific have been reported by M. Koslyaninov (Academy of Sciences, U.S.S.R.—personal communication to Mr J. E. Tyler, Scripps Institution).

Between the morning and afternoon casts the wind had increased from force 3 to force 4 and the sea from state 3 to state 5. The ship drifted less than 6 miles between casts and the possibility that this resulted in the sampling of different water masses at an oceanic station is slight.



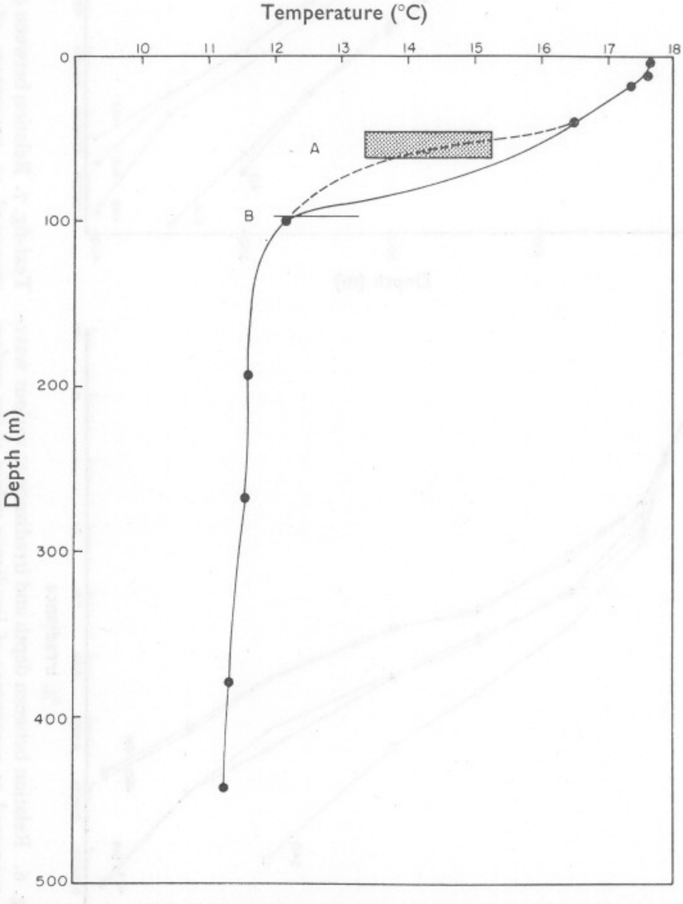
Text-fig. 6. Relation between depth and irradiance at various wavelengths expressed as percentage of irradiance values at the surface. The numbers at the ends of the curves indicate the wavelengths (in mμ) of maximum transmission of the interference filters used.



Text-fig. 7. Relation between depth and irradiance at various wavelengths expressed as percentage of irradiance values at the surface. The numbers at the ends of the curves indicate the wavelengths (in mμ) of maximum transmission of the interference filters used

TABLE 1. EXTINCTION COEFFICIENTS (*k*) OF LIGHT OF DIFFERENT WAVE-LENGTHS (λ) AT DIFFERENT DEPTHS AT STATION CAVALL

λ (mμ)	*D* (m)	*k*	*D* (m)	*k*	*D* (m)	*k*
			Morning cast			
540	0–60	0·126	60–300	0·047	—	—
514	—	0·112	—	0·034	300–405	0·045
491	—	0·102	—	0·026	—	0·032
460	—	0·101	—	0·026	—	0·033
434	—	0·118	—	0·031	—	0·052
			Afternoon cast			
421	0–98	0·111	98–300	0·048	—	—
470	—	0·081	98–350	0·039	350–400	0·050
482	—	0·083	—	0·037	—	0·035
498	—	0·096	—	0·035	—	0·072
528	—	0·111	—	0·047	—	—



Text-fig. 8. Thermal structure at Station Cavall. The stippled area A shows the vertical position of the turbid micro-layer observed in the morning. The line B shows the vertical position of the inflexion of the sunlight transmission curves in the afternoon. The positions of the thermocline in the morning (broken line) and afternoon (solid line) are inferred from the optical data.

We interpret this apparent destruction of the optically dense micro-layer and the sinking of the break between the surface and middle layers as being due to turbulence associated with this change in the weather. The high extinction coefficients in the surface layer could well have been caused by particulate matter due to the higher productivity of the layer. The vertical extent of this layer is consistent with the depth of the 'photic' zone (Hedgpeth, 1958) at this latitude. The sharp difference in the optical properties of the two layers was probably due to an accumulation of particulate matter at an interface associated with an apparently long-established thermocline.

TABLE 2. OXYGEN VALUES AT DIFFERENT DEPTHS AT STATION CAVALL

	Oxygen		
D (m)	ml./l.	% sat.	Defect (ml./l.)
97	5·52	93·6	0·37
100	5·45	94·8	0·30
193	5·57	94·6	0·32
268	5·59	95·0	0·29
381	5·38	90·7	0·55
442	5·32	89·6	0·62
537	5·02	83·9	0·96

Such turbulence would cause a slight sinking of the thermocline and this change in thermal structure is summarized in Text-fig. 8. The broken line shows the probable position of the thermocline in the morning, and the solid line the same in the afternoon. The shaded area (A) represents the turbid micro-layer present in the morning, and a line (B) shows the break between the optical properties of the upper and lower layers in the afternoon. This increase in the vertical extent of the surface layer would result in a greater dilution of the particles in it, and this is revealed by somewhat lower extinction values in this layer in the afternoon. The differences in extinction coefficients between the middle and lower layers, somewhere below 300 m, are less pronounced.

In California, Kampa (1955) found that the lower inflexion in the extinction curve was associated with the top of a sonic-scattering layer and inferred that this increased extinction was also of biological origin. We have no evidence of the existence of a sonic-scattering layer at Station Cavall at this time, but this does not preclude the possibility that one was present. The echo-sounder on the 'Sarsia' operates at a much shorter ping-length than most American instruments, and may well have not recorded a layer of the type found in California.

Cooper, who supplied the oxygen data in Table 2, writes 'between 268 and 391 m there was some evidence, particularly from oxygen, of a change in properties. It was not very marked, however'. It is apparent that the photometer entered a water mass with different optical properties at about this depth. Whether such changes in oxygen content and transparency are linked with some biological phenomenon is a moot point. There were no marked changes in temperature, salinity, or other properties at this depth.

This work was done under contract between the U.S. Office of Naval Research and the University of California. A grant-in-aid was made by the U.S. National Science Foundation. Part of the work was supported by the U.S. Bureau of Ships.

We wish to thank the Director, Dr F. S. Russell, F.R.S., for the unfailing hospitality of the Plymouth Laboratory, the scientific staff of the laboratory and the captain, officers and crew of the R.V. 'Sarsia' for their help under rather trying circumstances. Dr L. H. N. Cooper, for whom the cruise was scheduled, was extremely generous in granting us time and in making available the pertinent hydrographic data.

SUMMARY

A telerecording bathyphotometer embodying a multiplier phototube is described and the circuitry is illustrated. Measurements were made of the penetration and spectral characteristics of daylight to a depth of 400 m in the Bay of Biscay. It is suggested that the rapid attenuation of light in the upper 100 m was due in part to biological matter associated with a sharp thermocline. A change in the weather is presumed to have caused a change in the depth of the thermocline and this is reflected in a change in attenuation coefficients.

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J. mar. biol. Ass. U.K. (1960) 39, 239–248
Printed in Great Britain

CARBOHYDRATES IN SOME MARINE PLANKTONIC ANIMALS

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There have been few analyses of the fat, protein and carbohydrate fractions in zooplankton, and owing to the difficulty of sorting large numbers of single species, the majority of the earlier determinations were necessarily carried out on mixed zooplankton hauls (Brandt, 1898; Brandt & Raben, 1919; Moberg, 1926; Wimpenny, 1929; Drummond & Gunther, 1934; Vinogradov, 1953). Most of these analyses suggested a relatively high protein and fat content, and this was confirmed by Orr (1934*a*), who investigated the chemical composition of a single species, *Calanus finmarchicus*. Orr's result gave fat, protein and chitin as 20–40, 35–50 and 3%, respectively of dry weight. Similar high values were also reported by Orr (1934*b*) for *Euchaeta norvegica*. The carbohydrate content was not, however, estimated in either of Orr's investigations since large numbers of animals would have been required. Brandt (1898), after analysing mixed plankton hauls which were predominantly copepods, suggested a carbohydrate content of *ca*. 20%.

Although many workers have suggested that fat is used as substrate during the respiration of zooplankton, the role of carbohydrate is doubtful, since there is so little information on the glycogen content and on the amount of monosaccharides in plankton animals. Lane, Posner & Greenfield (1952) and Greenfield (1953) reported very high glycogen values in prenatal larvae of *Teredo*, and noted a sharp reduction in the amount in free-swimming larvae. Collyer (1957) found the glycogen reserves in the larvae of *Ostrea edulis* to lie between 13·4 and 15·4% of the dry organic matter, but found no correlation with size. It therefore appeared highly desirable to investigate the total carbohydrate content (i.e. glycogen and monosaccharides) in certain planktonic animals. It also was of interest to test whether the amount of carbohydrate varied with feeding and activity, since this might indicate whether carbohydrate was normally used as an energy source.

MATERIAL AND METHODS

Experiments were carried out with *Calanus finmarchicus* (Gunnerus)[1] and *Neomysis integer* (J. V. Thompson) at Plymouth, and with *Pleurobrachia pileus* (O. F. Müller) at Southampton. In each case the animals were picked

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[1] It is likely that since these specimens were collected in the English Channel they should be referred to the variety *helgolandicus*.

out from diluted plankton hauls. In the experiments with *Calanus*, over 100 animals were used for each carbohydrate determination. For experiments where the animals were first fed, batches of fifty animals were sorted into beakers, each containing a litre of filtered sea water enriched with cultures of diatoms and dinoflagellates. The beakers were placed in a light-tight box in a constant-temperature room at 12° C. For starvation experiments, batches of fifty animals were kept in tall rectangular Perspex vessels ($50 \times 7{\cdot}5 \times 3{\cdot}5$ cm) containing filtered sea water. These vessels, set up in the constant-temperature room (12° C), were supplied with fluorescent lighting from the top and side. This lighting was used as a stimulus to keep the animals active. The copepods were usually observed to be swimming upwards.

In the experiments with *Neomysis*, the same procedure as described for *Calanus* was followed, except that only twenty to fifty animals were used for each carbohydrate determination. With *Pleurobrachia* three to ten animals, depending on their size, were used. Owing to the high water content, the use of greater numbers of *Pleurobrachia* was of no advantage. A few experiments were attempted using dried *Pleurobrachia*, but as it was likely that the high salt content interfered with the analyses, those experiments were not continued.

The total carbohydrate content was determined by the micro-method of Mendel, Kemp & Myers (1954) and of Kemp and Heijningen (1954). Glycogen in the tissues was first hydrolysed to glucose, the final determination (made by a colorimetric method), including any glucose and fructose originally present as monosaccharides, and also saccharides yielding those sugars. Before each analysis the animals were concentrated by filtering through bolting silk, quickly rinsed with distilled water, and roughly dried on filter-paper. Except in the case of *Calanus*, the wet weight of the whole sample was then obtained. The animals were ground with 5 c.c. of 5% trichloracetic acid containing 0·2% silver sulphate. After boiling for 15 min and then centrifuging, a clear supernatant was obtained. To 1 c.c. of this fluid, 3 c.c. of concentrated H_2SO_4 (May & Baker, 98%, sp.gr. 1·84) was added and the mixture boiled for 6·5 min to develop colour. The intensity of the resulting pink colour was measured in a Unicam spectrophotometer (SP. 600) at 520 mμ. Usually three determinations were made on each sample; the agreement between the subsamples was good. The mean value was then converted into glucose units from a calibration curve, this curve being linear between 50 and 150 μg. glucose. Values below 50 μg. could not, however, be read with accuracy.

RESULTS

Calanus

The results of a few experiments with *Calanus*, mostly Stages V and VI ♀♀, suggested a rather low concentration of carbohydrates in the body (Table 1). Most of the determinations were made on copepods which had been kept in the laboratory and were either fed or starved, but in Expt. nos. 9 and 10 analyses of freshly caught *Calanus* were made and gave values of 1·7 and 1·4 μg sugar as glucose per copepod (Table 1). Copepods which were fed on phytoplankton in the laboratory gave rather variable carbohydrate contents (viz. 2·24–0·63 μg per copepod), and the same was true of those *Calanus* which were starved, though the values then tended to be lower (1·76 to < 0·25 μg per copepod). There is thus the suggestion that starvation (with continued activity of the copepods) tended to reduce carbohydrate, whereas feeding appeared to build up a small carbohydrate reserve. It is probable that the rise in body sugar with feeding would have been clearer, and the results less variable, had feeding been really active. Many workers, notably Marshall & Orr (1955), have commented on the variability of feeding activity seen in *Calanus* kept in the laboratory. In our experiments it appeared from a qualitative examination of the faecal pellet production that the *Calanus* were not feeding actively.

TABLE 1. CARBOHYDRATE CONTENT OF *CALANUS FINMARCHICUS*

Expt. no.	No. of animals used	Carbohydrate per copepod (μg)	% carbohydrate per wet weight	Remarks
1	125	2·24	0·18	Fed
2	125	1·76	0·14	Unfed
3	200	0·41	0·03	Unfed
4	200	1·15	0·09	Unfed
5	150	1·10	0·09	Fed
6	250	0·72	0·06	Fed
7	130	0·63	0·05	Fed
8	200	< 0·25	< 0·02	Unfed
9	140	1·70	0·13	Fresh animals
10	200	1·40	0·11	Fresh animals

In these preliminary experiments the *Calanus*, though counted, were generally not weighed. In Expt. no. 9, however, with freshly caught animals, the *Calanus* were weighed after roughly drying on filter-paper, and gave a mean of 1·26 mg per copepod (wet weight). This value (1·26 mg) has been used as a first approximation to convert the weight of carbohydrate per copepod to carbohydrate per body weight (Table 1). It then appears that in freshly caught *Calanus* carbohydrates amount to 0·11–0·13 % of the body (wet) weight. According to Marshall & Orr (1955) the water content of female *Calanus* is 78 % and that of Stage V 65 %. On the assumption of 70 % water content for a mixture of females and Stage V copepodites, the carbohydrate content of freshly caught *Calanus* expressed as percentage dry weight would be

$$0{\cdot}12 \times \frac{100}{30} = 0{\cdot}4\,\%.$$

In starved copepods the maximum carbohydrate (wet weight) was 0·14% and the minimum as low as < 0·02%. For fed copepods the values were slightly higher: range 0·18–0·05% of the body (wet) weight (Table 1).

Neomysis integer

It was possible to carry out rather more experiments on *Neomysis* and in all determinations the wet weight of the animals was first obtained. The results of experiments on animals which had been fed in the laboratory gave values of 0·42–0·20% sugar as glucose of the body (wet) weight. There was again the difficulty that although *Neomysis* fed on phytoplankton cultures, the intensity of feeding, as judged from faecal pellet production, appeared to be variable. Different periods of feeding were tried, but the intensity still varied considerably. It is of interest that the highest carbohydrate content (0·42%) was obtained in Expt. no. 13 (Table 2) where particularly marked feeding was noted.

TABLE 2. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*

(Fed Animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
11	160·0	0·31	1·55
12	142·0	0·20	1·00
13	180·4	0·42	2·10
14	353·4	0·22	1·10
15	243·6	0·24	1·20
16	228·0	0·28	1·40
17	251·0	0·23	1·15
18	208·0	0·22	1·10
19	310·0	0·25	1·25
20	276·7	0·20	1·00
21	318·8	0·22	1·10
22	980·0	0·22	1·10
23	389·2	0·29	1·45
24	403·0	0·26	1·30
25	333·3	0·23	1·18
26	278·0	0·39	1·95

The percentage of carbohydrate found in unfed *Neomysis* tended to be somewhat lower than in fed animals, though the range was considerable, viz. 0·28–0·15% glucose per body (wet) weight (Table 3). This suggests that carbohydrate is utilized to some extent with activity, and is stored during feeding. A somewhat closer comparison is possible for fed and unfed *Neomysis*, however. In some ten experiments the starved and fed cultures were set up simultaneously as paired experiments (Table 4). Only in one experiment (Expt. no. 28) was a greater percentage of glucose found in starved than in fed animals. In several of the pairs of determinations the reduction in carbohydrate with starvation was considerable (e.g. Expt. nos. 11 and 27, *ca.* 50%; Expt. nos. 13 and 29, *ca.* 40%), but in other experiments there was little or no change. In one of these experiments showing little change

(Expt. no. 33) duplicated unfed *Neomysis* cultures gave 0·21 and 0·24% carbohydrate against 0·23% for the fed animals (Expt. no. 17). But in the two unfed cultures, of a total of 300 mysids originally sorted, only 212 were recovered after 48 h starvation, although only a single intact dead mysid was seen. On closer examination several *Neomysis* were observed to be feeding on fragments of other mysids, suggesting that extensive cannibalism had occurred.

TABLE 3. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*

(Unfed animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
27	190·0	0·15	0·75
28	161·6	0·28	1·40
29	444·2	0·16	0·80
30	389·2	0·20	1·00
31	258·7	0·20	1·00
32	251·0	0·25	1·25
33*a*	334·2	0·21	1·05
33*b*	305·5	0·24	1·20
34	392·0	0·17	0·85
35	398·4	0·27	1·35
36	455·5	0·20	1·00

TABLE 4. A COMPARISON OF THE CARBOHYDRATE CONTENT OF FED AND UNFED *NEOMYSIS INTEGER*

(The pairs of experiments cited were set up simultaneously.)

Fed		Unfed	
Expt. no.	% carbohydrate per wet weight	Expt. no.	% carbohydrate per wet weight
11	0·31	27	0·15
12	0·20	28	0·28
13	0·42	29	0·16
14	0·22	30	0·20
15	0·24	31	0·20
16	0·28	32	0·25
17	0·23	*33*a*	0·21
		*33*b*	0·24
18	0·22	34	0·17
19	0·25	35	0·27
20	0·20	36	0·20

* Expt. 33 was run in duplicate.

A certain amount of cannibalism had been suspected in some of the earlier pairs of fed and unfed experiments, but only Expt. no. 33 gave clear proof. Lucas (1936) found *Hemimysis* carrying dead mysids and amphipods, and he observed that the prey was being masticated. Tattersall & Tattersall (1951) also claimed that mysids were partly carnivorous.

It may be suggested that in those experiments listed in Table 4, where the unfed mysids showed very little or no reduction in carbohydrate as compared with fed animals, the reserves of carbohydrate were maintained to some extent by some of the so-called unfed *Neomysis* feeding on their less active fellows.

Attempts were made to limit cannibalism by reducing the starvation period (e.g. Expt. nos. 34–36: 4–5 h starvation), but this in turn raised difficulties in that the period was then likely to be insufficient to reduce carbohydrate reserves markedly. The short-term starvation results, in fact, fell well within the range for the whole unfed series—0·27 and 0·20 %—and were by no means the lowest values obtained. While, therefore, it is difficult to ensure complete starvation conditions experimentally for *Neomysis*, there is little doubt that where marked reduction in feeding occurred, carbohydrate content was lowered.

The water content was determined on two samples of *Neomysis*, and the dry weight was found to be 19·0 and 19·9 %, respectively, of the wet weight. As an approximation, therefore, the dry weight was reckoned as 20 % of the wet weight, and the percentage of carbohydrate to dry body weight has been calculated for all the experiments. For fed animals the values varied from 2·10 to 1·00 % (mean 1·30 %); for unfed mysids, from 1·40 to 0·75 % (mean 1·06 %) (Tables 2 and 3).

Pleurobrachia pileus

The carbohydrate values found in *Pleurobrachia* varied from a maximum of 0·05 % of the body (wet) weight to as little as 0·001 %. In two experiments (Expt. nos. 42 and 50) the value was below 0·001 %, though the precise level was uncertain. The very low values are explainable largely on the high water-content characteristic of ctenophores. The minimal values were barely detectable by the spectrophotometric method used, but the use of greater quantities of *Pleurobrachia* was not advantageous, since this also increased the volume of fluid. Although the figures for the lowest concentrations may be open to some criticism, there is no doubt that they are of the correct order of magnitude, and it therefore appears that there is an unusually wide range in the carbohydrate values obtained. This is in contrast to the results for both *Calanus* and *Neomysis*, where although a range was experienced, this was not nearly so great, unless animals were specifically starved. All the results quoted for *Pleurobrachia* in Table 5 were for fresh animals analysed as soon as possible—certainly the same day as collected. However, some hours elapsed, with the sorting of plankton hauls and preparation of the material, before the analyses, and this was especially true where several sets of determinations were made in one day. It is well known that *Pleurobrachia* is an active swimmer, and also a voracious and destructive carnivore, feeding on zooplankton. It is probable that like many other marine carnivores, the speed of digestion and assimilation is high, and the great variability in the carbohydrate content of freshly caught animals may reflect the variation between those that have fed very recently and those animals which have not eaten for a few hours. Some support for this theory comes from the analyses in Expt. nos. 58–62 (Table 5) which were specifically carried out on *Pleurobrachia* which were caught, sorted and used as rapidly as possible. The results gave carbohydrate contents varying from 0·010–0·007 %, i.e. the range was not so great, and no extraordinarily low values were obtained. By contrast, a few *Pleurobrachia* were left to starve in the laboratory in breffits of filtered sea water for 48 h. They were still healthy and active after starvation, but when analysed gave very much lower sugar values (viz. 0·0015– 0·0010 %).

TABLE 5. CARBOHYDRATE CONTENT OF *PLEUROBRACHIA PILEUS*

Expt. no.	% carbohydrate per wet weight	% carbohydrate per dry weight
37	0·011	0·275
38	0·057	1·425
39	0·002	0·050
40	0·007	0·175
41	0·005	0·125
42	< 0·001	< 0·025
43	0·006	0·150
44	0·001	0·025
45	0·009	0·225
46	0·007	0·175
47	0·001	0·025
48	0·001	0·025
49	0·001	0·025
50	< 0·001	< 0·025
51	0·046	1·150
52	0·003	0·075
53	0·004	0·100
54	0·002	0·050
55	0·003	0·075
56	0·001	0·025
57	0·002	0·050
58	0·007	0·175
59	0·006	0·150
60	0·009	0·225
61	0·008	0·200
62	0·009	0·225

Expt. nos. 58–62 refer to determinations made on animals immediately following capture.

Though the evidence is not strong, these last experiments suggest that carbohydrate is utilized by *Pleurobrachia* fairly rapidly. Some *Pleurobrachia* were fed on zooplankton in the laboratory, but we were unable to feed a sufficient number to obtain a reliable analysis for experimentally fed animals. Analyses made by one of us (S. K.) on *Pleurobrachia* suggested that the dry weight of the body amounted to only 3·75 and 4·62 %, respectively, of the wet weight. This agrees fairly well with the values of 4·6 % (Cooper, 1939), and 4·5 % (Vinogradov, 1953). We have assumed a mean value of 4 % for all our experimental animals and from this we have calculated the percentage of carbohydrate to dry weight of body. The maximum obtained is 1·43 %, but values as low as 0·025 % were also found (Table 5).

DISCUSSION

The data presented on the carbohydrate reserves of certain planktonic animals, though preliminary, suggest that the amount of sugar in the body is low. For *Calanus* the maximum would appear to be of the order of 0·2% of the wet body weight; for *Neomysis*, where our values are a little more certain, the maximum is approximately 0·4% of the wet body weight. It is of some interest that in a determination made on the copepod *Anomalocera patersoni* the amount of carbohydrate was 0·17% of the wet body weight. This is of the same order as the mean figure for freshly caught *Calanus*. For *Pleurobrachia*, as would be expected from the very high water content, even the maximum percentage (0·057%) is much lower than for the crustaceans, but the difference is less obvious if we calculate carbohydrate as a percentage of dry body weight. Thus, for *Neomysis* the maximum is 2·1%, whereas for *Pleurobrachia* it is 1·4%. These values are very much lower than those suggested by Brandt (1898) and Brandt & Raben (1919) for plankton. For example, for 'copepods', Brandt (1898) gives a summary: protein 59%, fat 7%, carbohydrate 20%, chitin 4·7%, ash 9·3%. Thus his figure for the amount of carbohydrate reckoned on a dry-weight basis is approximately × 10 our suggested values. However, Brandt's values are based on a few analyses of mixed marine plankton hauls (predominantly copepods) and also on some analyses of freshwater copepods, and it is difficult to compare his data with analyses of single species of zooplankton. It may be significant that Brandt & Raben (1919) give an analysis for a named zooplanktonic species (*Sagitta*) and the percentage of carbohydrate is then lower (*ca.* 14%).

Our preliminary data also suggest that there is a rise in carbohydrate in our animals with feeding. This agrees with the findings of previous workers, who showed a rise in blood sugar levels with feeding in crayfish and insects (Hemmingsen, 1924). There also appears to be a fall in the total carbohydrate content in starving planktonic animals, as has been found in the shore form *Carcinus* by Kleinholz & Little (1949), and this fall could be associated with activity, suggesting thus that sugars may be metabolized to some extent. However, as the rate of utilization of sugar is not rapid, it might be inferred that fat is utilized to a greater extent.

A few preliminary analyses of the fat content of *Neomysis integer*, using the method of Kumagawa & Suto (1908), as modified by von Brand, Weinstein, Mehlman & Weinbach (1952), gave fat values varying from 0·2 to 0·8% of the wet body weight. Since the dry weight is only a fifth of the wet weight of the body (p. 244) the amount of fat varies from 1 to 4% of dry body weight. Orr (1934*a*, *b*) quotes values of 20–40% as the fat content in *Calanus* and *Euchaeta*, reckoned on a dry-weight basis. Brandt (1898), however, gave a value of *ca.* 7% for copepods which is more comparable to the present figures.

It is generally known that carbohydrates may be converted into fats by many vertebrates. Whether a similar process is involved in these planktonic animals is uncertain, but it could be responsible for the low carbohydrate, as compared with high fat values, in zooplankton. It is also of interest to recall the suggestion made by Zeuthen (1955), based on respiratory quotient studies in butterflies, that carbohydrates, when they are metabolized, are first converted to fat before combustion in the muscles. Whether a similar process goes on in crustaceans is not known.

We are grateful to the Director and Staff of the Marine Biological Laboratory for all facilities during our work at Plymouth.

SUMMARY

The carbohydrate content of three species of planktonic animals (*Calanus finmarchicus*, *Neomysis integer*, *Pleurobrachia pileus*) was estimated.

In *Calanus* fed on phytoplankton the carbohydrate content varied from 2·24 to 0·63 μg per copepod or 0·18–0·05 % of the wet body weight. In fed *Neomysis* the carbohydrate content was 0·42–0·20 % of the wet body weight. Analyses of *Pleurobrachia* gave values for carbohydrate of 0·05–0·001 % wet body weight.

In all three species it appeared that starvation tended to lower the carbohydrate content.

The mean percentage of carbohydrate expressed as dry body weight is approximately 0·4 % for *Calanus*, 1·3 % for *Neomysis* and 0·2 % for *Pleurobrachia*.

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J. mar. biol. Ass. U.K. (1960) 39, 249–254
Printed in Great Britain

THE FECUNDITY OF ENGLISH CHANNEL PLAICE

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(Text-figs. 1–2)

This paper is the fourth in a series dealing with the fecundity of flatfish (Bagenal 1957*a*, *b*, 1958), and is concerned with the egg numbers in ripening female plaice *Pleuronectes platessa* L. caught in the English Channel.

On 27 November 1957, eighty-five plaice with maturing ovaries were caught in Rye Bay, Sussex; on 1 December, eight similar fish were caught in Lyme Bay, and during December sixty-four locally caught female plaice were brought in to the Plymouth Laboratory. The dates of the collections were chosen because in January 1957 I had found that a small proportion of the Plymouth plaice were spent. All the fish caught in November and December were at a suitable stage for fecundity estimation: that is, the eggs were well developed though none had begun to turn translucent.

The treatment of the fish was similar to that already described (Bagenal, 1957*a*) for long rough dabs, except that the Rye Bay and Lyme Bay plaice were weighed on a spring balance to the nearest quarter ounce and these weights were subsequently transformed to grammes; the Plymouth fish were weighed to the nearest 5 g. The paper on long rough dabs should be consulted for details of the laboratory methods of preservation, the estimation of the fecundity and the statistical analysis of the data.

I would like to thank Captain C. A. Hoodless and the crew of R.V. 'Sarsia' for their help at sea and Mr A. D. Mattacola and the Plymouth Laboratory staff for their help on land and also Miss Sheila Morris who counted the eggs.

RESULTS

The data are summarized in Tables 1 and 2 along with the fecundity data for the Clyde (from Bagenal, 1958) and for the Southern Bight of the North Sea (from Simpson, 1951). The relations of fish length and fecundity are shown in Figs. 1 and 2. The relations of age and fecundity are given in Table 3.

Plymouth

The fecundity of the Plymouth female plaice is the same as that of the Clyde fish; the difference between the two values for the expected fecundity ($\hat{F}$) of a 37 cm plaice could easily be due to random subsampling errors.

Simpson (1957) has found the fecundity of plaice from the Irish Sea to be similar to Clyde and Plymouth fish. The nearest locality from which he determined the fecundity was Cardigan Bay. It would be interesting to know the fecundity of the plaice that spawn off St Ives.

Plaice seem to be rare off Plymouth until mid-December at which time they begin to appear in increasing numbers prior to spawning in early January. We do not know where they come from.

TABLE 1. SUMMARY OF PLAICE FECUNDITY DATA

	Clyde	Plymouth	Lyme Bay	Rye Bay	North Sea
Number of fish	61	64	8	85	223
Mean length (cm)	38·33	42·47	37·57	38·35	37·13
Mean weight (g.)	585·8	758·8	688·1	518·8	518·4
Mean age	5·2	6·3	5·0	6·4	7·3
Mean fecundity	158,845	212,769	255,888	139,127	84,928
$\hat{W}$ for 37 cm	526·4	516·4	661·4	470·97	517·27
$\hat{F}$ for 37 cm	137,266	137,470	244,311	127,093	84,019

TABLE 2. THE MEAN FECUNDITY (IN THOUSANDS) OF EACH 3 CM LENGTH GROUP OF ENGLISH CHANNEL FEMALE PLAICE

Length group	Plymouth Number	Plymouth Fecundity	Lyme Bay Number	Lyme Bay Fecundity	Rye Bay Number	Rye Bay Fecundity
30	—	—	—	—	6	70·21
33	5	125·06	4	172·80	23	89·62
36	8	113·88	2	131·20	16	117·82
39	10	129·62	—	—	14	125·83
42	13	207·71	1	324·95	12	186·60
45	14	247·20	—	—	6	173·25
48	8	266·62	—	—	2	250·60
51	3	313·82	—	—	2	268·53
54	2	419·85	—	—	1	230·35
57	—	—	1	768·55	1	264·15
60	1	709·55	—	—	—	—
63	—	—	—	—	2	442·63

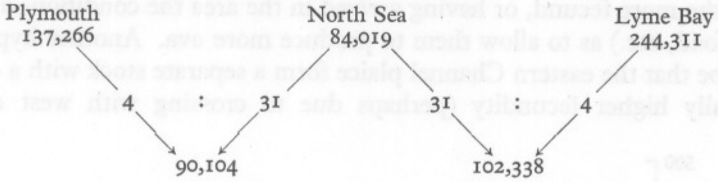
Rye Bay

The fecundity of the eighty-five Rye Bay plaice is intermediate between that of Plymouth and North Sea fish. From marking experiments in Rye Bay (Wimpenny, 1953) we know that the plaice migrate both into the North Sea and to the west. Wimpenny's results are summarized below.

Released	No.	Local returns	Eastward movement	Westward movement
January	300	56	31	4
April	?	87	49+	—
July	No tendency to move to the westward			
October	Suggested that what little movement there had been was in a westerly direction			

Three of the four westerly moving plaice were caught off Brixham (West end of Lyme Bay) and one from off South Ireland. Mixtures of west channel and

North Sea plaice in the ratio of 4:31 should produce a mean fecundity for 37 cm fish of between 90 and 102 thousand eggs.



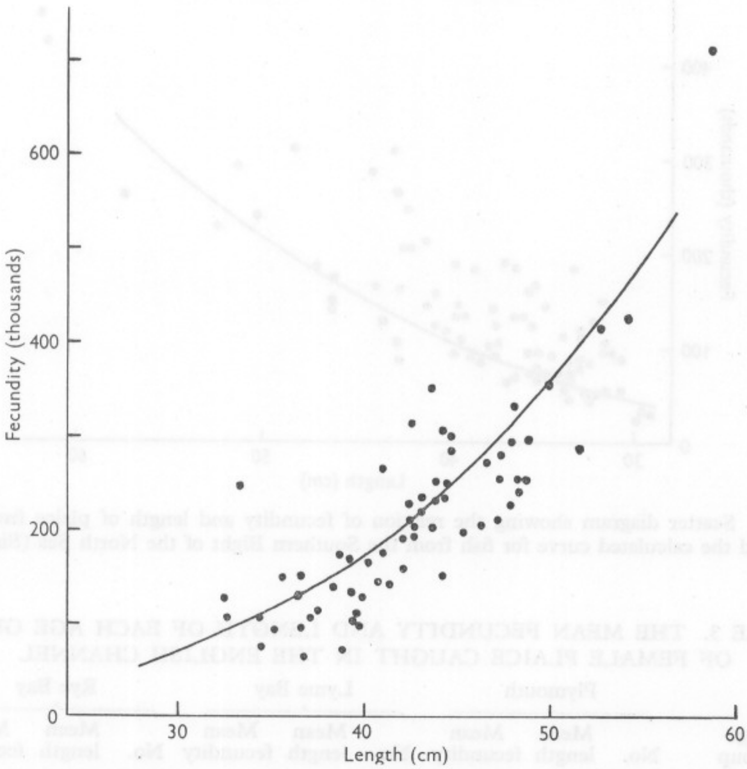


Fig. 1. Scatter diagram showing the relation of fecundity and length of plaice from Plymouth and the calculated curve for Clyde fish (Bagenal, 1958).

The actual fecundity of 127 thousand eggs for 37 cm plaice might be the average of fish mainly derived from the North Sea, but with a mixture of more plaice from the west than marking experiments suggest do exist in the area: over one-third of the population would have to be of western origin. Moreover, the scatter diagram (Fig. 2) shows that the general level of fecundity for the Rye Bay population as a whole is above that of the North Sea.

Simpson (1959) discusses the spawning of North Sea plaice and believes that 'the spawning area in the eastern English Channel is not an independent spawning area, but is, in effect, a spill-over from the main Southern Bight area'. If this is true either the spill-over is not of typical North Sea fish but selects the more fecund, or having arrived in the area the conditions are such (more food, etc.) as to allow them to produce more ova. Another hypothesis would be that the eastern Channel plaice form a separate stock with a characteristically higher fecundity (perhaps due to crossing with west channel

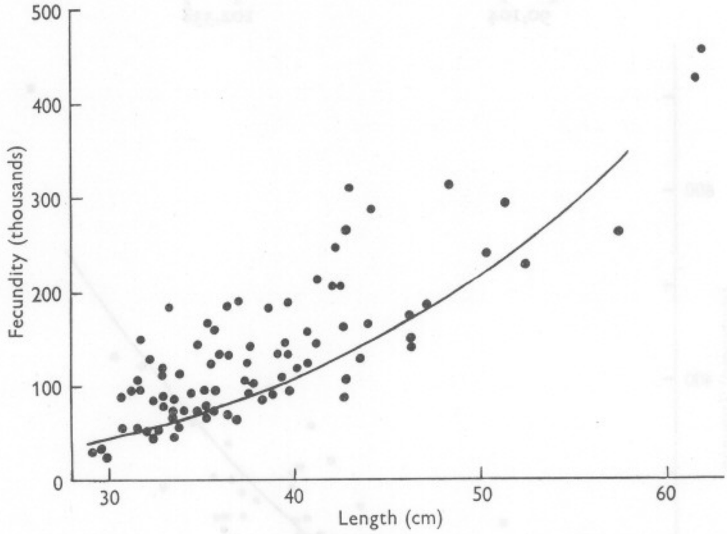


Fig. 2. Scatter diagram showing the relation of fecundity and length of plaice from Rye Bay and the calculated curve for fish from the Southern Bight of the North Sea (Simpson, 1951).

TABLE 3. THE MEAN FECUNDITY AND LENGTH OF EACH AGE GROUP OF FEMALE PLAICE CAUGHT IN THE ENGLISH CHANNEL

	Plymouth			Lyme Bay			Rye Bay		
Age group	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity
II	—	—	—	—	—	—	4	31·3	96·4
III	4	36·2	162·1	2	32·7	242·6	10	32·9	77·6
IV	4	38·6	164·9	1	36·2	158·8	9	34·9	124·3
V	15	40·6	172·8	3	33·1	103·2	16	34·6	107·8
VI	11	42·3	198·6	1	41·8	325·0	13	37·6	124·0
VII	12	41·5	183·6	—	—	—	9	37·0	122·9
VIII	6	46·9	298·5	—	—	—	4	42·7	221·1
IX	6	46·6	239·3	1	57·9	768·6	8	43·3	139·3
X	2	53·4	419·9	—	—	—	3	43·7	154·0
XI	—	—	—	—	—	—	2	44·5	206·0
XII	—	—	—	—	—	—	2	46·7	277·1
XIII	—	—	—	—	—	—	—	—	—
XIV	—	—	—	—	—	—	1	52·5	230·4
XV	—	—	—	—	—	—	1	57·5	264·2
XVI	—	—	—	—	—	—	1	51·3	296·6
XVII	—	—	—	—	—	—	1	61·7	427·9

fish). This would involve the return of those adult fish that migrate into the North Sea as well as the return of the young that have drifted there as eggs and larvae The return of young to the exact breeding place of their parents is well known in salmonids and birds.

The growth rate of eighty-five Rye Bay plaice as shown in Table 3 is comparable to that given by Wimpenny (1947) after allowance is made for the time of year of the collections. The rate of growth is faster than that of North Sea plaice, and this is similar to the situation at Flamborough.

It is perhaps significant that the smaller areas such as Flamborough and Rye Bay that are out-lyers of the main North Sea plaice grounds carry stocks with higher fecundities, and faster growth rates.

Lyme Bay

The eight Lyme Bay plaice have a high mean fecundity but this is to some extent increased by one fish of 58 cm in length which was exceptionally fecund.

Four hours fishing off Brighton, and some 12 h trawling in Poole Bay did not yield any plaice and the eight females from Lyme Bay were caught in over 4 h fishing.

In the middle region of the Channel therefore plaice are very scarce in late November, and even at Plymouth they do not appear to become plentiful until mid-December. It is not possible at this stage to confirm an inverse relation between fecundity and population density, because of the complications imposed by migration. Nor is a relation between fecundity and condition immediately apparent. This is shown by the North Sea plaice which were in better condition than those in Rye Bay (a 37 cm fish has a heavier expected weight) but had a lower fecundity.

SUMMARY

The plaice off Plymouth are shown to have a level of fecundity comparable to the Irish Sea and Clyde. The plaice in Rye Bay have a fecundity intermediate between that of the Clyde–Irish Sea–Plymouth fish, and the North Sea plaice, but this is apparently not produced by a mixing of the two populations, either the environment favours a high fecundity, or the Eastern Channel plaice form a separate stock.

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J. mar. biol. Ass. U.K. (1960) 39, 255–262
Printed in Great Britain

THE FECUNDITY OF PLAICE FROM THE SOUTH AND WEST COASTS OF IRELAND

By T. B. Bagenal

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(Text-figs. 1–3)

This paper is the fifth in a series dealing with the fecundity of flatfish (Bagenal, 1957*a*, *b*; 1958, 1960), and is concerned with the numbers of eggs in the roes of ripening female plaice *Pleuronectes platessa* L. caught off the south and west coasts of Ireland during November and December 1958. The fish were obtained from Wexford, Ballycotton, Schull, Dingle, Galway and Killybegs (Fig. 1).

The fish were bought immediately after being landed either direct from the fishermen, when the whole female catch was obtained, or through An Bord Iascaigh Mhara when a predetermined number were taken as they lay in a fish box. The fish bought from the fishermen were ungutted, but those obtained from the Board had been gutted. A few of the latter fish had to be rejected as the ovaries were damaged, but it was an insignificant percentage. Thereafter the treatment of the fish, storage of the ovaries, the subsampling and counting of the eggs and the statistical analysis of the results were all as described in an earlier paper (Bagenal, 1957*a*) except that the four aliquot samples of eggs consisted of 1/410 instead of 1/200. This greatly reduced the time and labour of egg counting.

I would like to thank the employees of An Bord Iascaigh Mhara who helped me in Ireland and Miss Sheila Morris for her help in the laboratory.

RESULTS

The data are summarized in Tables 1–3, and the relation of fish length and fecundity are shown in Figs. 2 and 3. The expected weight ($\hat{W}$) and the expected fecundity ($\hat{F}$) of a fish 37 cm long are also shown in Table 1. They were calculated from the regression equations of log length on log weight and on log fecundity, respectively, and may be used for comparing the different populations. The regression coefficients (*b*) are also shown. (For details of the calculations see Bagenal, 1957*a*.) Numerous tests were made to see if any of the differences in fecundity and condition were significant.

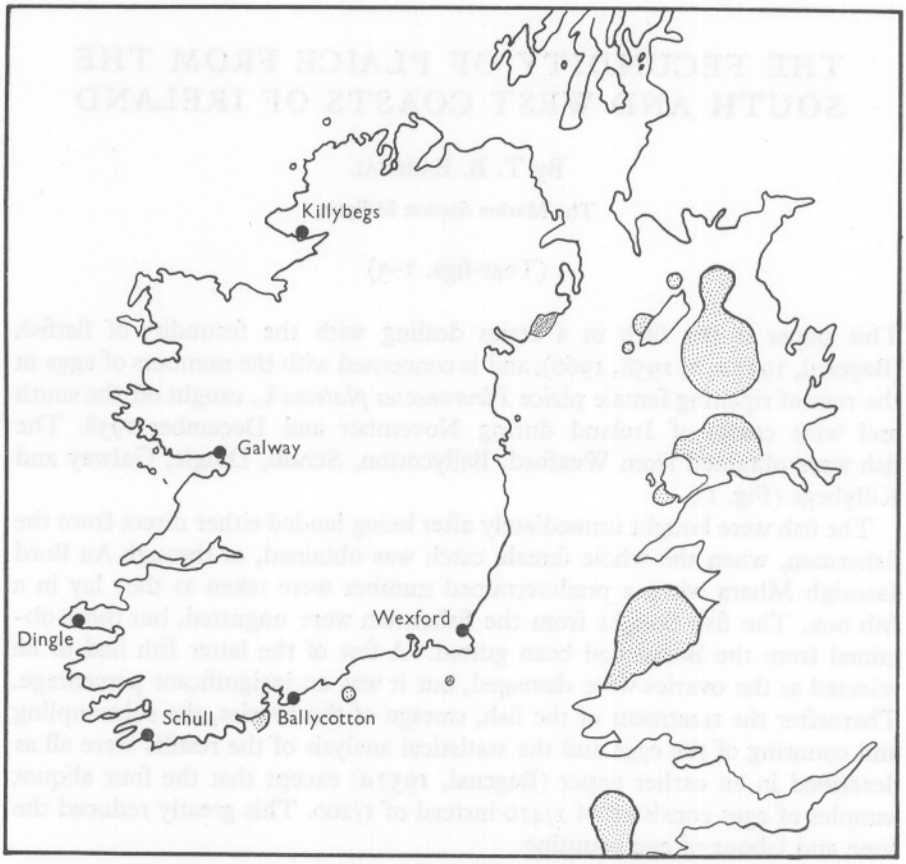

Fig. 1. Map of Ireland and the Irish Sea, showing localities from which plaice were collected, and (stippled) the spawning areas found by Simpson.

Wexford

Simpson (1959*b*) made a survey of plaice eggs in 1952 and 1953 in the Irish and Celtic Seas from Newcastle (Co. Down) to west of Cork. He gives maps indicating the occurrence of newly spawned eggs. The largest concentration of eggs nearest to Wexford was found in Cardigan Bay (about 60 miles to the east across St George's Channel on the Welsh coast), and, although one egg was found south of Saltee Island, the Wexford plaice probably belong to the Cardigan Bay stock. The fecundity of the Wexford plaice was not found to differ from that of the Plymouth plaice (Bagenal, 1960) or from those of the Clyde (Bagenal, 1958) and appear to be similar to those in the Irish Sea for which Simpson (1957) has given the preliminary results. The plaice on the north–south line through the Clyde–Irish Sea–West Channel on longitude 5° west have similar fecundities.

Ballycotton

Simpson found one planktonic plaice egg off Minehead in 1955 (Survey 1, 23 January–3 February). I found plaice very scarce at Ballycotton, 20 miles west. Their fecundity, however, was high.

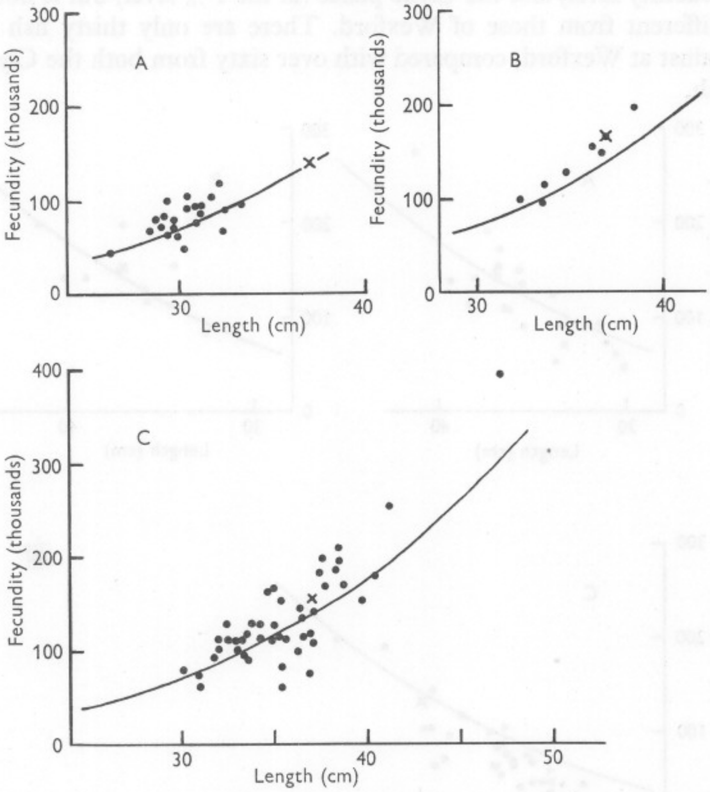

Fig. 2. Scatter diagrams showing the relation of fecundity and length of plaice from (A) Wexford, (B) Ballycotton and (C) Dingle. In some cases dots are superimposed on others. The expected fecundity ($\hat{F}$) of fish of 37 cm is shown in each diagram by × and the calculated curve for Clyde fish is given for comparison.

Schull

West of Cork Simpson appears to have found the edge of a concentration of plaice eggs whose centre lay farther still to the west. At Schull, plaice were again scarce and only ten could be got in a reasonable time. Even though the Schull and Ballycotton plaice have very high fecundities, they are not statistically significantly different from those of Wexford, but the samples are unfortunately very small.

Dingle

At Dingle, plaice were plentiful and the roes from a good sample of fifty fish were easily obtained. These, like those from Schull, have a high fecundity. Their fecundity is significantly higher than that of Plymouth fish (at the 5 % probability level) and the Clyde plaice (at the 1 % level) but is not statistically different from those of Wexford. There are only thirty fish to test them against at Wexford, compared with over sixty from both the Clyde and Plymouth.

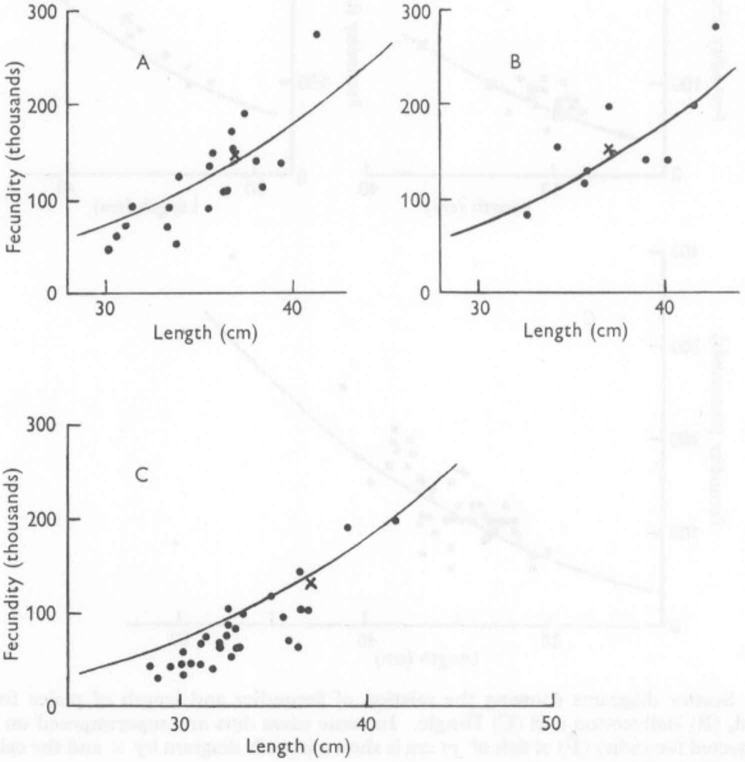

Fig. 3. Scatter diagrams showing the relation of fecundity and length of plaice from (A) Galway and (B) Schull and (C) Killybegs. In some cases dots are superimposed on others. The expected fecundity ($\hat{F}$) of fish of 37 cm is shown in each diagram by × and the calculated curve for Clyde plaice is given for comparison.

Galway

The Galway plaice were caught off Clare Island. Their fecundity is lower than that of the Dingle fish, but the difference is not statistically significant.

TABLE 1. SUMMARY OF IRISH PLAICE FECUNDITY DATA

	Wexford	Bally-cotton	Schull	Dingle	Galway	Killybegs
Number of fish	30	8	10	50	20	31
Mean length (cm)	30·67	35·40	37·59	35·51	35·41	33·17
Mean weight (gr)	292·63	458·50	549·90	483·56	464·70	358·52
Mean age (years)	2·9	3·3	2·8	3·1	3·2	3·8
Mean fecundity	84,002	139,336	158,137	133,195	120,811	82,162
W for 37 cm	505·3	539·2	523·8	549·4	521·4	501·2
F for 37 cm	139,612	169,342	150,641	152,775	146,182	132,120
Regression coefficient (*b*)	2·71	4·15	3·10	3·33	4·33	4·35

TABLE 2. THE MEAN FECUNDITY (IN THOUSANDS) OF EACH 3 CM LENGTH-GROUP OF IRISH FEMALE PLAICE

Length group	Wexford		Ballycotton		Schull		Dingle		Galway		Killybegs	
	No.	Fecundity	No.	Fecundity	No.	Fecundity	No.	Fecundity	No.	Fecundity	No.	Fecundity
27	1	45·72	—	—	—	—	—	—	—	—	—	—
30	21	81·39	—	—	—	—	3	70·42	3	60·92	9	47·83
33	8	95·63	3	104·76	2	116·65	17	107·77	5	87·74	13	78·21
36	—	—	4	150·42	4	146·19	19	122·98	7	132·11	7	101·08
39	—	—	1	198·75	2	140·48	8	181·57	4	148·04	1	192·60
42	—	—	—	—	2	241·18	2	216·17	1	277·88	1	199·67
45	—	—	—	—	—	—	—	—	—	—	—	—
48	—	—	—	—	—	—	1	394·83	—	—	—	—

TABLE 3. THE MEAN FECUNDITY AND LENGTH OF EACH AGE-GROUP OF FEMALE PLAICE CAUGHT OFF SOUTH AND WEST IRELAND

Age group	Wexford			Ballycotton			Schull			Dingle			Galway			Killybegs		
	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity
II	6	31·4	103·6	—	—	—	3	35·8	115·8	16	33·2	109·2	4	34·0	96·5	3	30·6	61·5
III	21	30·4	79·5	4	34·0	117·5	5	38·9	178·5	18	35·3	123·5	10	34·0	98·6	12	31·7	61·9
IV	3	31·1	76·2	2	35·8	139·8	1	37·0	198·0	10	37·4	156·7	4	38·9	196·7	9	34·0	93·3
V	—	—	—	—	—	—	—	—	—	1	40·5	178·2	2	38·4	129·0	3	33·4	68·8
VI	—	—	—	—	—	—	—	—	—	1	35·2	122·8	—	—	—	3	35·9	124·7
VII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	41·6	119·7
VIII	—	—	—	—	—	—	—	—	—	1	47·3	394·8	—	—	—	—	—	—

Killybegs

Thirty-one female plaice were sampled at Killybegs, the fish having been caught in Donegal Bay. The fecundity is lower than at Galway, and significantly lower at the 1 % level than the fecundity of the Dingle fish, but the mean fecundity of the Killybegs plaice does not differ significantly from the Clyde fish, though the slopes of the lines ($b = 3{\cdot}21$ for the Clyde and $4{\cdot}35$ for Killybegs) are nearly significantly different at the 5 % level.

DISCUSSION

The fecundity of plaice increases westwards along the south coast to Dingle and then decreases northwards along the west coast to Killybegs. Added to these general trends there is a further feature that small populations of plaice which are living in 'bleak' habitats appear to have a higher fecundity than neighbouring larger populations. This is seen at Ballycotton and Schull, as well as at Lyme Bay (Bagenal, 1960). The mechanism behind these differences in fecundity is still obscure, but the survival value of them is quite clear. Dingle and Schull, being in the south-west of Ireland, are not only in an extremely exposed region, but also are in the track of the prevailing south-westerly winds and currents. There will therefore be a much greater chance of the planktonic eggs and young being transported long distances, than for example in the North Sea. Similarly, in small populations the dispersal of the planktonic eggs and larvae may at times be catastrophic. In both cases a high fecundity will increase the chances of sufficient of the progeny being able to return to the breeding area. This view implies that the fish return to the area where they themselves were spawned regardless of their movements in the meantime.

A similar explanation (Bagenal, 1960) has been put forward for the higher fecundities that have been found with Flamborough and Rye Bay plaice, both of which are small outliers of the main North Sea population. The North Sea plaice that spawn to the south of the Dogger Bank, and particularly the largest concentration in the Southern Bight (Simpson, 1959*a*, fig. 35), have the lowest fecundities that have been recorded for this species (Simpson, 1951), and this is a relatively sheltered and enclosed area.

A further point of significance is the ranked order of fecundity and condition. For the Irish data given in Table 1, the ranks are

Condition		Fecundity	
Dingle	549	Ballycotton	169
Ballycotton	539	Dingle	153
Schull	524	Schull	151
Galway	521	Galway	146
Wexford	505	Wexford	140
Killybegs	501	Killybegs	132

The ranked order for fecundity and condition of fish including data from other British areas is given below.

Condition		Fecundity	
Lyme Bay	661	Lyme Bay	244
Dingle	549	Ballycotton	169
Ballycotton	539	Dingle	153
Clyde	526	Schull	151
Schull	524	Galway	146
Galway	521	Wexford	140
North Sea	517	Plymouth	137·5
Plymouth	516	Clyde	137·3
Wexford	505	Killybegs	132
Killybegs	501	Rye Bay	127
Rye Bay	471	North Sea	84

The difference here, apart from the interchange of positions by Ballycotton and Dingle, and by Wexford and Plymouth, are due to Clyde and North Sea being four places higher in the fecundity rank. The most likely reason for the greater weight of these fish is that they were probably caught earlier in the year, that is, a longer time before the spawning season. As the time of spawning approaches the condition of the somatic tissue decreases very rapidly though the gonads of course are increasing in weight. It is for this reason that I attach little importance to the weight of the fish or their gonads in fecundity work (cf. Kändler, 1959), unless the spawning season is well known. That these weights are important factors to be considered if the spawning dates are known is obvious, and they may be useful when comparing two nearby localities at nearly the same time. In this case the fish will probably be at comparable stages in their breeding development. This, I think, is true of the Irish data.

Another point that is apparent from Table 3 is that the growth rate also increases along the south coast, and decreases again northwards. At Dingle the mean length of eighteen fish in the III age-group was 35·3 cm, though in the North Sea plaice often do not reach this length until their sixth year. The order of localities ranked for the rate of growth of fish is not the same as for condition or fecundity, though as has been found elsewhere (Simpson, 1951; Bagenal, 1958) the fast growing fish do tend to be those with the higher fecundity.

SUMMARY

The fecundity of plaice from six localities on the south and west coasts of Ireland has been analysed. For a 37 cm fish the fecundity increases from about 140 thousand eggs at Wexford to 153 thousand eggs at Dingle, and decreases northwards to 132 thousand at Killybegs, though at Ballycotton and Schull where plaice are scarce the fecundity is unusually high. It is suggested that the fecundity is an adaptive character, being highest in the poorer habitats and in regions where the dispersal of the planktonic stages will be greatest. This

implies that plaice, like other fish, return to an hereditary spawning area. In the poor habitats the fish have to be in good condition, grow fast and have a high fecundity in order to survive.

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J. mar. biol. Ass. U.K. (1960) 39, 263–274
Printed in Great Britain

THE MOTILE (*CRYSTALLOLITHUS HYALINUS* GAARDER & MARKALI) AND NON-MOTILE PHASES IN THE LIFE HISTORY OF *COCCOLITHUS PELAGICUS* (WALLICH) SCHILLER

By Mary Parke and Irene Adams

The Plymouth Laboratory

(With 43 Figures on Plates I–IV)

A new coccolithophorid, *Crystallolithus hyalinus*, was described with the help of electron micrographs by Gaarder & Markali in 1956 from preserved material in which the cells lacked the appendages. From temporary cultures set up from our September 1957 sea-water samples a coccolithophorid was isolated which appeared, under the light microscope, very similar to this newly described coccolithophorid but which possessed, as does the genus *Chrysochromulina*, a coiling haptonema in addition to the two flagella. Electron micrographs, taken for us by Prof. I. Manton, have shown that the holococcoliths from our organism are identical in structure with those from the *Crystallolithus hyalinus* (cf. Pl. I, and Gaarder & Markali, 1956, pl. I).

In addition, we have shown by culturing that the motile *C. hyalinus* bearing holococcoliths (crystalloliths) is in fact the motile phase in the life history of another coccolithophorid previously known only in the non-motile phase. This non-motile phase, bearing heterococcoliths (placoliths) which are structurally different from those borne on the motile phase, can be referred to the well-known species *Coccolithus pelagicus* (Wallich) Schiller.

The finding of two distinct structural types of coccoliths (see Braarud, Deflandre, Halldal & Kamptner, 1955; Halldal & Markali, 1955; Kamptner, 1958) in the life history of one coccolithophorid will necessitate a complete reassessment of the problems connected with the classification of the Coccolithophoridae.

Very grateful thanks are due to Prof. Irene Manton for examining our organism under the electron microscope and for compiling for us Plate I of this paper. We are also indebted to Dr L. H. N. Cooper and Mr E. I. Butler for the collection of sea-water samples, and to Mrs B. Hepper for testing this organism for its possible toxicity to fish.

THE MOTILE 'CRYSTALLOLITHUS' PHASE

As two strains (Plymouth no. 182, at position 50° 02′ N., 04° 22′ W., at 10 m on 17 September 1957, deposited with the Collection of Algae and Protozoa, Cambridge; Plymouth no. 217, at position 47° 19′ N., 07° 23′ W., at 20 m on 20 April 1958) are being maintained in the Plymouth culture collection, additional information from living material can be given to supplement the description given by Gaardner & Markali from preserved material.

The Crystallolithus phase swims only for short periods in one direction and moves comparatively slowly, rotating slowly also but showing sometimes considerable gyration. It can swim with the flagella and haptonema in front, or behind the body with the haptonema coiled or extended. As in some *Chrysochromulina* species (Parke, Manton & Clarke, 1955, 1956) swimming is more rapid when the flagella and haptonema are directed backwards, but unlike most of the *Chrysochromulina* species in which the haptonema is coiled during rapid swimming, the haptonema in this form is seen more usually fully extended when swimming in either direction.

In culture the cells of this phase are globose to subglobose, measuring 8–18 (exceptionally 6–20) μ in diameter (in a rapidly growing culture 18% of the cells are 6–10 μ, 55% 10–15 μ, and 27% 15–20 μ). The uninucleate cells have two or four deep golden brown parietal saucer-shaped to oblong chromatophores, deeply cleft into two at the non-flagellar pole. Conspicuous lipid bodies lie near the inner faces of the chromatophores, and leucosin vesicles are developed towards the non-flagellar pole. Two acronematic flagella, usually homodynamic, and one haptonema arise close together at one pole (Pls. I, II). The flagella are very fine and rather stiff, equal or unequal in length, 1·5–2·5 times the cell diameter in length. There can be a difference of up to 6 μ in the length of the two flagella of an individual cell. The short haptonema, thinner than the flagella and coiled round once or twice when not extended as a rod, usually measures ½ to ¾ of the cell diameter in length when fully extended; it has a small club-shaped tip and shows a basal swelling (Fig. 2, Pl. I) similar to that found in *Chrysochromulina kappa* (Parke *et al.*, 1955, pl. IV) and *C. ericina* (1956, pl. II).

The periplast of the cell has embedded, in its surface layer, very thin transparent oval to elliptical sculptured plate-scales, the sculpturing being visible only with the electron microscope. The scales show on one face a radiating pattern of ridges which reach to the edge (Fig. 4, Pl. I), while the other face usually shows either a network of fibres (Fig. 5, Pl. I) or sometimes roughly concentric surface ridges of varying width. In any one cell the scale size can range from 0·4 to 3·3 μ in diameter but the most frequent size is from 1·5 to 2·0 μ.

The Crystallolithus phase of *Coccolithus pelagicus* differs from the motile phases of members of the genus *Chrysochromulina* in having calcite microcrystals deposited on the scales, and also apparently in the composition of the periplast. In addition to showing that scale size is extremely variable the electron micrographs have shown also that the calcite microcrystals, deposited on the scales in a definite pattern, the 'holococcolith' or 'crystallolith' (Braarud *et al.*, 1955), vary considerably in size depending on scale size. Scales below 1 μ show no crystals, but scales about 1 μ in length show a deposit of microcrystals which are clearly distinguishable (see centre Fig. 3, Pl. I). The edge length of the microcrystals can vary from 430 to 2500 Å according to the size of the scale.

In the Crystallolithus phase the body has a two-layered covering, an inner distinct layer, which is clearly visible in Figs. 13–16, Pl. II, and an outer hyaline striated layer in which the scales, bearing the crystalloliths on their outer face, are embedded (Figs. 8–16, Pl. II). With Schultze's solution the inner layer gave a reaction suggesting cellulose, but the outer hyaline layer failed to give any reaction for pectic material with Ruthenian Red; its composition therefore is unknown. This outer hyaline layer varies very considerably in thickness in different individuals, the range of thickness being from apparently absent (Fig. 7, Pl. II) to being about 2·5 μ thick (Figs. 8–16, Pl. II). The change in thickness of this outer layer will be dealt with in the section on reproduction.

Frequently more than one layer of crystalloliths can be distinguished in this outer striated layer (Figs. 11, 13, 16, Pl. II) but in spite of these layers of material surrounding the body, the Crystallolithus phase can exhibit phagotrophy as do the marine species of *Chrysochromulina* that have been studied (Parke *et al.*, 1955, 1956, 1958, 1959). Phagotrophy occurs very frequently, the cells ingesting graphite, bacteria and plant cells up to a size of 5 μ (Figs. 27, 28, Pl. III). Ingested material is taken in at the non-flagellar pole and is digested usually in the region towards that pole. An unusual procedure for the discarding of waste material then occurs which has not previously been recorded, although the discarding of empty walls of plant cells through a tube was reported for *Chrysochromulina ericina* (Parke *et al.*, 1956, p. 398). In the Crystallolithus phase waste material, still in active Brownian movement, is passed out of the body into the outer hyaline layer where it collects in a globule (or vacuole) which is pushed out gradually from the hyaline layer, taking part of this layer with it including the crystalloliths. It is then cut off from the cell surface and discarded as a sack or sphere. This process takes place more usually near the non-flagellar pole, but it has been seen to occur near the flagellar pole. The discarded globules can measure up to 7·5 μ in diameter. Under dark field it can be seen clearly that they are covered by coccoliths, and filled with minute granules still in active Brownian movement, but in preserved material these discarded globules could quite easily be mistaken for small coccolithophorids. The Crystallolithus stage has been tested and found non-toxic to fish.

Reproduction of the motile Crystallolithus phase is by fission to produce generally two daughter-cells of equal or unequal size. Incipient fission stages (Fig. 15, Pl. II) measure 18–21 μ in diameter but double fission stages producing more usually three daughter-cells but occasionally four and measuring 28–30 μ in diameter are not uncommon (cf. *Chrysochromulina*, Parke *et al.*, 1955, figs. 11, 44, 70). In the incipient fission stages the outer hyaline layer containing the crystalloliths has reached its maximum thickness and during fission appears to swell up and become detached from the body surface so that the two daughter-cells when they have rounded off lie free inside it. The daughter-cells emerge from this outer layer leaving it behind as an empty case (Fig. 31, Pl. IV) and in cultures the bottom of the flasks have a thick covering of these empty cases which persist for a considerable time. In the newly liberated daughter-cells (Fig. 7, Pl. II) the hyaline layer cannot be detected although both it and the sculptured scales may be present. The crystalloliths are definitely not developed at this stage but as the daughter-cell secretes a new hyaline covering, apparently in concentric layers, the crystalloliths are gradually produced on the scales (Figs. 8–14, Pl. II). Although the usual procedure is for the daughter-cells to emerge from the outer clear layer as 'naked' stages it is not unusual for the outer hyaline layer of the mother-cell, or part of it, to remain attached to the outside of the daughter cells so that when the new hyaline layer of the daughter-cell containing the crystalloliths is laid down, there is a second outer layer containing crystalloliths covering part of, or the whole of, the cell (Fig. 13, Pl. II).

THE NON-MOTILE *COCCOLITHUS PELAGICUS* PHASE

The stages in the life history found so far suggest very strongly a type of life history similar to that found in the *Chrysochromulina* species that have been studied (cf. Parke *et al.*, 1955, p. 593). The motile Crystallolithus cells pass into the non-motile phase when a culture is 5–8 weeks old. The cells collect on the bottom of the flask as a dark olive brown skin, which, if examined soon after its formation, shows masses of Crystallolithus-sized cells, the majority of which still retain the outer hyaline layer containing the crystalloliths (Fig. 16, Pl. II; Figs. 19, 29, Pl. III). At this early stage the cells, although lacking flagella, appear to retain their haptonemata as organs of attachment, as do the cells of the coccolithophorid, *Pleurochrysis scherffelii* Pringsheim, during the early stages of the non-motile phase. If samples of this skin from a Crystallolithus culture are not examined until about 2 weeks after its formation then the non-motile stages illustrated on Pl. III can usually be found. Among the smaller non-motile Crystallolithus individuals (Fig. 19), cells of much larger size (25–60 μ) have developed (Figs. 20–26) but their origin has not so far been traced. Fusion stages have been looked for consistently in cultures in this stage, but without success. Although knowledge of the first stage in the production of the large cells is lacking (cf. *Chrysochromulina*, Parke *et al.*, 1955, p. 593), unless it is just a type of cyst formation in which there is a gradual increase in cell size, the later stages in their development have been recorded. Whether or not the initial stage in the production of the large cells is a fusion of two cells there is still further enlargement during the later stages of development.

In the earlier stages of enlargement the cells (25–35 μ), still surrounded by the hyaline layer (Fig. 20), develop very large leucosin vesicles, which can fill up to three quarters of the volume of the cell (Figs. 20, 21). Later stages show either four (Fig. 30) or eight disk-shaped chromatophores (Fig. 22) and leucosin vesicles usually of smaller size. With further increase in cell size (35–60 μ) the leucosin reserve disappears (Fig. 20, bottom cell), the chromatophores become more lobed (Fig. 23) and numerous spheroidal to ovoid vesicles (2·5–5·5 μ), which darken on the outside with osmium tetroxide, gradually develop in the cells (Figs. 24–26). The production of these vesicles is an indication that the large placoliths of the *Coccolithus pelagicus* phase are beginning to form inside the cell. Single placoliths have been seen inside these large cells which still retain a very thin outer hyaline layer round the body (Fig. 26).

Normally the placoliths are deposited on the cell surface inside the thin hyaline layer (Fig. 17, Pl. II) before the double division of the large *C. pelagicus* mother-cell (Figs. 32, 36) to produce four *C. pelagicus* daughter-cells (Figs. 38–40, 42, 43); nevertheless, fission of the mother-cell into two (Fig. 25, Pl. III) or four (Fig. 26, Pl. III) can start while the placoliths are being deposited on the body surface. Our measurements of the different stages indicate that the mother-cells contract considerably in size while the placoliths are being deposited on the body surface (cf. similar stage in *Chrysochromulina* species, 1955, p. 593).

In culture, both the *Coccolithus pelagicus* mother- and daughter-cells show a wide range in size. The mother-cells are usually ovoid (Figs. 32, 36), measure from 25 to 40 μ in diameter, and bear from 25 to 35 placoliths, while the daughter-cells are always spheroidal in shape, measure from 10 to 22·5 μ in diameter, and bear from 8 to 17 placoliths. Sometimes the two *C. pelagicus* cells, product of the first division of the mother-cell (Figs. 38, 39), separate before the second fission; their size is from 20 to 30 μ and they bear from 16 to 28 placoliths. The placoliths on all stages are generally ovate in surface view (Fig. 33) with a central oval pore, usually subdivided by a bar into two equal parts (Fig. 6, Pl. I; Fig. 33, Pl. IV), but it is not uncommon for the dividing bar to be lacking; they measure usually from 8 to 11 μ in length but lengths of from 4·4 to 13 μ have been recorded. Placoliths circular in surface view, with a single central round pore, have also been observed, usually on daughter-cells, and placoliths abnormal in shape are also occasionally produced (Fig. 37). Thus, from the measurements obtained from culture the range of size of *C. pelagicus* cells that might be found in the sea is from 10 to 40 μ with the cells bearing from 8 to 35 placoliths, the placoliths themselves varying from 4·4 to 13 μ in length.

Although the natural emergence of a Crystallolithus motile cell from a *C. pelagicus* daughter-cell has not been witnessed, it is possible to force out the Crystallolithus cell from its covering by exerting slight pressure on a daughter-cell ready to liberate its contents. The cell which emerges has two chromatophores and is similar in appearance to the Crystallolithus cell illustrated in Fig. 7, Pl. II, except that the flagella and haptonema are lacking. Cells released in this way have a diameter 3–5 μ less than that of the placolith covering. Normal release is by a pore produced by the casting off of a single placolith (Fig. 41, Pl. IV), which can be seen frequently still attached by one edge to the empty daughter-cell.

Cultures of this organism have been started each month throughout the year by inoculating with the motile phase. In the spring, the *C. pelagicus* phase can occasionally be found in cultures 5–7 weeks old, but at other times of the year the cultures are more usually 10–12 weeks old, sometimes older, before the *C. pelagicus* phase is produced. *C. pelagicus* can persist in unialgal culture in a healthy condition for at least 12 months (records for longer period not yet available) without being subcultured and without the addition of nutrients other than those in the medium (Erd-Schreiber) when the culture was started. Our records for the 12-month period, for a number of cultures, show that there is a regular alternation of the motile Crystallolithus and the non-motile *C. pelagicus* phase during the period. The persistence in unialgal culture of this species for such a long period in a healthy and vigorous state, without requiring additional nutrients (including iron) for rapid growth, suggests that the phagotrophy shown by the motile Crystallolithus phase may be in part responsible for this behaviour.

For the years 1921–22, Lebour (1923) records *C. pelagicus* (non-motile phase) as occurring at all depths from the surface to 100 m almost all the year round from the Plymouth region, the western part of the Channel and outwards towards the Irish Sea and the French coast. It was most frequent in March and October and less frequent from June to August than in the remaining months. Our records, for the nanoplankton occurring at Stations E1 and L2 to 6 for 1957–59, show that this phase occurs now much less commonly in the waters off Plymouth than it did in 1921 and 1922. In the three years 1957-59 its presence was recorded during three periods only, September 1957 to January 1958 (frequent, surface to 70 m), February and March 1959 (rare, surface to 20 m), and October to December 1959 (frequent, surface to 70 m).

The Crystallolithus phase, however, was recorded five times during the same period from the following stations and depths: E1, 17. ix. 57, 10 m with *C. pelagicus* phase; L6, 15. x. 57, surface, with *C. pelagicus* phase; L5,

9. vii. 58, surface; L4, 9. vii. 58, surface; E1, 26. viii. 58, surface. It has also been recorded from the southern Celtic Sea and the north-eastern Bay of Biscay in slope and oceanic water during March and April 1958, at a depth of 10–20 m but at no other depth. In March, the *C. pelagicus* phase was also present at 20 m in the oceanic water.

Recent records for the occurrence and distribution of the Crystallolithus and *C. pelagicus* phases can be found in Braarud, Gaarder & Grøntved (1953), Gaarder & Markali (1956), Smayda (1958), and for the *C. pelagicus* phase only, in Bernard (1942), Lecal-Schlauder (1951), Halldal (1953), and Gaarder (1954). For the Norwegian Sea in May 1948, Braarud, Gaarder & Grøntved (1953) record the Crystallolithus phase as reaching a maximum density of 17,500 cells/l. at the surface and the *C. pelagicus* phase as reaching a maximum density of 20,000 cells/l. at 50 m.

DISCUSSION

We have called this organism by the name in current usage (Schiller, 1930; Lecal-Schlauder, 1951; Kamptner, 1954), *C. pelagicus* (Wallich) Schiller, and Mrs Karen Ringdal Gaarder has confirmed (private communication) that this name is the legitimate name for this organism.

When Gaarder & Markali (1956) described *Crystallolithus hyalinus* they suggested it might be identical with *Pontosphaera borealis* Ostenfeld (1910), described from arctic water of the East-Greenland Sea, but they were doubtful because coccoliths 3–4 μ long were recorded for *P. borealis*, while their preserved material of *Crystallolithus* had coccoliths only 2 μ long. We have shown earlier that the coccoliths on the Crystallolithus phase can be up to 3·3 μ long, and, as further supporting evidence of the two motile forms being identical, Ostenfeld (1910) nearly always found the non-motile *Coccolithus pelagicus* phase of *Crystallolithus* associated with the *Pontosphaera borealis*. In fact Ostenfeld (1910) states he found both *Coccolithus pelagicus* and *Pontosphaera borealis* in the outer part of the pack ice and outside it, the *Coccolithus pelagicus* was dead (contents having been released—authors), but the *Pontosphaera* was most probably living when caught. Smayda (1958) supports this finding of the two phases occurring together by means of his records from around Jan Mayen Island where he reports the presence of *Crystallolithus hyalinus* and *Coccolithus pelagicus* 'at similar temperatures in the same habitat coupled with an identical habitus' to that in which Ostenfeld found the *Pontosphaera borealis*. It now appears certain that *Crystallolithus hyalinus* is synonymous with *Pontosphaera borealis* Ostenfeld.

The occurrence of a haptonema in a coccolithophorid was recorded by von Stosch (1955) for a form closely resembling, but not identical with, *Hymenomonas carterae* (Braarud & Fagerl.) Braarud. We have at the present time in culture in the Plymouth Collection three coccolithophorids, in addition to the *Coccolithus pelagicus*, which possess haptonemata. Two we have not yet related to any described species and the third is *Pleurochrysis scherffelii* Pringsheim (1955). In *P. scherffelii* the short haptonema is visible on the motile phase for only a very short period after release from the non-motile phase, since the coccoliths, which are produced gradually on the body surface, eventually mask it from view. This may also be the case for many other coccolithophorids and therefore many described forms may possess haptonemata which have not so far been detected, or alternatively, they have have been seen but not recognized in preserved material. For example, Prof. Chadefaud brought to our notice a paper by Schlauder (1945) in which she records three flagella in *Pontosphaera triangularis*, saying that the third flagellum appeared to be more rigid; it may therefore be a haptonema.

The secretion of coccoliths inside the cells of coccolithophorids has been recorded by a number of workers (see also p. 267), but the process by which they are produced inside the cell is still unknown. Prof. Manton's findings (Manton & Parke, 1960, p. 282 of this number) from the examination under the electron microscope of sections of a small green flagellate, which possesses surface body scales, may be the answer also to the internal production of coccoliths; she found inside the body of *Micromonas squamata* Manton & Parke evidence of the production of complete scales within more or less deep-seated vesicles. The large vesicles which appeared inside the *Coccolithus pelagicus* mother-cells prior to placolith deposition on the body surface suggest that coccoliths may originate in vesicles in a manner similar to scales.

There is little detailed and precise information available in the literature on the stages in the life history of coccolithophorids with the exception of the studies by Bernard (1948, 1949) on the life history of *C. fragilis* Lohm. Spore formation has been reported for some species and spores, morphologically different and more simple than the parent cell, have been recorded by Bernard (1938) for *Rhabdosphaera subopaca* Bern. and *Scyphosphaera elegans* (Ost.) Defl., suggesting that these two species may have a type of life history similar to the one we have recorded for *Coccolithus pelagicus*.

The few studies already published on the life history of coccolithophorids in culture—Braarud & Fagerland (1946), Pringsheim (1955), von Stosch (1955, 1958), and the present work—as well as our unpublished records from the ten species we have in culture, show undoubtedly that a great deal of valuable knowledge concerning the behaviour of these organisms (e.g. the demonstration of phagotrophy) and the stages in their life history can be obtained from the study of cultures.

Kamptner (1958), in his recent classification of the Coccolithineae, places the motile Crystallolithus phase of *C. pelagicus* in the tribe Syracosphaereae and the non-motile phase in the tribe Coccolitheae, both tribes being placed in the family Coccolithaceae. If this organism is classified on the micro-structure of its coccoliths, however, according to the units proposed tentatively by Braarud *et al.* (1955) and Halldal & Markali (1955), the motile Crystallolithus phase would be placed in the section with holococcoliths and the non-motile phase in the section with heterococcoliths. It appears, therefore, that a coccolithophorid, which produces two morphological types of coccolith, cannot be placed satisfactorily in the present systems adopted for the classification of the Coccolithophoridae, and so these systems need revision.

SUMMARY

The study of *Crystallolithus hyalinus* Gaarder & Markali in culture has shown it to be the motile phase in the life history of the non-motile *Coccolithus pelagicus* (Wallich) Schiller; two distinct morphological types of coccolith can therefore be produced by different phases of the one species.

Additional information from living material is given to supplement the original description of the Crystallolithus phase; sculptured scales are recorded under the crystalloliths in the hyaline outer layer of the body. This phase possesses a haptonema as well as two acronematic flagella; it exhibits phagotrophy and shows an unusual procedure for the discarding of waste material; its swimming and reproductive behaviour are recorded. The stages in the development of the *Coccolithus pelagicus* phase from the Crystallolithus phase are described. The occurrence of the two phases in the sea off Plymouth is recorded for the years 1957–59.

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EXPLANATION OF PLATES I–IV

Coccolithus pelagicus (Wallich) Schiller

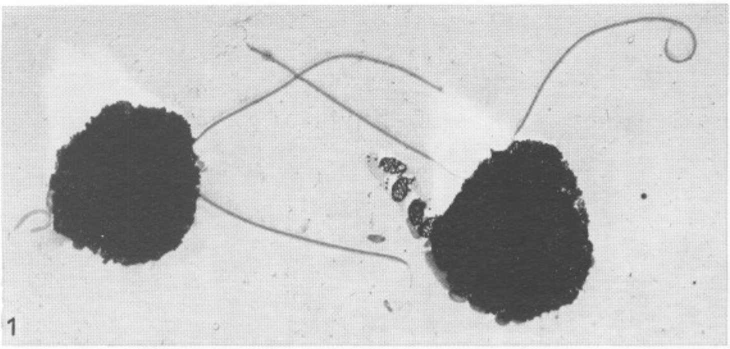
I

Electron micrographs of shadow-cast whole mounts taken with a Philips microscope carrying a 25 A pole-piece with astigmator, used at 60 kV.

Fig. 1. Two Crystallolithus cells with bodies completely covered by crystalloliths. Exposure M 577.14, magnification × 1400.

Fig. 2. Part of a Crystallolithus cell showing a coiled haptonema between the two flagella. Exposure M 577.17, magnification × *c.* 8000.

Fig. 3. Crystalloliths and translucent plate-scales from the motile Crystallolithus phase, direct print. Exposure M 577.6, magnification × 23,000.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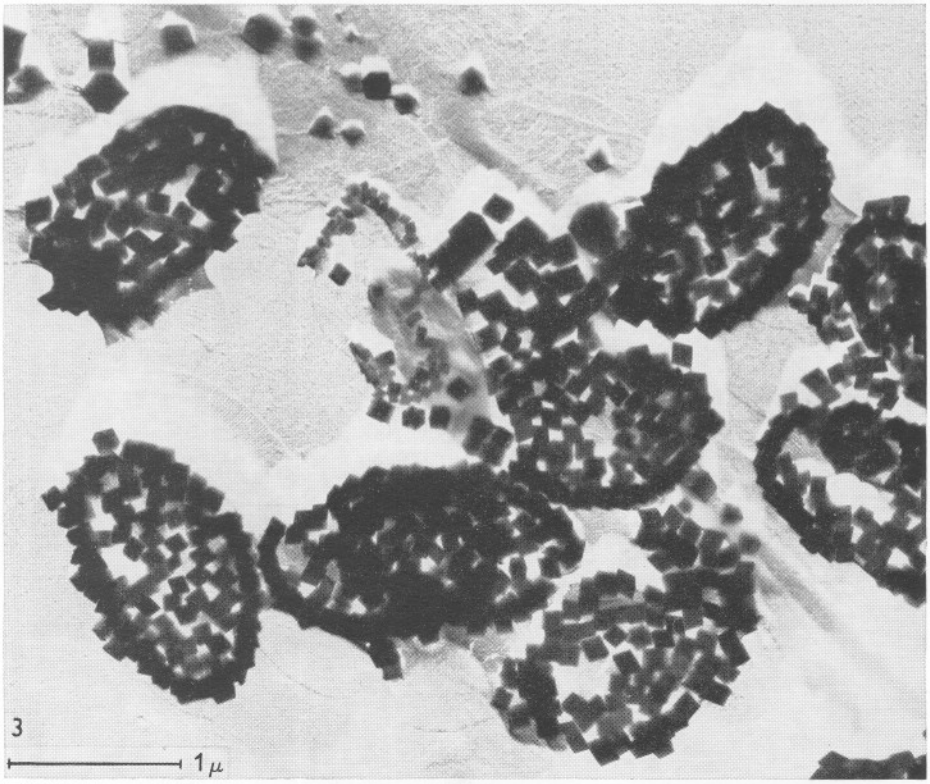
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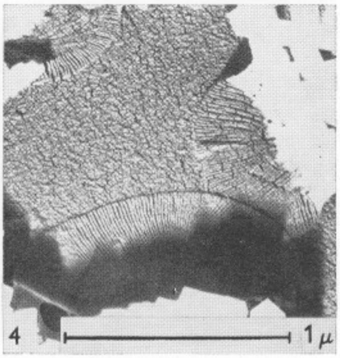
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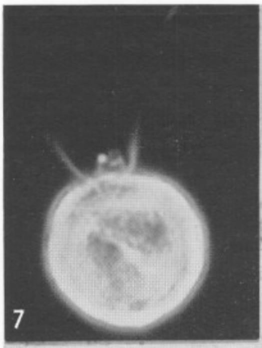
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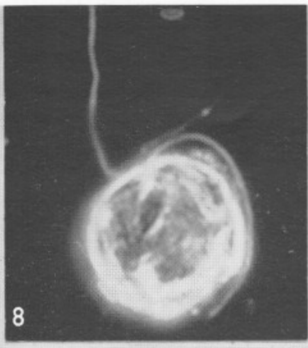
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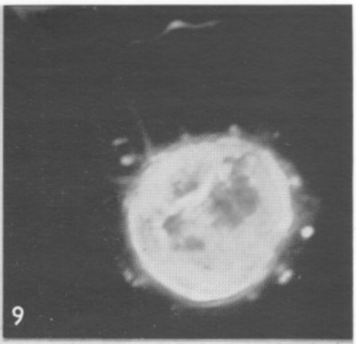
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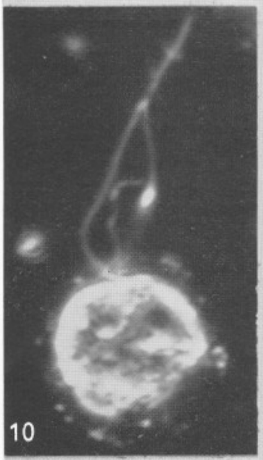
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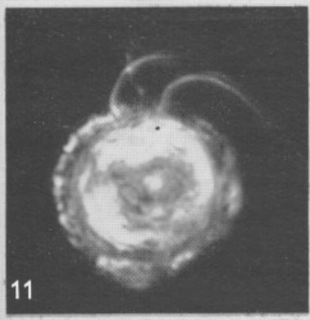
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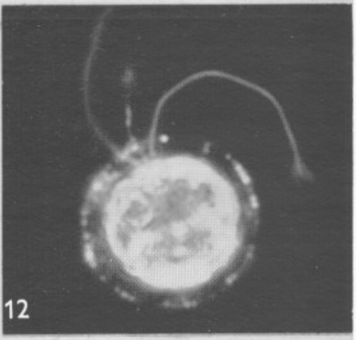
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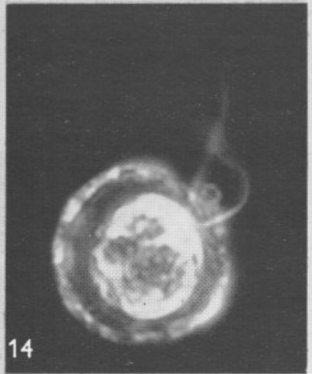
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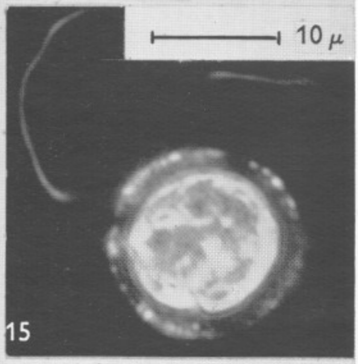

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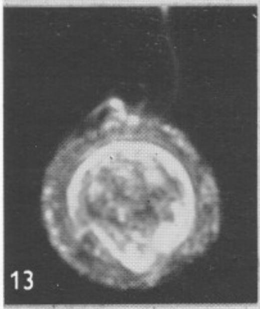
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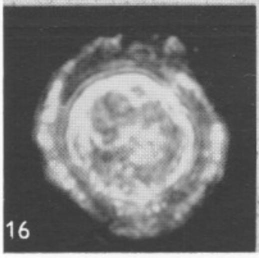
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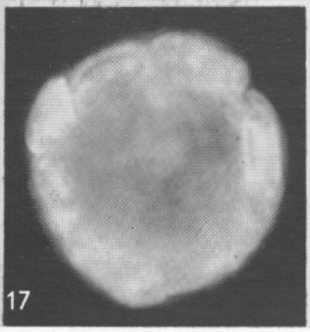
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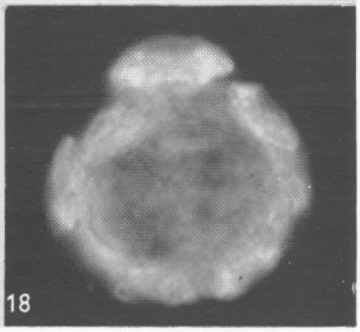
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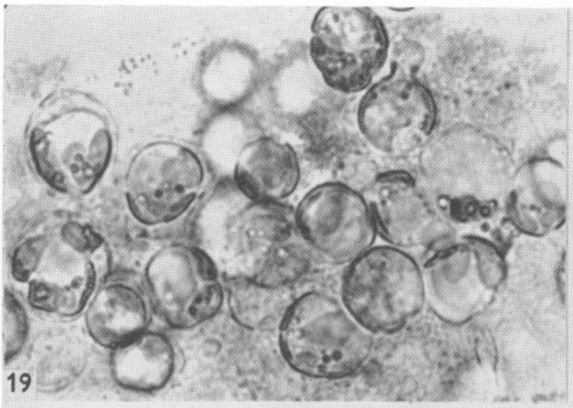
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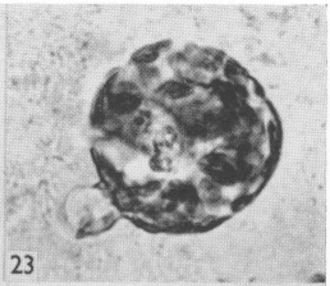
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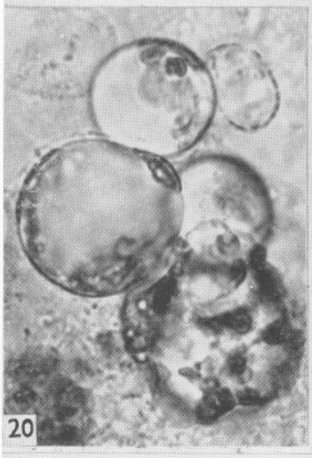
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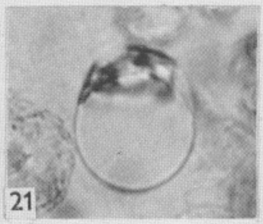
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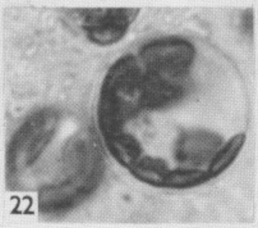
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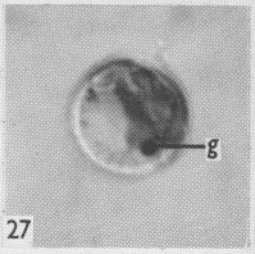
Figs. 19–25 ⊢——⊣ 20 μ

Figs. 26–30 ⊢————⊣ 20 μ



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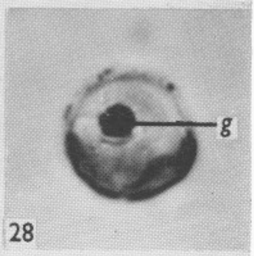

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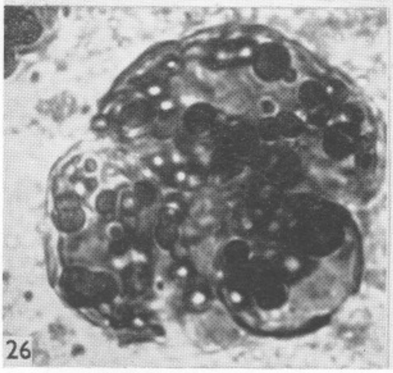
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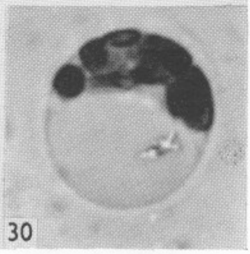
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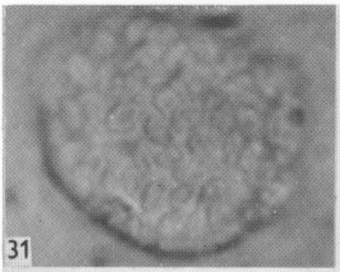
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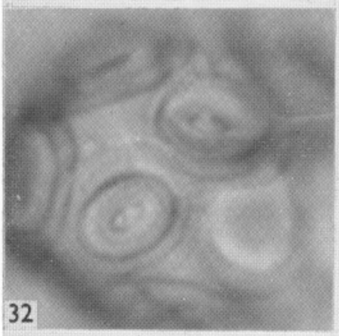
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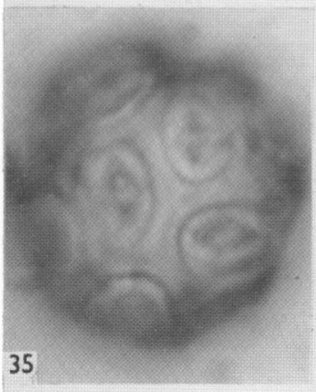
Figs. 31–37 ⊢——⊣ 10μ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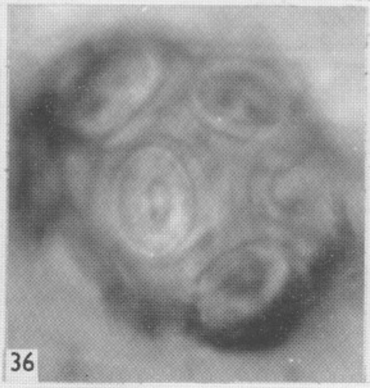
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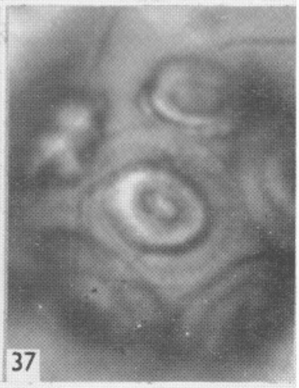
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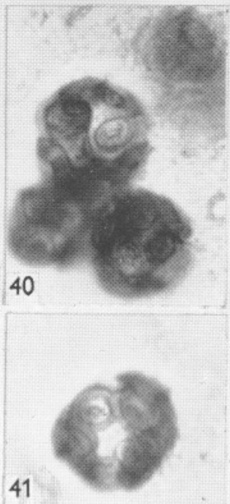
Figs. 38–42 ⊢——⊣ 20μ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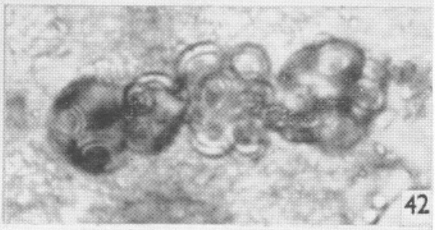
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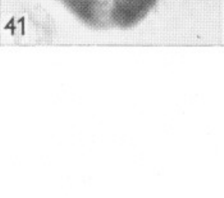
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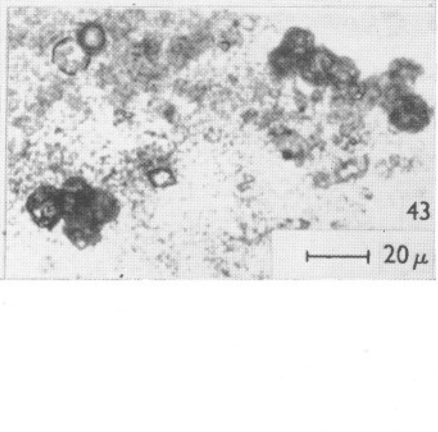
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⊢——⊣ 20μ

Fig. 4. Part of the field of fig. 3, reversed print, to show details of the markings on one side of the scales on which the crystalloliths are deposited. Exposure M 577.6, magnification × 30,000.

Fig. 5. Another field as fig. 4 but showing the markings on the other side of the scales. Exposure M 577.8, magnification × 30,000.

Fig. 6. Part of a placolith from the non-motile *Coccolithus pelagicus* phase. Exposure S. 686.7, magnification × *c*. 6000.

II

(Figs. 7–16, × 1650, Crystallolithus phase; Figs. 17, 18, × 1650, *Coccolithus pelagicus* phase.)

Fig. 7. Cell lacking visible hyaline layer round body; no crystalloliths formed.

Fig. 8. Cell with fully extended haptonema visible between the two flagella; very few crystalloliths present in outer thin hyaline layer of body.

Fig. 9. Cell with haptonema coiled and thin hyaline layer, few crystalloliths.

Fig. 10. Cell with two flagella, unequal in length, and haptonema fully extended; hyaline layer round body thicker than in fig. 9.

Figs. 11–14. Series of cells to show increase in thickness of hyaline layer round body and also the increase in the number of crystalloliths on the scales in this layer.

Fig. 15. Early fission stage.

Fig. 16. Non-motile Crystallolithus cell from bottom of a flask.

Fig. 17. Daughter-cell of *Coccolithus pelagicus* phase immediately after formation showing very thin hyaline layer covering the placoliths round the body.

Fig. 18. Same cell as fig. 17 after slight squashing to burst outer layer.

III

(Figs. 19–25, × 750; figs. 26–30, × 1250. Figs. 19–26, 29–30: stages in the development of the non-motile *Coccolithus pelagicus* mother-cell.)

Fig. 19. A group of non-motile Crystallolithus cells from a sample of the skin taken from the bottom of a flask.

Fig. 20. Four cells at different stages in development.

Fig. 21. Early stage with two chromatophores and very large leucosin vesicle.

Fig. 22. Later stage than fig. 21 with eight chromatophores and large leucosin vesicle.

Fig. 23. Mother-cell with lobed chromatophores at later stage than figs. 20–22, showing increase in size and disappearance of large leucosin vesicle.

Fig. 24. Two mother-cells with numerous small vesicles inside; cells fixed with osmium tetroxide.

Fig. 25. A mother-cell starting to divide before the placoliths are deposited on the body surface.

Fig. 26. A mother-cell dividing to produce four daughter-cells before the placoliths are deposited on the outside; many vesicles, darkened by osmium tetroxide, clearly visible inside the body; thin hyaline outer layer showing round part of the cell.

Fig. 27. A Crystallolithus cell showing a small pellet of ingested graphite (*g*).

Fig. 28. Another Crystallolithus cell showing a larger pellet of ingested graphite (*g*).

Fig. 29. A non-motile Crystallolithus cell showing a thick striated hyaline layer round the body.

Fig. 30. Slightly later stage (at higher magnification) than Fig. 21 with four dividing chromatophores and a large leucosin vesicle.

IV

(Figs. 31–37, × 2335; figs. 38–42, × 750; fig. 43, × 375.)

Fig. 31. Crystallolithus phase—empty hyaline casing containing the crystalloliths from which the daughter-cells emerged after fission of the parent-cell.

Fig. 32. Part of a *C. pelagicus* mother-cell, ovoid in shape, showing the overlapping of the placoliths on the body surface.

Fig. 33. Three placoliths from the *C. pelagicus* stage in surface view.

Fig. 34. A *C. pelagicus* daughter-cell squashed to liberate the cell inside the placoliths; liberated cell lying beside placoliths.

Fig. 35. A *C. pelagicus* daughter-cell, spheroidal in shape.

Fig. 36. A small *C. pelagicus* mother-cell, ovoid in shape.

Fig. 37. A *C. pelagicus* daughter-cell showing placoliths of normal and abnormal shape.

Figs. 38–39. First fission of *C. pelagicus* mother-cell.

Fig. 40. Second fission of mother-cell to produce four *C. pelagicus* daughter-cells.

Fig. 41. *C. pelagicus* daughter-cell from which contents have been liberated.

Fig. 42. Four *C. pelagicus* daughter-cells united together in a linear series, as described for a coccolithophorid by Wallich (1861, 1877).

Fig. 43. Low power photograph of groups of four *C. pelagicus* daughter-cells from sample of the skin taken from the bottom of a flask.

J. mar. biol. Ass. U.K. (1960) 39, 275–298
Printed in Great Britain

FURTHER OBSERVATIONS ON SMALL GREEN FLAGELLATES WITH SPECIAL REFERENCE TO POSSIBLE RELATIVES OF *CHROMULINA PUSILLA* BUTCHER

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and M. Parke

The Plymouth Laboratory

(With total of 59 Figures on Plates I–IX and in text)

CONTENTS

INTRODUCTION

The observations to be recorded here have been carried out primarily for the purpose of clarifying the taxonomic position and naming of the small organism previously known as *Chromulina pusilla* Butcher. This had been shown (Manton, 1959*a*) to possess the pigments and fine structure appropriate to a position in or near the Chlorophyceae but quite inappropriate to a position within the Chrysophyceae to which the genus *Chromulina* properly belongs. Before selecting a new generic name, it was highly desirable to make some comparative electron microscopical observations on authentically named material of appropriate kinds since the fallibility of the light microscope for study of organisms of this order of size (1–3 μ) had been all too clearly exposed. A search was therefore made for a representative or representatives of the only genus of green flagellates known to us from the literature to possess a single posteriorly directed flagellum, namely *Pedinomonas*.

No species of *Pedinomonas* has so far been encountered among flagellates isolated from the sea at Plymouth, and most of those described in the literature have been from fresh water. The Culture Collection at Cambridge, however, contains two species referred to this genus, one a recent isolation from brackish water made by E. A. George who had provisionally identified it as *Pedinomonas minor* Korsch., and the other a freshwater species, *P. tuberculata* (Vischer) Gams.

When these two species were investigated electron microscopically it at once became apparent that they were so unlike each other that they could not possibly be regarded as representatives of one genus. This rather disconcerting discovery necessitated close attention to the taxonomic credentials of the two cultures since one showed many more points of resemblance to *Chromulina pusilla* Butcher than the other and therefore the correct allocation of the name *Pedinomonas* was a matter of critical importance.

There proved to be a substantial difference between the two cultures in the authenticity of the specific names attributed to them. The original culture of *P. tuberculata* had been presented to the Cambridge collection by the describer of the species and it still agrees with the published description (Vischer, 1945, 1949) in all details ascertainable with the light microscope; its specific identity cannot therefore be called in question. The other culture was, however, a recent isolate from British estuarine waters which had been named provisionally from the literature. Close comparison with Korschikov's original description (1923) of *Pedinomonas minor* (a freshwater species from Poland) soon convinced us that though superficially similar our material could not be this species. Moreover, the differences detectable with the light microscope, notably those concerned with the character of the starchy food store, were also differences from the situation found in the culture of *P. tuberculata*. Since *P. minor* Korschikov itself is generally assumed to be the type species of *Pedinomonas* we are forced to conclude that the material supplied to us under this provisional name is not only not this species but is a new and undescribed species of an, at present, untypified genus.

The fine structure of our new species is, however, similar in many respects to that of *Chromulina pusilla* Butcher, allowance being made for a difference in cell size. There are also substantial morphological differences, notably in the long hair point terminating the flagellum in the latter and the very unusual covering of scales on the flagellar surface in the former; but as long as we have, as at present, only one species of each type on record, and since some of the characters in which the two species differ most from each other are completely invisible with the light microscope, it seems not unreasonable in the present state of knowledge to regard these differences as specific and not as generic criteria. It is then possible to construct a new generic diagnosis which will separate both these species from *Pedinomonas minor* on light microscope characters and from *P. tuberculata* on light microscope and electron microscopical characters.

We therefore propose to describe our new species as *Micromonas squamata* sp.nov., referring it to *Micromonas* gen.nov. of which *M. pusilla* (Butcher) comb.nov. will be the type. In designating *M. pusilla* and not *M. squamata* as the type species of *Micromonas* we are hoping to safeguard *M. pusilla* from further name changes should it become necessary in the future to subdivide this genus.

Our observations contribute only indirectly to an understanding of *Pedinomonas* itself since we still lack electron microscopical information about the type species. We therefore propose to limit the account of *P. tuberculata* to the minimum necessary to substantiate our view that generic separation from *Micromonas* is essential. It will be possible to deal briefly with *M. pusilla* since all the electron microscopical facts have already been placed on record in Manton (1959*a*). Our new species, *M. squamata*, will however be described as fully as is normally necessary in dealing with a new species, and since the fine structure has in this case been of critical importance in indicating the probable affinities we propose, in the account which follows, to present the electron microscopical evidence first. To meet the needs of the light microscopists, however, and to facilitate cross-reference we have supplied a table (p. 292) listing all the more important specific characters of all three species and have assembled together (Pl. IX and p. 291) all the photographs and drawings made with the light microscope instead of following our usual practice of grouping these beside the electron micrographs of the species to which they refer.

We are able to dispense with a special section on material and methods since the methods used are exactly the same as in our previous studies on marine flagellates (Parke, Manton & Clarke, 1955, 1956, 1958, 1959; Manton, 1959*a*) and the few additional details about our sources of material will be inserted with the specific descriptions.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE ON *MICROMONAS SQUAMATA* SP.NOV.

External morphology

Low-power views of intact cells are uninformative except as evidence of size (Fig. 1). The single posteriorly directed flagellum is about 12 μ long and though it is sometimes accompanied by a second, or even a third (Fig. 2) or fourth flagellum, such supernumeraries being of any length from very short to equal, there is no doubt that these all relate to growth stages of cells in division or to giant cells representing double-divisions. In normal undivided cells, which make up the majority in any culture, only one flagellum is present.

At higher magnifications (Figs. 3–6, 7–8) the scales and other surface appendages become visible. Almost always the arrangement of scales is disturbed by the act of drying the preparation though they commonly remain in close proximity to the surface from which they have fallen. These surfaces include not only the body of the cell but the entire length of all flagella from their base to extreme tip as may be seen in the various specimens included in Figs. 3–6. Only one of the five individual flagella depicted, namely that of Fig. 5, shows the scaly covering intact. In this particular specimen the flagellar axis has shrunk in drying and has therefore drawn away from the tubular sheath of scales which covers it. The scales themselves in this sheath are, however, still in their original positions and the regular imbrication over the entire surface is a striking feature; the few loose scales present in the field near this flagellum come almost certainly from the body of the same cell.

The fine structure of the scales is best shown in Figs. 7 and 8. There is a considerable range of sizes on any one cell, but all show a highly characteristic spider's-web pattern which we have not previously encountered on the other organisms described by us.

In addition to scales, many flagella also show hairs of an unusual kind. They are sometimes present in abundance on both sides of the flagellum and others emerge from the tip as in Fig. 4. The lateral hairs seem to fall off very

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Explanation of Plates I–VI

Micromonas squamata sp.nov.

I

Fig. 1. A dried cell photographed with the light microscope. × 1000.

Fig. 2. A double-division cell with three flagella photographed with the light microscope. × 1000.

Fig. 3. Tips of two of the flagella of fig. 2, the apex of the right flagellum damaged, that of the left flagellum intact, both showing a layer of detached scales throughout their length. Electron micrograph S 702.15, × 15,000.

Fig. 4. Tip of another flagellum to show presence of hairs as well as scales. Electron micrograph S 668.37, × 20,000.

Fig. 5. Tip of an unusually well preserved flagellum with the scaly covering intact and showing their regularly imbricated arrangement. Electron micrograph M 586.4, × *c.* 30,000.

Fig. 6. A flagellar tip showing detached hairs and scales and three long terminal hairs replacing the attenuated apex of the left-hand specimen in fig. 3. Electron micrograph H 4867, × 30,000, reversed print.

II

Fig. 7. Detached hairs and scales. Electron micrograph S 680.18, × 50,000, reversed print.

Fig. 8. Detached scales. Micrograph H 5760, × 70,000, reversed print.

Fig. 9. Part of a TS of a cell with two flagella transected near it; covering of imbricated scales visible on both. Micrograph H 246, × 30,000.

Fig. 10. LS of a flagellum attached to the body and showing imbricated scales in position over it. Micrograph H 2833, × 30,000.

Figs. 11, 12. Thick sections of two cells transecting the chloroplast in directions approximately at right angles; the translucent area around the core of the pyrenoid visible in both; the nucleus present only in fig. 11. Micrographs S 690.24 and 20, × 12,000.

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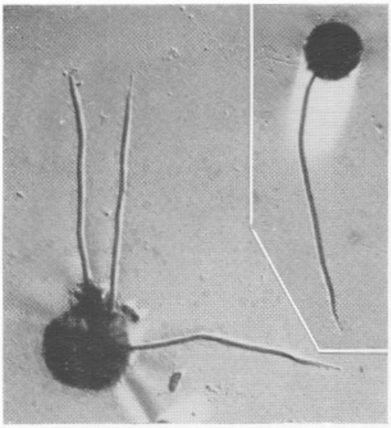

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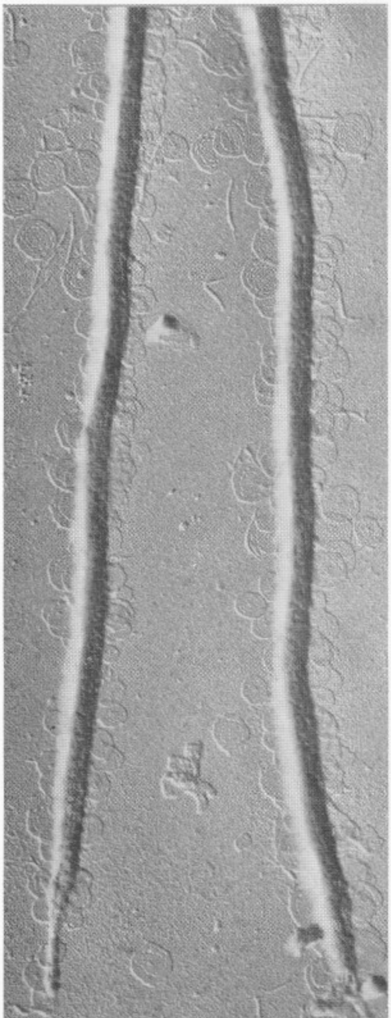

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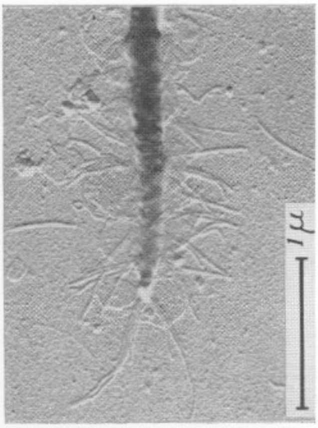

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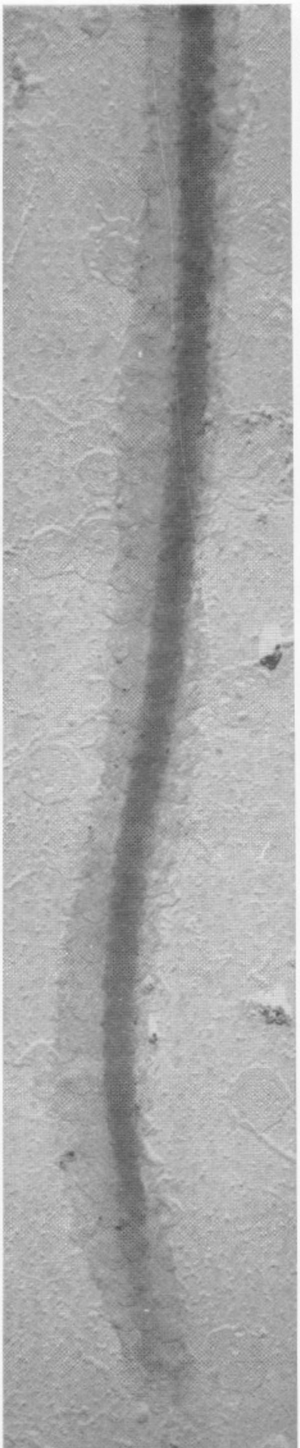

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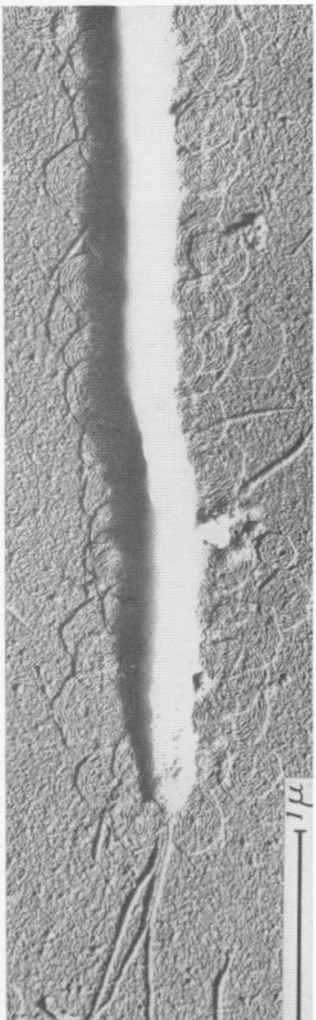

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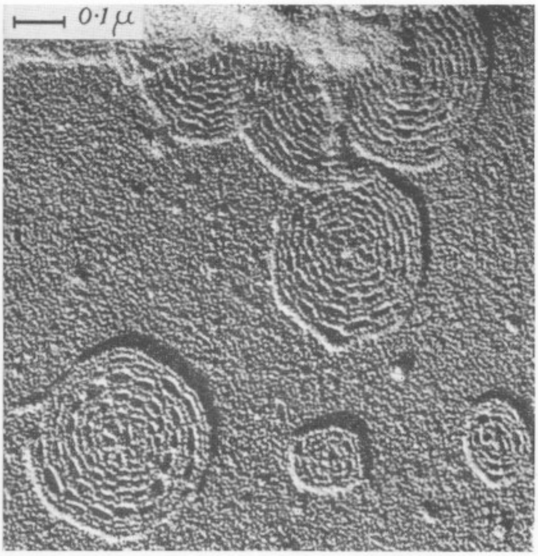

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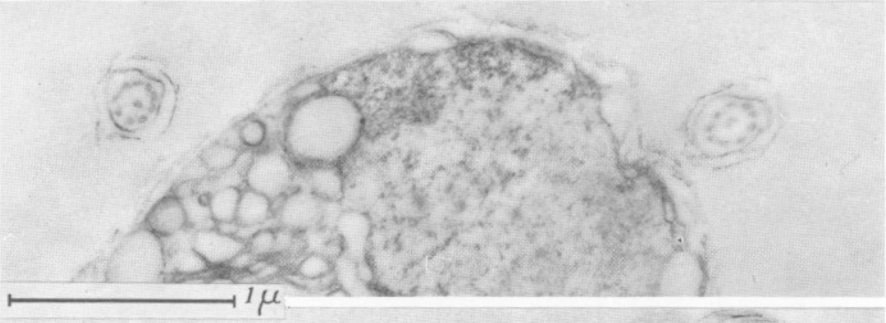

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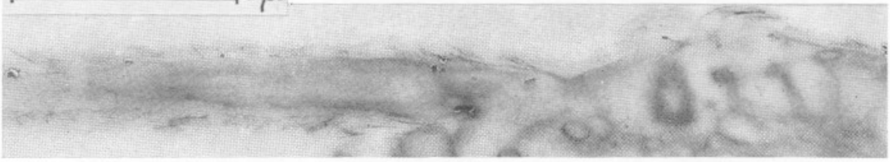

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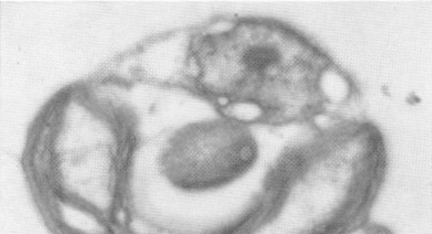

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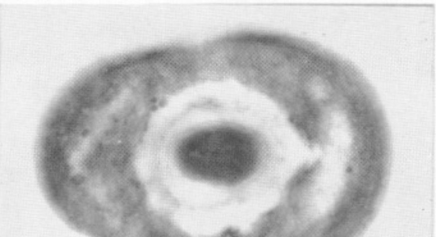

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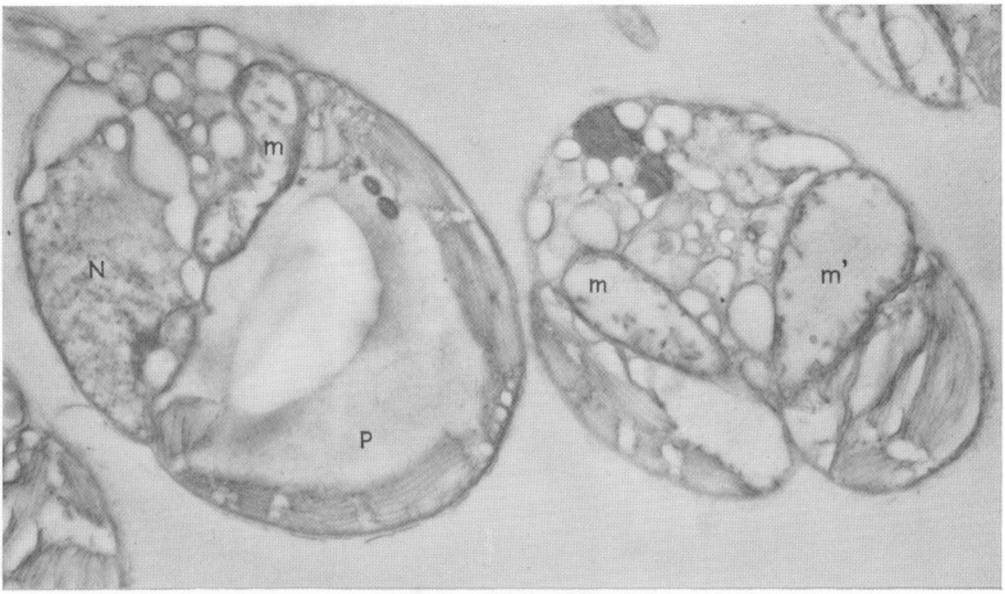

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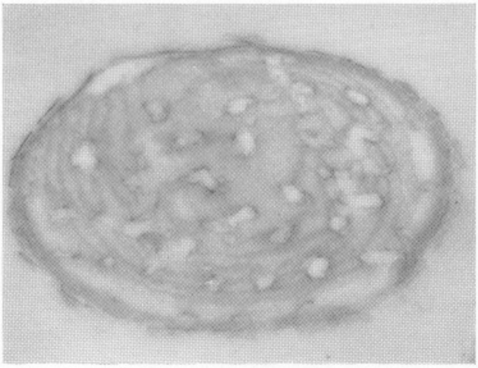

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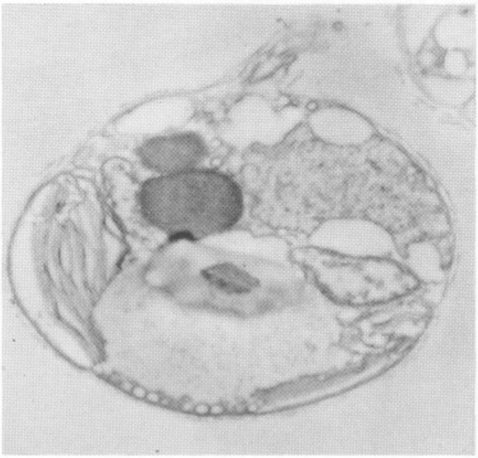

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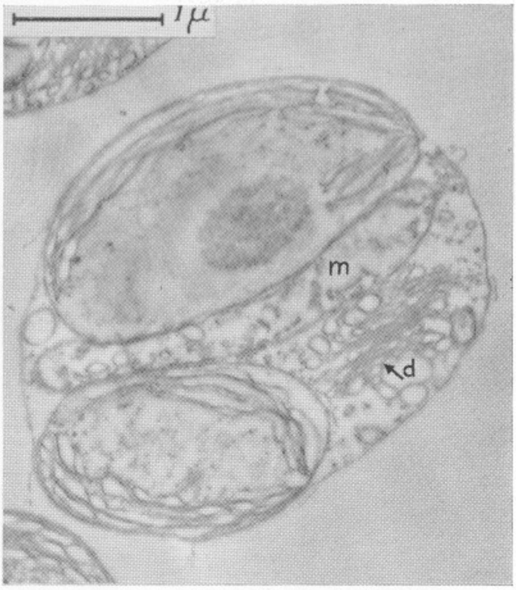

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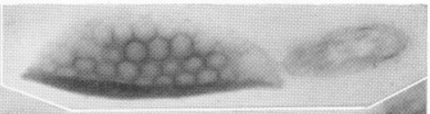

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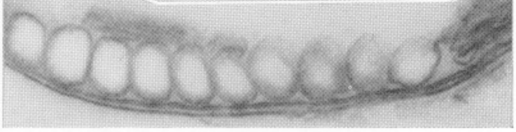

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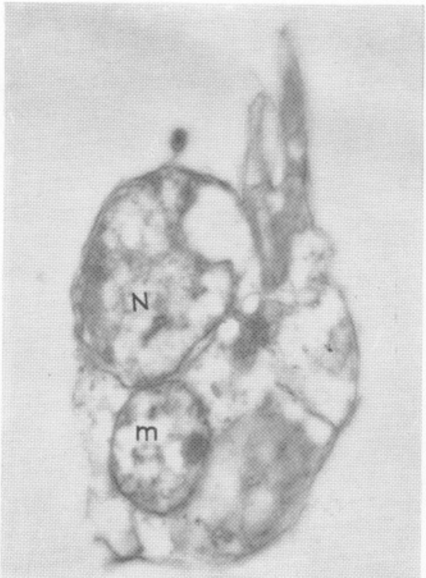

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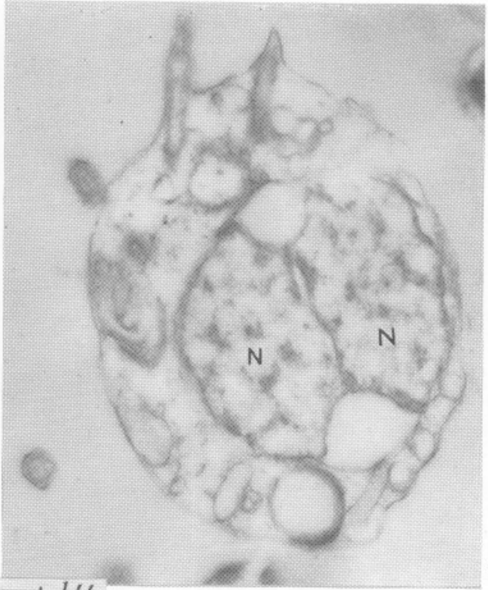

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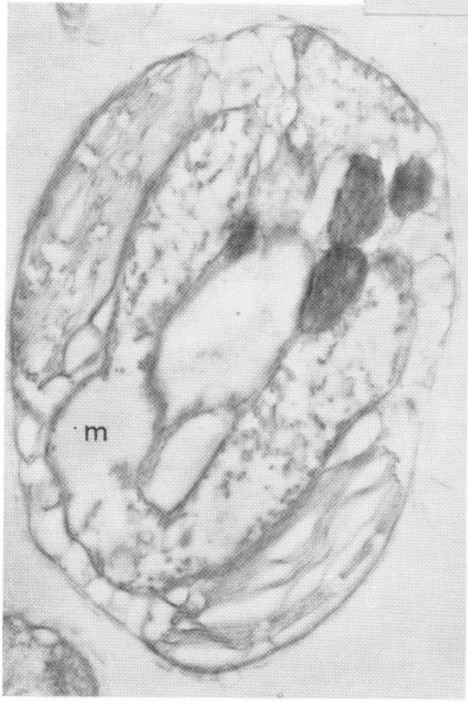

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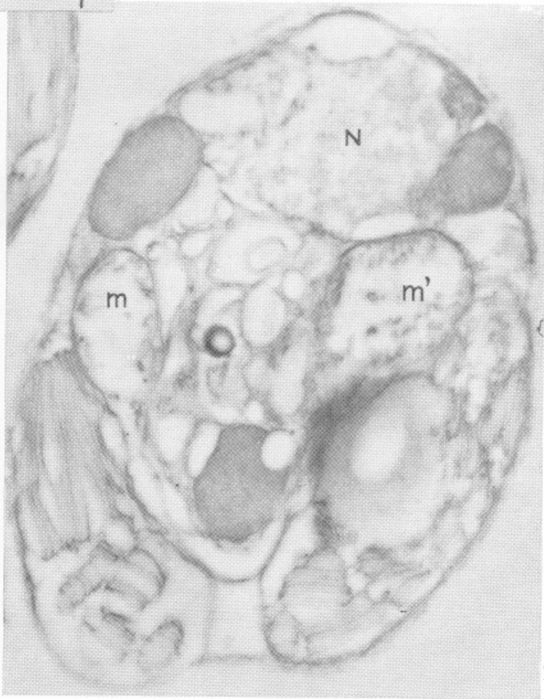

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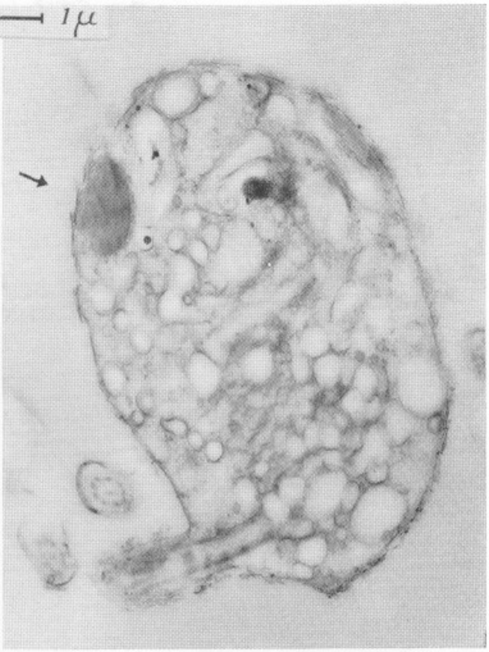

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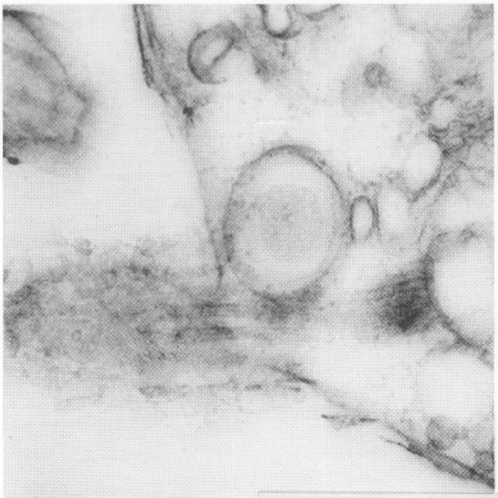

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25 (inset)

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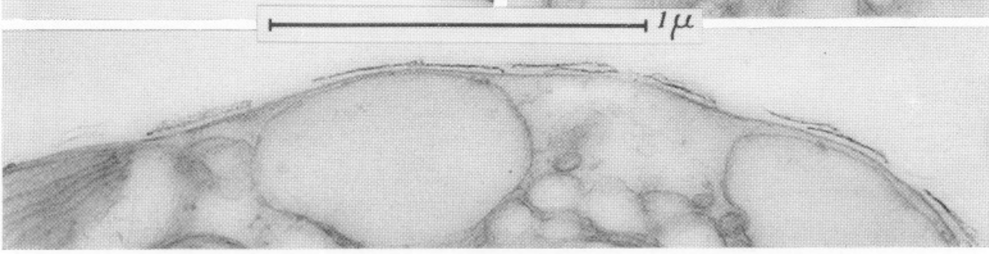

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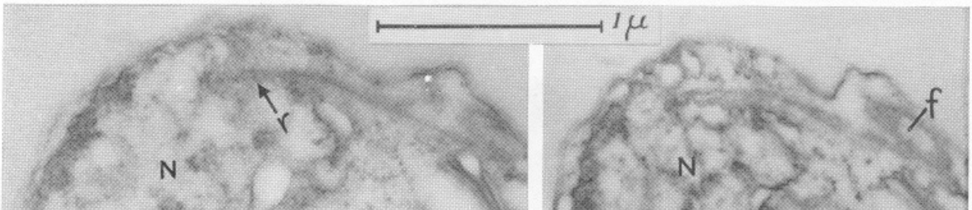

29a

29b

Explanation of Plates I–VI continued

Micromonas squamata sp.nov.

III

Fig. 13. Two cells, the left-most passing through the nucleus (*N*), the mitochondrion (*m*), the plastid (*P*) cut near but not through the pyrenoid and showing the stacks of paired plastid lamellae near the surface with fenestrations at intervals; the right-hand cell a division stage with two lobes of a bent U-shaped mitochondrion (*m* and *m′*) associated with the two halves of the plastid (another section of this cell, not reproduced, showed the centre part of the mitochondrion connecting the two lobes). Micrograph H 247, × 20,000.

Fig. 14. Tangential section near the surface of a plastid showing the fenestrations in face view. Micrograph H 5777, × 20,000.

Fig. 15. Part of a dividing cell showing golgi (*d*) and a long arm of a mitochondrion (*m*) between two plastids. Micrograph H 5467, × 20,000.

Fig. 16. A section passing through the plastid to show a structure resembling an eyespot (bottom centre) but without sign of pigment. Micrograph H 2728, × 15,000. For further details of eyespot region see figs. 17 and 18.

Fig. 17. Tangential section near the surface of a plastid in the region of the putative eyespot showing the close-packing of objects resembling pigment chambers, an obliquely cut flagellum near. Micrograph H 5777, × 20,000.

Fig. 18. More highly magnified view of plastid surface with putative pigment chambers covered by plastid double-membrane and cell body membrane. Micrograph H 2635, × 50,000.

IV

Figs. 19, 20. Two successive stages of a division showing different degrees of separation of the two flagella for the daughter-cells; two nuclei side by side visible in fig. 20. Micrographs H 2995 and H 3010, × 20,000.

Fig. 21. Stage in a cell-division showing a very long U-shaped mitochondrion (*m*) between two plastids or plastid lobes. Micrograph H 242, × 20,000.

Fig. 22. Another specimen at a stage similar to that of fig. 21 but cut in a slightly different plane and showing two plastids (or plastid lobes), a nucleus (*N*), a U-shaped mitochondrion (*m*, *m′*) with the arms in contact with the two plastids, some fat bodies and vesicles with other contents in the trough of the U. Micrograph H 698, × 20,000.

V

Fig. 23 *a*, *b*. Two successive sections through a flagellar insertion cut near the surface of a cell and showing disposition of vesicles and other details represented more highly magnified in figs. 24–26. Micrographs H 2647 and H 2639, × 20,000.

Fig. 24. Part of the section of fig. 23 *a* near the flagellar base showing a vesicle containing a scale in full face view immediately above the flagellar insertion. Micrograph H 2647, × 50,000.

Fig. 25. A scale in face view outside the body for comparison with that of fig. 24, from the region of the arrow on the right of fig. 23 *a*. Micrograph H 2647, × 50,000.

Fig. 26. Part of the cell surface showing imbrication of body scales, from the field near the arrow in fig. 23 *b*. Micrograph H 2639, × 50,000.

Fig. 27. Imbricated scales on the surface of part of another cell. Micrograph H 2639, × 50,000.

VI

Fig. 28. LS of a cell passing through the pyrenoid *P*, the starch shell *S*, the nucleus *N*, the mitochondrion *m* and showing the fibrous connection (*r*) between the base of the flagellum and the nuclear surface. Micrograph H 2986, × 40,000.

Fig. 29 *a*, *b*. Two adjacent sections through another specimen showing the fibrous connection (*r*) from the flagellar base (*f*) ending on the nuclear surface (*N*). Micrographs H 5459 and H 5461, × 30,000.

easily, but even when none are retained on the flagellum itself they are always to be found scattered on the field in the neighbourhood, e.g. Fig. 3, top centre. It seems necessary to believe therefore that they are normal structural features and not fixation artifacts.

The average length of the lateral hairs is of the order of half a micron and their width approximately 200 Å; they are therefore relatively coarse, considerably more so than bacterial flagella. They are usually slightly curved with one end attenuated; this end appears to be that by which the hair is attached to the flagellum. These features are well seen on some of the detached hairs included in the field of Fig. 7.

The tuft of hairs at the tip of the flagellum is perhaps of a different nature. The tips of flagella in general are known to be specially sensitive to post-mortem changes and it is not always self evident which condition of several which may occur is the least altered. In the present material it seems likely that the apex of the left-hand flagellum of Fig. 3 is in fact in the most undamaged state since it corresponds in general shape to the normal condition in many other organisms. On the right-hand flagellum of Fig. 3 the tip is partly broken away, while the abrupt termination of the flagellar column immediately below the terminal tuft of three hairs in Fig. 6 suggests that these particular hairs may perhaps be part of the distal extremity of the flagellar axis from which the outer skin has been removed leaving three of the longest component fibrils within it exposed. If this interpretation is correct the terminal hairs would here correspond to the internal parts of the attenuated distal apex of the left-hand flagellum of Fig. 3; if incorrect it would be necessary to assume that a terminal garniture of three hairs has in fact been present on the tips of all these flagella but in the case of those in Fig. 3 has fallen off. The first alternative is the more probable.

Internal structure

A preliminary view of most of the essential body organs can perhaps best be obtained from the most highly magnified section, reproduced in Fig. 28. This is comparable in attitude and plane of cutting with Fig. 11 of Manton (1959*a*) and the strong resemblance to the arrangement and structure of the cell of *Chromulina pusilla* Butcher will at once be apparent if the two are examined together. There is the same large plastid with superficial lamellations and conspicuous eccentric pyrenoid with dark central contents surrounded by shells of lighter material. There is the same single mitochondrion, and the positions relative to the flagellum of both these organs and of the nucleus are also comparable. The cells of our present species are, however, considerably larger (3–6·5 μ instead of 1–3 μ) and therefore certain features, notably the fibrous root connecting the base of the flagellum with the surface of the nucleus, can be demonstrated here relatively easily though looked for in vain in the smaller organism. This root is visible in Fig. 28, and two adjacent sections of another specimen are reproduced in Figs. 29*a* and *b*. The root undoubtedly terminates on the nuclear surface without either passing beyond or penetrating it. The distal tip is perhaps covered by a spirally wound sheath since diagonal lines sloping in opposite planes are detectable in the two sections (Figs. 29*a*, *b*).

The only other constant organs not included in Fig. 28 are fat bodies, seen incidentally in several other sections, notably Figs. 13, 16, 21 and 22, and golgi areas (dictyosomes), one of which is indicated in Fig. 15. A single dictyosome is always present near the flagellar base, as in the previous species.

Within these various organelles certain additional structural details deserve attention. The structural arrangement within the plastid is perhaps more clearly revealed by the two thick sections cut in planes approximately at right angles to each other included in Figs. 11 and 12 which amplify previous information on the general shape and distribution of storage and pigment materials. The thinner sections of Figs. 13 and 14 add further details of the pigmented layers. Thus in Fig. 13 (left) the section misses the pyrenoid but passes perpendicularly through the pigmented layers showing them to be stacks of paired lamellae interrupted at intervals by spaces which in surface view (Fig. 14) appear as roughly isodiametric holes scattered in a fairly uniform distribution over the surface.

Figs. 16–18 show some of the details associated with the region resembling an eyespot in the middle of the outer surface of the plastid. Here the ordinary lamellae are replaced by a layer of close-packed cylindrical chambers with well marked walls resembling those encountered in eyespots of other organisms, e.g. *Fucus* (Manton & Clarke, 1956), though here with translucent contents suggesting that special pigmentation was either absent at the time of fixation or has dissolved out.

The region of the putative eyespot is very suitable for demonstrating the compound nature of the plastid membrane (Fig. 18). Its over-all thickness is somewhat greater than that of the cell-body membrane overlying it which is also compound (better seen underlying the scales in Fig. 27).

The single mitochondrion, which is in itself one of the more striking features by which this species resembles *Chromulina pusilla* Butcher, is very strikingly shown in the early division stages during which the mitochondrion may become very long and bent into a U or V shape before dividing. Different manifestations of this are included in Figs. 13, 21 and 22, but it should be noted that if the plane of section does not coincide with the plane of elongation of the mitochondrion the two ends may be found so far apart (e.g. Fig. 13) that at first they might be mistaken for two separate organelles. That this is not so is clearly indicated by the constant position of the component parts lying in what is effectually a groove between the plastid rim and the centre bulge caused by the pyrenoid and marking the eventual place of cleavage. The number of cristae, i.e. internal projections within the mitochondrion, is far larger than in *C. pusilla*; they appear to be somewhat flattened tubes, rather short and not displaying the peculiar curved paths characteristic of the other species (Manton, 1959*a*).

The most important new facts from the point of view of a general understanding of algae are those associated with the origin of the scales. It is probable that the scales are slightly mineralized since, though no thicker than the scales of the species of *Chrysochromulina* described by us, they are slightly more opaque than these when seen in section (e.g. Fig. 27), appearing distinctly denser than the cell membrane over which they lie. This circumstance makes them slightly more conspicuous in various planes of section than the unmineralized scales more familar to us and it is probably for this reason that the following observations as to their mode of formation have been obtainable. It had previously been thought probable that scales of any kind when encountered on the surface of a 'naked' cell would have been produced in one way or another from the surface membrane underlying them. That this is not so here is however proved by finding completed scales inside the cell as in Fig. 24 where a perfect spider's-web scale is encountered in face view in the centre of a large vesicle below the cell surface near the insertion of the flagellum. Figs. 23*a* and *b* are introduced to show the exact position on the specimen from which this detail was taken and other scales outside the body or in position on it are illustrated in Figs. 24–26. Since all attempts to demonstrate phagotrophic feeding by this species have proved vain it is necessary to conclude that internal scales are part of a developmental process and have not been swallowed from outside.

It has not been possible to follow all the developmental details, since scales can scarcely be recognized as such in a very incomplete condition. The probable site of synthesis is, however, in the group of vesicles with contents which commonly occupies the space between the arms of a V-shaped mitochondrion in a dividing cell (Fig. 22). These vesicles contain contents of various kinds including, usually, some densely opaque material and also objects possessing a type of refringence reminiscent of that of the scales. If this is a true identification these vesicles are too large and too full of contents to be engaged in production of single scales. It therefore seems probable that the early stages are passed through in groups within these large, relatively central, vesicles, and that the transferrence of single scales into separate vesicles near the cell surface is part of the final act of deposition. If this is so the very regular imbrication of the scales covering the flagellum, already seen in Fig. 5 and detectable both in LS and TS in Figs. 9 and 10, is readily understandable as the expression of the successive opening on to the surface of a cluster of vesicles each containing one scale and arranged round the base of a growing flagellum. The great difficulty of imagining any mechanism by which scales could be produced from the apparently normal flagellar surface itself is thereby eliminated.

OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *MICROMONAS SQUAMATA* SP.NOV.

Examples of cells photographed with the light microscope, using dark-ground illumination, will be found grouped under one number as Fig. 40, Pl. IX (facing p. 288); some are in the uniflagellate condition and the remainder are division stages with two or four flagella, unequal to equal in length. Fig. 39, Pl. IX, illustrates two cells of *Chromulina pusilla* Butcher at the same magnification for comparison; their much smaller size has made it impossible to obtain effective photographs of the flagella by this method.

Cells of the organism that we propose to name *Micromonas squamata* sp.nov. can swim fairly quickly, rotating rapidly with only slight gyration and moving in straight lines for short distances, but more usually they move fairly slowly with slow rotation of the body and more pronounced gyration. They can also glide along for short distances without rotation, or they can show periods of jerking about very actively by the lashing of the flagellum. During movement, the region of the body at which the flagellum arises is always foremost. The proximal 1–2 μ of the flagellum becomes pulled out into what appears, when the cell is moving, to be a short stiff spine-like organ which lies in *front* of the body (Figs. 44–45); the remainder of the flagellum is curved sharply backwards down the side of the body to lie behind the cell. When cells are moving rapidly the flagellum appears to vibrate but when moving more slowly definite undulations can be observed; the undulations are usually small but can on occasion be large. A cell stops swimming suddenly by bringing the flagellum up with a sharp jerk of the body into a curved position round and under the body (Fig. 42), sometimes coiled twice round the body (Fig. 43), after which the cell will commonly move off in a different direction. In fission stages when a second flagellum has developed, the two behave homodynamically, both twisting round the body simultaneously when a cell stops swimming to change direction.

The region of the body close to the point of origin of the flagellum can show considerable metaboly and, in addition, fine pseudopodium-like filaments have several times been seen produced; they appear to attach to the surface of the slide but so far only cells in the incipient fission stage have been seen producing these filaments (Fig. 46).

In an actively growing culture 15% of the cells are 3 μ in size, 20% 3·5 μ, 40% 4·0 μ, 13% 4·5 μ, while the remaining 12% are incipient fission stages ranging from 5 to 6·5 μ in size. The smallest cells (newly divided daughter-cells) may show some slight flattening of the body but the larger cells and the fission stages are more globose. The flagellum length in relation to the body size can vary from 2½ to 4 times the length of the body but 80% of the cells have a flagellum 3–3½ times the length of the body.

This organism shows a distinct phototactic reaction but there is no evidence of phagotrophy. In culture it is yellow-green, i.e. is similar in colour to *Chromulina pusilla* Butcher, and it contains, as does the latter, chlorophyll *a*, chlorophyll *b*, β-carotene and α-xanthophyll (Dr G. Y. Kennedy, personal communication).

In the living cell the most obvious of the cell contents are the chloroplast with its embedded pyrenoid and, when present, the refractive lipid body or bodies. The chloroplast is situated on the side of the body opposite to that from which the flagellum arises; under the high power it appears striated with the pigmented outer region crescentic in optical section. The pyrenoid, immersed in the inner side of the chloroplast, is surrounded by a starch shell staining violet with iodine. The starch shell shows considerable variation in shape and size in different cells and it may be studied either in intact stained cells or loose among the debris taken from broken cells at the bottom of the flask. Examples of such isolated but intact starch shells are drawn in Fig. 47. When least developed the starch shell is a hollow sphere a little over 1 μ in diameter surrounding the pyrenoid on all sides except that nearest to the unpigmented face; an isolated starch shell is therefore a hollow sphere with a hole at one pole. As the shell thickens its outline becomes more ovoid and irregular, the starch appearing to be laid down unevenly, more being deposited on the sides than in the centre but the hole on the inner plastid face never becoming covered. The largest starch shells are about 3 μ in diameter.

There is usually one lipid body, about 0·5 μ in diameter, situated in the cell on the side opposite to the chloroplast, but occasionally none are present. After a culture has been grown in strong light for some time additional lipid globules can be seen in the cells; there may be from 1 to 4 and they lie against the inner face of the chloroplast. The stigma, orange-red, and oval to oblong in the surface view, measuring up to $1 \times 0{\cdot}5\,\mu$, lies centrally in the outer face of the chloroplast and is not always readily detected. A single elongated mitochondrion, $1 \times 0{\cdot}75\,\mu$ in size when stained with Janus Green, lies on the inner face of the chloroplast while the ovoid nucleus, $1{\cdot}5 \times 1\,\mu$ in size, lies outside it towards the side of the cell from which the flagellum arises. The golgi area, situated close to the nucleus, stains with Janus Green to give a bluer colour than the mitochondrion. Neither the body scales nor the flagellar scales stain with cresyl blue, but the flagellar basal body can be detected after fixation with osmium tetroxide.

Asexual reproduction can occur in either the motile or non-motile phase. In the motile phase fission is usually into two daughter-cells but it is not uncommon for double-fission to occur producing three or four daughter-cells at the same time from the parent cell (Figs. 40, 48, 49). The first indications of fission are the simultaneous elongation of the stigma and pyrenoid accompanying the first appearance of the second flagellum; occasionally the stigma divides and the daughter-flagellum appears before the elongation of the pyrenoid. By the time the daughter-flagellum has nearly reached its full length the nucleus, mitochondrion, golgi, chloroplast, pyrenoid and stigma have divided. The daughter-flagellum is fully developed and the chloroplasts have separated before actual fission of the body commences at the flagellar pole. In the non-motile (palmelloid) phase, the cells become surrounded by what appears to be a very thin membrane lying close to the body; such cells divide into four or occasionally eight daughter-cells (Figs. 50, 51). The apparent membrane shows up a little more clearly after treatment with Schultz's solution but its precise nature is uncertain.

If this description is compared with that of Korschikov (1923) for *Pedinomonas minor* the following differences from *P. squamata* should be noted: habitat in standing fresh water of inland areas in Poland and west Russia (more recently reported from similar habitats from Hungary by Fott & Ettl (1959)), in contrast to the brackish habitat of *M. squamata*; presence of a contractile vacuole reported in *P. minor*, not detectable in *M. squamata*; the flagellum in *P. minor* considerably shorter (only 1½ times body length) than in *M. squamata* (where it is 2½–4 times body length); starch grains present round the pyrenoid as opposed to the continuous starch shell of *M. squamata*.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE ON *PEDINOMONAS TUBERCULATA* (VISCHER) GAMS

External morphology

The cells of this species make very elegant preparations when dried down and they also possess an unusual capacity for informative dismemberment. One intact cell is illustrated in Fig. 30 with the tip of its plume-like flagellum shown more highly magnified in Fig. 33. The profuse garniture of very delicate hairs spread on the field on both sides of the flagellar axis are highly characteristic. They are individually so slender, however, that the bacterial flagella lying loose in various parts of the field of Fig. 31 appear coarse in comparison.

Where cells have dismembered as in Figs. 31 and 32, four stout roots arranged in a cruciform manner are seen to be attached to the lower end of the flagellar base. These roots have a fibrous core and a membranous covering which in some if not all exhibit conspicuous diagonal striations as of a spiral winding of alternating bands of different electron opacity. This diagonal cross-banding is clearly visible in the lowermost root of Fig. 32.

Internal structure

One morphological detail, namely, the superficial tubercles from which this species gets its name, is better seen in sections than in our whole mounts. They occur as spine-like excrescences on various parts of the body as may be seen in Figs. 34–35. These tubercles are covered by the normal body membrane and they therefore represent local deposits of material beneath the membrane. This material is unidentifiable by the electron microscope alone but the presence of cellulose, calcite and quartz (SiO_2 in micro-crystalline form) has been indicated by X-ray analysis by Brandenburger & Frey-Wyssling (1947) and one or other of these components could be represented here. In addition, the surface membrane, which bears no resemblance in section to a normal cell wall, is covered by small spicules and traces of amorphous material among which fine particles of metallic osmium commonly become lodged as a fixation artifact. It therefore seems probable that though entirely devoid of either scales or a cell wall of algal type the membrane of this species is not completely naked on its outer side.

When viewed in section (Pl. VIII) the cells of *P. tuberculata* appear strongly flattened. Internally the cell is dominated by the large starch-filled chloroplast which is here curved (see especially Fig. 37), surrounding the other cytoplasmic organs which lie in the hollow. In a section cut in another direction (Fig. 36, approximately at right angles to Fig. 37) the nucleus is seen to be strongly flattened against the outer surface of the body on one side. There are several rather small mitochondria in the hollow of the curved plastid, one conspicuous golgi body (dictyosome) near the flagellar insertion and an array of small vesicles and granular cytoplasm. A few larger vesicles containing traces of opaque fat-like material are often conspicuous, though

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Explanation of Plates VII and VIII

Pedinomonas tuberculata (Vischer) Gams

VII

Fig. 30. A dried cell. Micrograph S 672.26, × 3000.

Fig. 31. Field containing a dismembered cell represented by an intact flagellum with four roots arranged in a cruciform manner; bacterial cells and bacterial flagella loose upon the field and appearing relatively coarse in comparison with the very fine lateral hairs on the flagellum of *Pedinomonas*. Micrograph S 669.30, × 10,000.

Fig. 32. Base of the flagellum and roots from another specimen showing fibrous structure in the roots and traces of cross-banding probably carried by a covering membrane on the longest of the roots shown. Micrograph S 669.29, × 20,000.

Fig. 33. Tip of the flagellum of the cell of fig. 30 more highly magnified to show the details of the hairs. Micrograph S 672.28, × 20,000, reversed print.

Fig. 34. Section through a tubercle. Micrograph H 4957, × 30,000.

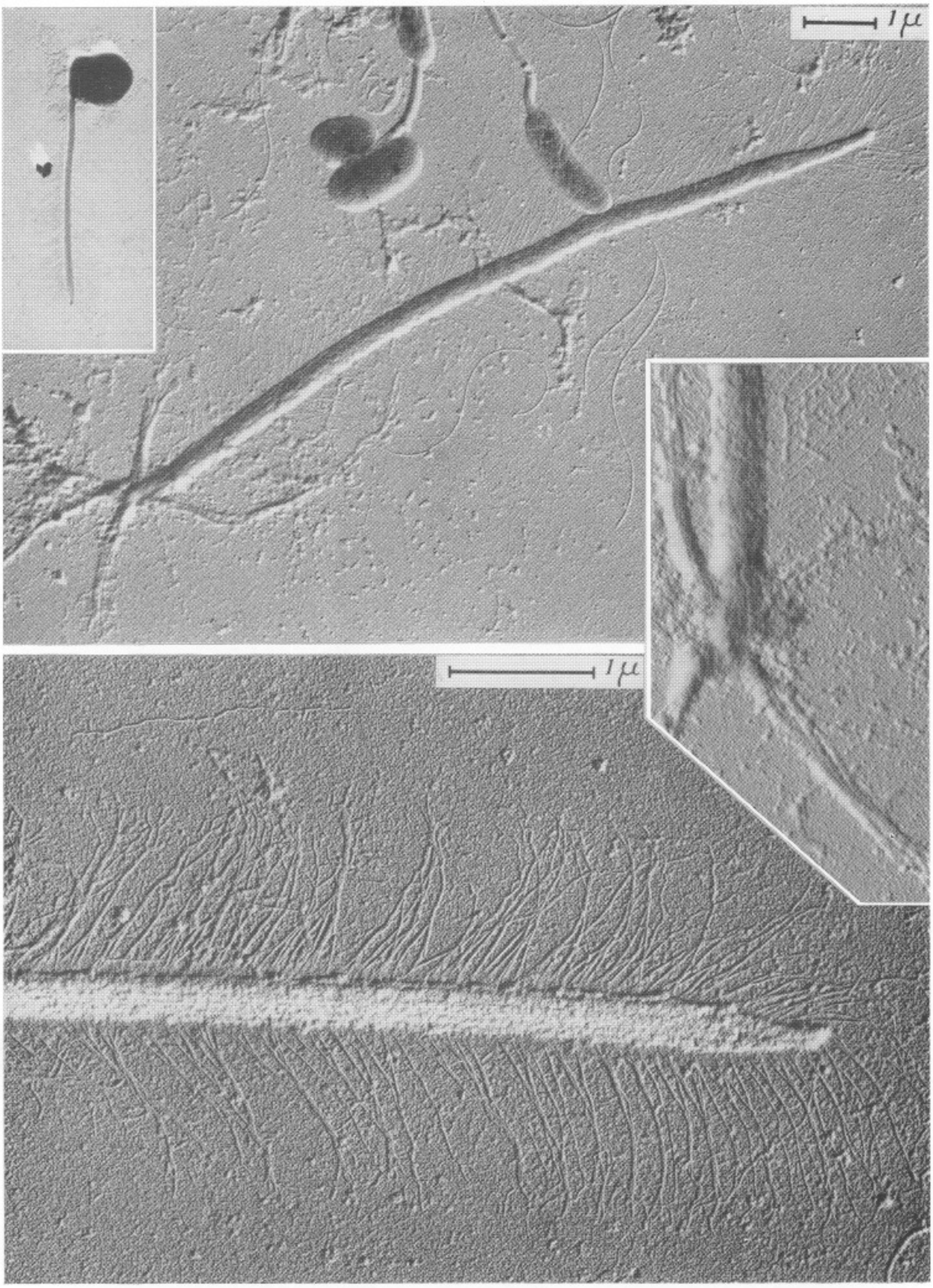
Fig. 35. Section through a tubercle, another specimen. Micrograph H 4985, × 40,000.

VIII

Fig. 36. Section of a cell showing parts of all the main organelles; nucleus (*N*), pyrenoid (*P*) starch grains (*S*), mitochondria (*m*), golgi (*d*). Micrograph H 4993, × 40,000.

Fig. 37. Section cut in another plane showing the curved plastid surrounding the other organelles in the hollow, the flagellar base cut transversely at the top of the section. Micrograph H 5047, × 30,000.

Fig. 38 *a*, *b*. Two successive sections through a flagellar base (*f*) in the region of a root (*r*), to show its superficial position and close relation with the edge of the plastid; a golgi area (*d*) also included in Fig. 38 *b*. Micrographs H 4981 and H 4978, × 50,000.



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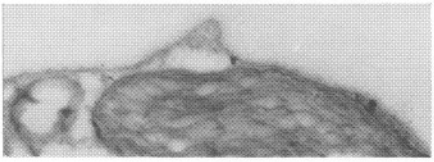

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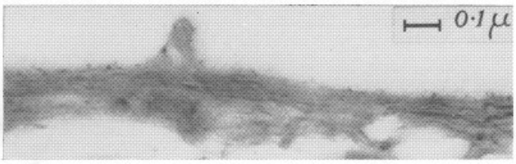

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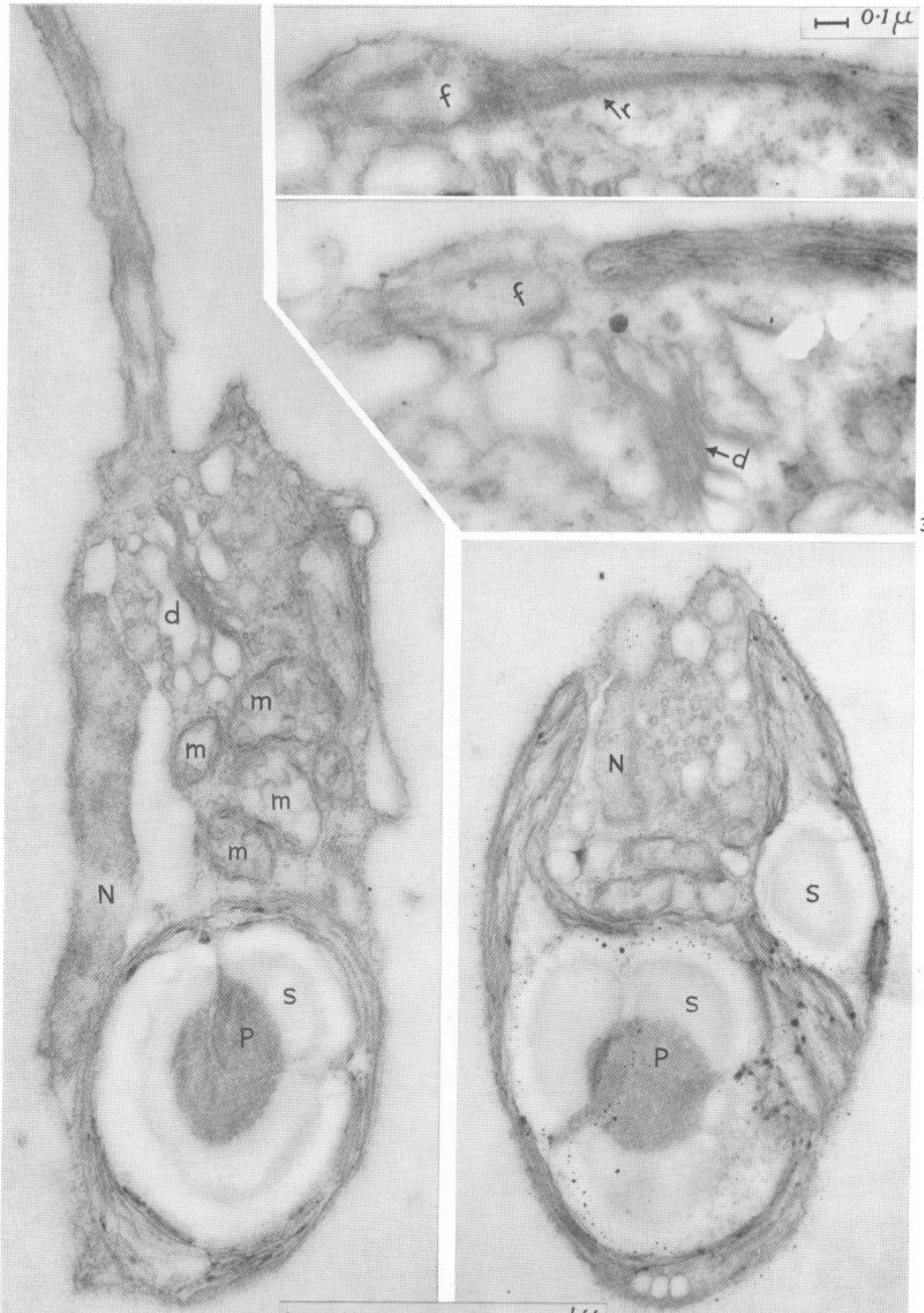
(*Facing p.* 286)



38*a*

38*b*

36

37

not included in the section reproduced. The cavity at first suggestive of a large vesicle on the right of the nucleus in Fig. 36 is a distortion of the perinuclear space.

Within the plastid the stacks of paired lamellae are conspicuous outside and between the starch accumulations; dark granules are conspicuous among them and there are traces of fenestrations comparable to those of *Micromonas squamata* here and there (Fig. 36). The pyrenoid itself has a dense core traversed by channels connected with the lamellated surface; large starch grains occupy the space between the lamellae and the core. Additional starch grains occur singly in other parts of the plastid (Fig. 37).

Some details concerning the attachment of the flagellum are illustrated in Fig. 38*a* and *b*. The flagellum itself is situated close to one edge of the plastid, as may clearly be seen in the specimen transected in Fig. 37. Fig. 38*a* shows the position of one of the cross-banded roots in relation to the subtending basal body (*f*). This root (*r*) remains close to the cell surface running along the plastid edge (cf. Fig. 38*b*) and apparently terminating on it (Fig. 38*a*). There is no sign of a direct attachment to the nucleus which in this particular specimen is situated in the direction of the bottom right-hand corner of Fig. 38*b*. The disposition of the other three roots is uncertain and it is possible that some may proceed in the direction of the nucleus, but it is probable that all are relatively superficial in position since this would adequately explain the ease with which they tear out of the cell when it dismembers.

This species thus differs from *M. squamata* in the shape of the plastid and structure of the pyrenoid, in the possession of conspicuous starch grains both in the pyrenoid and outside it, in the size, number and position of the mitochondria, in the position and shape of the nucleus, in the nature of the cell surface, and in the character and mode of attachment of the flagellum.

OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *PEDINOMONAS TUBERCULATA* (VISCHER) GAMS

Vischer's descriptions (1945, 1949) are sufficiently accurate and detailed to make it unnecessary for us to quote many new observations on *P. tuberculata*. The presence of chlorophyll *a* and chlorophyll *b* has been demonstrated by Harder & Koch (1954), but even though both species of *Micromonas* also contain these pigments there is a readily perceptible difference of actual colour, *P. tuberculata* being a bright grass green both in the mass and in individual chloroplasts, whereas both species of *Micromonas* appear no more than yellowish green. The presence of starch in definite grains round the pyrenoid and elsewhere in the chloroplast is easily attested by staining with iodine.

A small eyespot as claimed by Vischer can sometimes be seen, ovoid in shape, 0·5–1·0 μ long and pale orange-red in colour, situated centrally on the surface of the plastid (Fig. 52). It is not, however, always detectable and the extreme insensitivity of the organism to the direction of incident light added to our inability to detect an eyespot structurally in the sections so far examined with the electron microscope suggests that perhaps the pigment spot observed may be of some other kind.

The organism swims fairly rapidly, travelling sometimes in straight lines for short distances or sometimes in circles; stops are frequent, the flagellum then curving towards the body (Fig. 54), after which the cell will move off in the same or another direction. During movement the body rotates and can show considerable gyration. The flagellar insertion is always directed backwards during swimming with the flagellum trailing (Figs. 41, 52, 53). The insertion itself is slightly off centre (Figs. 52–54).

FURTHER OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *MICROMONAS* (*CHROMULINA*) *PUSILLA* (BUTCHER) COMB.NOV.

The following new observations on living cells may be quoted to supplement the account of the fine structure already published (Manton, 1959*a*). The cells can be very fast moving, with frequent changes of direction (relative speed in culture quoted by Knight-Jones & Walne (1951) as fifty times the body length per second). When a cell changes direction it frequently moves round in circles for a time before swimming off in a different direction. During rapid swimming the cell travels with the rounded end, containing the chloroplast, foremost and with the clear end curved towards the side from which the flagellum arises (Fig. 55). The flagellum proper is then at right angles to the body, arising from the concave surface and with its distal long hair-point curving outwards and backwards (Figs. 55, 56); the shape of the whole cell is then strongly reminiscent of a comma. It is probable that the body does rotate when the cell is swimming very rapidly, but rotation can be seen only when movement becomes slower since there seems to be no gyration. The cells can also swim for short periods with the flagellum directed forwards (Figs. 57, 58) but the speed is then slower. This species characteristically has considerable periods of remaining in one position attached to a surface by the clear end of the body which tends to show metaboly, the cell

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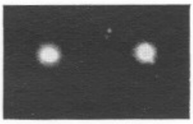
Explanation of Plate IX

Photographs of cells under oil immersion with the light microscope arranged for dark ground illumination, all magnified × 1000.

Fig. 39. Two cells of *Micromonas pusilla* (Butcher) comb.nov., the small tubercle on the right-hand cell is the flagellum, its hair-point not visible.

Fig. 40. *Micromonas squamata* sp.nov. A series of exposures to show the uniflagellate condition and various division stages.

Fig. 41. *Pedinomonas tuberculata* (Vischer) Gams. A series of exposures to show uniflagellate cells and division stages.



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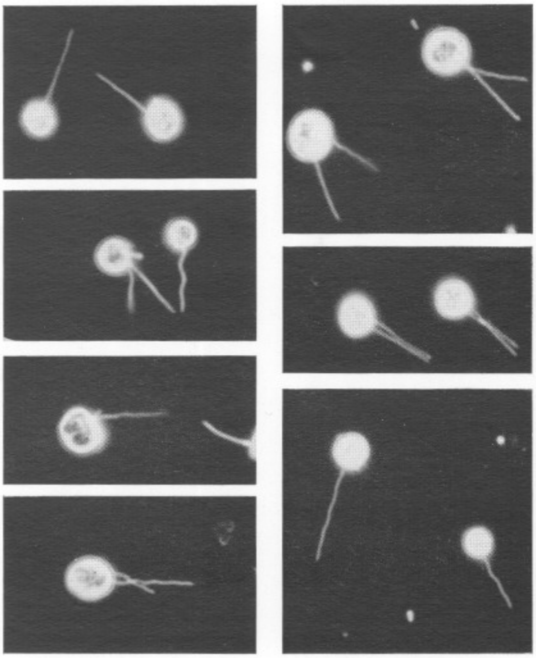

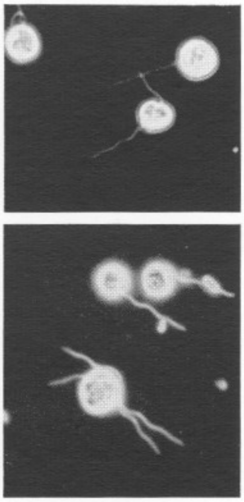

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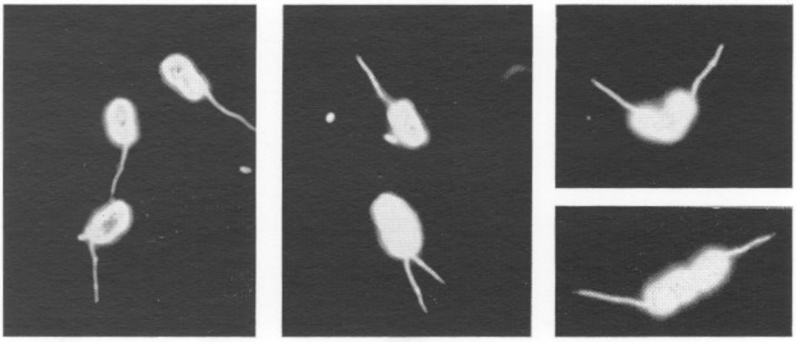

41

(*Facing p.* 288)

meanwhile either swinging round in circles from the point of attachment (Fig. 59) or exhibiting a dithering movement which is very characteristic for this organism.

The species is strongly phototactic and is not toxic to fish (tested by Mrs B. Hepper). Motile cells in culture measure 1·0–3·0 μ long × 0·75–1 μ wide. Fission occurs in both motile and non-motile condition. A non-motile palmelloid phase with cells measuring 2·5–5 μ and showing a translucent area round each also occurs, the cells dividing into 2 or 4. No trace of cellulose is detectable in either motile or non-motile phases and no positive signs of starch when tested with iodine. Signs of a sexual process have been looked for by mixing five different strains, without success.

In occurrence this marine flagellate is very widespread; it has been recorded from surface samples taken from estuaries, creeks and the open sea around the British Isles (Knight-Jones, 1951, 1952; Knight-Jones & Walne, 1951). According to Knight-Jones it is the most generally abundant organism in British coastal waters and the North Sea, the greatest density he recorded for it being 3500 cells per ml in October 1946 from the Helford River, Cornwall.

Our records, covering a period of several years (Tables 1 & 2, Appendix) amplify those of Knight-Jones and Walne and show that this species occurs commonly in the English Channel throughout the year from the surface down to 70 m (Table 2). It occurs also in oceanic water and has been recorded from oceanic stations from the surface down to a depth of 500 m (Table 1). In Table 1 of the Appendix (p. 297) its occurrences are listed other than for International Station E1 and Plymouth Laboratory Stations L 2–6 from 17 September 1957 to 8 September 1959, the records for which are included in Table 2 (p. 297). This table includes densities at different depths sampled on one day at International Station E1.

SUMMARY OF TAXONOMIC CONCLUSIONS AND DIAGNOSES

We can now summarize in tabular form the more important facts ascertained or verified by us for the three organisms under discussion. From this table (p. 292) it will be seen that the organism formerly known as *Chromulina pusilla* Butcher agrees with *Micromonas squamata* in all salient features of internal organization, including plastid structure and form, the possession of one mitochondrion and in the position, relative to other cell organs, of the single flagellum. It differs in the absence of a scaly covering, in the absence of any trace of lateral hairs on the flagellum and in the very unusual relative proportions of the flagellum and its hair-point.

In contrast, *Pedinomonas tuberculata* differs from both the other species in the shape of nucleus and chloroplast, in the position and number of the mitochondria, in the presence of starch in definite grains, in the presence of canaliculi traversing the core of the pyrenoid, in the possession of tubercles beneath the surface membrane and of traces of calcite, quartz and cellulose indicated by X-rays in association with the body membrane, and perhaps most of all in the morphology and mode of attachment to and within the cell, of the flagellum with its four large roots attached apparently to the chloroplast rather than to the nucleus and its very profuse array of exceptionally delicate hairs down the two sides. The resemblance between *P. tuberculata* and either of the other species is limited to very general features such as the plastid pigments, which are similar in all three in spite of the apparent difference of colour when viewed under the microscope, and to the possession of a single chloroplast and a flagellum directed backwards in swimming though arriving at this position in a somewhat different way. This degree of resemblance is perhaps sufficient to permit the placing of *P. tuberculata* within the same family or class as the other two species though not in the same genus.

It is not necessary for us to discuss the genus *Pedinomonas* further here, except to point out the strong probability that all the characters enumerated above as differentiating *P. tuberculata* from our other two species may need to be added to the specific diagnosis of *P. tuberculata* if the time ever comes to characterize this genus more fully in terms of its proper type species. With regard to our new genus *Micromonas* we are in no doubt that this can be

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Legends to Text-figs. 42–59, all × 5,000

Micromonas squamata sp.nov.

Fig. 42. Cell stationary with flagellum curved round under body in characteristic position when at rest.

Fig. 43. Cell stationary with flagellum coiled twice round body.

Figs. 44, 45. Individuals swimming with the flagellum and body in the position characteristic for the species when swimming; point of origin of flagellum *anterior*.

Fig. 46. Early fission stage showing second short flagellum and pseudopodium-like filament; cell with two nuclei, pyrenoid, stigma and mitochondrion dividing.

Fig. 47. Examples of different sizes and shapes of isolated starch shells; for further description see p. 284.

Fig. 48. Fission stage showing chloroplast divided.

Fig. 49. Double-fission stage producing four motile daughter-cells.

Fig. 50. Palmelloid phase with four daughter-cells.

Fig. 51. Palmelloid phase with eight daughter-cells.

Pedinomonas tuberculata (Vischer) Gams

Figs. 52, 53. Individuals with the flagellum and body in the position characteristic for the species when swimming; point of origin of flagellum *posterior*.

Fig. 54. Cell with flagellum in characteristic position when cell is at rest.

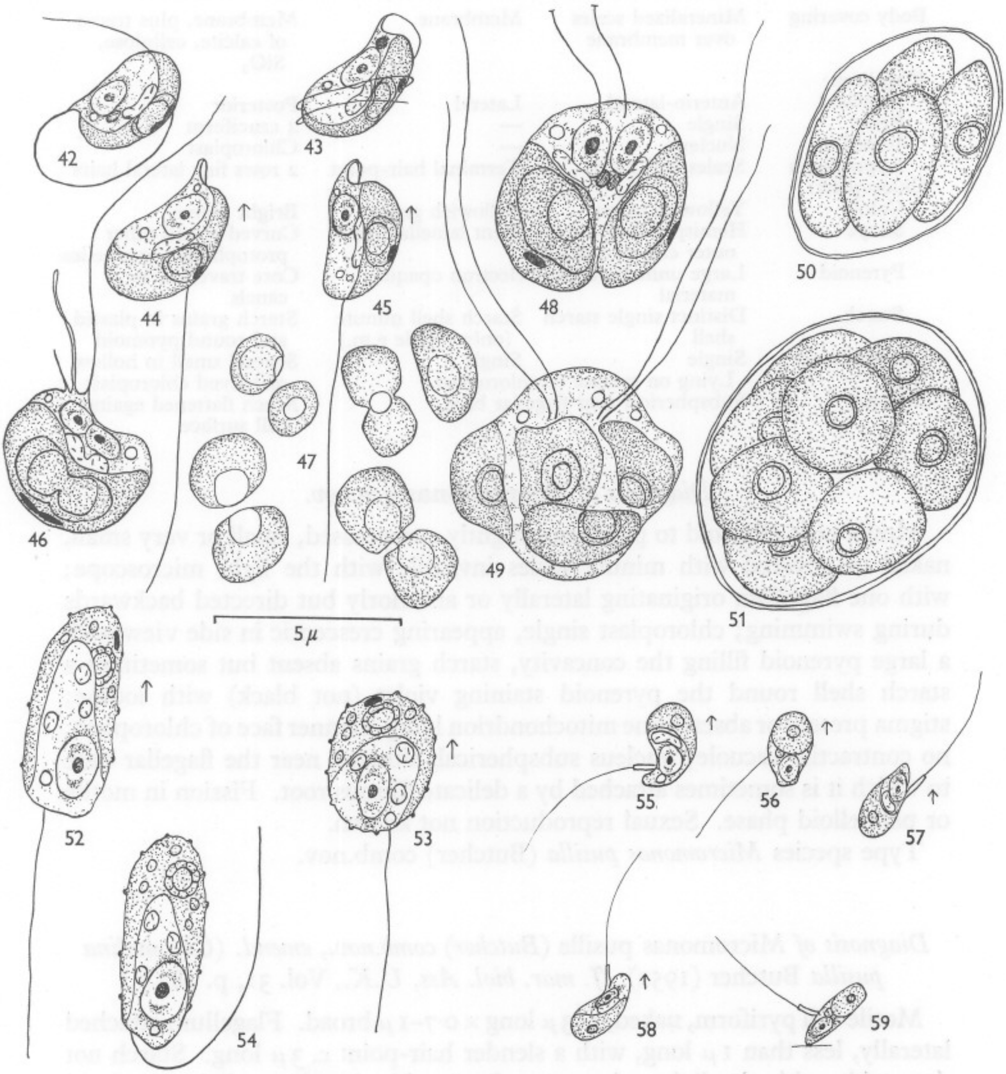
Micromonas pusilla (Butcher) comb.nov.

Figs. 55, 56. Individuals with the flagellum and body in position characteristic for the species during rapid swimming; point of origin of flagellum *lateral*.

Figs. 57, 58. Individuals swimming slowly with flagellum directed forwards.

Fig. 59. Cell attached at clear end of body; body swinging round in circles from point of attachment.

differentiated clearly from the type species of *Pedinomonas* (*P. minor*), as described by Korschikov, on the light microscopy alone. We recognize, however, that while this applies with equal force to both our species of *Micromonas*, the decision to group these together as one new genus and not as two is to some extent arbitrary, depending on our decision, on grounds of convenience, to regard the differences between these two species as less significant than the resemblances and to treat such differences as specific and not as generic criteria,



Text-figs 42–59

as explained in the introduction. The way is then clear to summarize these conclusions still further by constructing formal diagnoses for the new genus *Micromonas* and for the two species which it at present contains.

TABLE OF MORPHOLOGICAL AND ANATOMICAL CHARACTERS AVAILABLE FOR DIFFERENTIATING THE THREE SPECIES UNDER DISCUSSION FROM EACH OTHER

	Micromonas squamata	*Micromonas pusilla*	*Pedinomonas tuberculata*
Body covering	Mineralized scales over membrane	Membrane	Membrane, plus traces of calcite, cellulose, SiO_2
Flagellum:			
Attached	Anterio-lateral	Lateral	Posterior
Roots	Single	—	4 cruciform
Joined to	Nucleus	—	Chloroplast
Appendages	Scales and hairs	Terminal hair-point	2 rows fine lateral hairs
Chloroplast:			
Colour	Yellowish green	Yellowish green	Bright green
Shape	Hemispherical with pigment lamellae near outer curved surface		Curved round other protoplasmic organelles
Pyrenoid	Large uniform core of electron opaque material		Core traversed by canals
Starch	Distinct single starch shell	Starch shell minute (only visible e.m.)	Starch grains in plastid and round pyrenoid
Mitochondria	Single Lying on surface of chloroplast	Single	Several small in hollow of curved chloroplast
Nucleus	Subspherical near flagellar base		Much flattened against cell surface

Diagnosis of **Micromonas** *gen.nov.*

Motile cells ellipsoid to pyriform, slightly compressed, small or very small, naked or covered with minute scales invisible with the light microscope; with one flagellum originating laterally or anteriorly but directed backwards during swimming; chloroplast single, appearing crescentic in side view with a large pyrenoid filling the concavity, starch grains absent but sometimes a starch shell round the pyrenoid staining violet (not black) with iodine; stigma present or absent; one mitochondrion lying on inner face of chloroplast; no contractile vacuole; nucleus subspherical, situated near the flagellar base to which it is sometimes attached by a delicate fibrous root. Fission in motile or palmelloid phase. Sexual reproduction not known.

Type species *Micromonas pusilla* (Butcher) comb.nov.

Diagnosis of Micromonas pusilla (*Butcher*) *comb.nov.*, *emend.* (*Chromulina pusilla* Butcher (1952). *J. mar. biol. Ass. U.K.*, Vol. 31, p. 182.)

Motile cell pyriform, naked, 1–3 μ long × 0·7–1 μ broad. Flagellum attached laterally, less than 1 μ long, with a slender hair-point *c.* 3 μ long. Starch not detectable with the light microscope but a thin layer round the pyrenoid thought to be a narrow starch shell visible with the electron microscope. Stigma absent.

Habitat in estuaries and the open sea round the British coasts. Neo-type culture Plymouth no. 27, isolated by M. Parke from the sea at position 50° 15′ N., 04° 13′ W. (13 April 1950) at surface.

Diagnosis of **Micromonas squamata** *sp.nov.*

Motile cell ovoid with anterior pole depressed, 3–5 μ diameter; the flagellum attached anterio-laterally, 3–3·5 times cell diameter in length. Surface of cell and flagellum completely covered with slightly mineralized plate-like scales of a spider's web pattern, 0·15 to 0·4μ in diameter; a few short stout curved hairs borne laterally on the flagellum but easily detached. Single starch shell demonstrable with iodine round the pyrenoid; a small stigma sometimes present on outer face of chloroplast close to the pyrenoid.

Habitat in brackish water. Type culture Cambridge no. 1965/1, isolated by E. A. George from Brancaster Salt Marsh (salinity *c.* 15‰) in August 1951.

GENERAL DISCUSSION

Apart from the taxonomic conclusions only three general points need to be singled out for discussion. The observations on scale formation in *Micromonas squamata* constitute perhaps the most generally interesting contribution that this organism has made to botanical knowledge. Detachable surface scales are now known in great variety in pigmented micro-organisms of many groups but it is usually tacitly supposed that their place of origin is the cell surface itself, either on, in or immediately below the body membrane. Satisfactory direct evidence of mode of origin has hitherto eluded us, even in those species, notably of *Chrysochromulina* for which we have detailed electron microscopical information on the appearance and pattern of the finished scale. The observation in *Micromonas squamata* that the scales are here elaborated in the interior of the cell before being deposited on the surface individually from separate vesicles does not necessarily apply to any other flagellate. It is, nevertheless, strongly suggestive of a primitive and more plausible mechanism than any other yet suggested. It is therefore greatly to be hoped that precise observations on this particular matter may be obtainable from other genera.

Secondly, the various manifestations of hairs on the flagella on the two species described here offer many points of unusual interest. The presence of hairs as lateral appendages on certain flagella is well known in and characteristic of all the major heterokont groups (Xanthophyceae, Phaeophyceae Chrysophyceae, Saprolegniaceae, etc.) though not of the green algae as such. Nevertheless, reports claiming the presence of hairy flagella in individual genera of green flagellates have appeared in the literature more than once (e.g. Benešová, 1949; Butcher, 1959) and though these records vary very much in the degree of clarity with which the facts have been ascertained a few comparisons and contrasts can usefully be made. Thus the peculiar curved hairs encountered by us in *Micromonas squamata* bear a suggestive resemblance to hairs illustrated by one micrograph of *Chilomonas paramecium* (a colourless Cryptomonad) published by Pitelka & Schooley (1955). *C. paramecium* is described by these authors as also possessing, on the same flagellum, another type of hair more nearly comparable in morphology to those commonly known as Flimmer in some of the heterokont groups. It is therefore possible that both in this *Chilomonas* and in our *Micromonas squamata* the peculiar curved hairs represent some entirely different category of appendage from ordinary Flimmer. A comparison based on only one micrograph reproduced at a very low magnification (17,000 in Pitelka & Schooley's Pl. 22*c*) must necessarily be substantiated by fuller information before it can become more than a tentative suggestion. It would, nevertheless, be a matter of considerable interest if a real resemblance in this particular feature were to be found between two such apparently different organisms.

On the other hand, *Pedinomonas tuberculata* with its profuse garniture of very fine hairs is peculiar in several respects. The hairs here are individually far more delicate than those hitherto encountered in the heterokont groups, though in this particular character they may prove to be comparable with the Euglenoids, in some of which (e.g. *Phacus*, Manton, 1952) the hairs are also individually more delicate than average bacterial flagella. A marked difference from the Euglenoids is nevertheless provided by the presence in *Pedinomonas tuberculata* of hairs on both sides of the flagellum and also on the conspicuously posterior position of the flagellum both in point of attachment and in direction of movement. The usual position of the 'Flimmergeisel', in the heterokont types, as in the euglenoids, is forwards, even when, as in *Dictyota*, the cell may have become uniflagellate by suppression of one (the smooth) member of the pair (Manton, 1959*b*). The particular situation in *P. tuberculata* is thus at present without exact parallel.

A conclusion of some importance which these observations suggest is that outside the major heterokont groups the mere presence or absence of flagellar hairs cannot yet be used with the same precision as a phyletic guide as within the heterokont groups. Where hairy flagella are encountered among forms with chlorophycean pigments, notably chlorophyll *b*, there is reason to think that parallel evolution, possibly of more than one kind, may have taken place. If this were so, by no means all, and perhaps none, of the hairs encountered among green pigmented flagellates could be treated as homologous with those of the Phaeophyceae, Chrysophyceae, Xanthophyceae and Saprolegniaceae.

This may perhaps give point to the final comment that in very small organisms of the size range of those immediately under investigation in this communication, far greater care is necessary in formulating descriptions and in postulating phyletic affinities than has sometimes been used. The electron microscope as it can now be applied to the study of both morphology and internal structure has a uniquely important part to play in elucidating the facts regarding a region of the plant world about which very little has hitherto been known. It is of the greatest importance to clarity of thinking that hasty generalizations should not be made on insufficient evidence. If restraint is practised, however, it is to be hoped and indeed expected that when a greater number of individual taxa have been studied by comparable means some clearer general principles about how to interpret them may become available than we have at present.

Grateful thanks are due to Mr E. A. George of Cambridge for supplying the two cultures and for co-operating with information. We have to thank Dr G. Y. Kennedy of Sheffield for the pigment analyses, Miss I. Adams for assistance in the routine examination of samples and Mrs B. Hepper for testing *Micromonas pusilla* for its possible toxicity to fish. For help with the Latin diagnoses we have to thank Dr T. Christensen. We have also to thank Dr L. H. N. Cooper, Mr E. I. Butler, Mr D. Vaux and Mr A. Burd ('Sir Lancelot') for the collection of sea-water samples. Mention should also be made of the technical staffs of both Leeds and Plymouth for help in maintaining cultures, making preparations and completing the photography for publication.

SUMMARY

Pedinomonas tuberculata (Vischer) Gams has been investigated electron microscopically to the extent necessary to show that the generic name *Pedinomonas* cannot be used to include the flagellate formerly known as *Chromulina pusilla* Butcher.

A new genus, *Micromonas*, has been defined with *M. pusilla* (Butcher) comb.nov. emend. as the type species.

A second species of *Micromonas*, *M. squamata* sp.nov., has been described electron microscopically and with the light microscope. Special attention is drawn to one specific character of unusual interest, namely, the presence all over the flagellar and cell surface of an external covering of detachable plate-scales of characteristic pattern which have been shown to originate within vesicles in the body of the cell.

Attention is drawn to some of the comparative problems raised by the existence of lateral hairs of very different types on the flagellum in *Pedinomonas tuberculata* and *Micromonas squamata* respectively.

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APPENDIX

TABLE 1. RECORDED DISTRIBUTION OF *MICROMONAS PUSILLA* (BUTCHER) MANTON & PARKE

(Excluding Stations E 1 and L 2–6, September 1957–59)

Date	Position N.	Position W.	Depth (m)
12. xi. 48	50° 19·5′	04° 10′	5
8. vi. 49	50° 19·5′	04° 10′	10
29. ix. 49	50° 19·5′	04° 10′	10
14. xi. 49	50° 19·5′	04° 10′	10
8. iv. 50	49° 51′	04° 00′*	10
13. iv. 50	50° 15′	04° 13′†	0·5
9. v. 50	49° 21′	04° 54′*	0·5
30. v. 50	50° 15′	04° 13′	0·5
13. vi. 50	48° 38′	06° 20′	5
14. vi. 50	49° 19′	07° 26′	5, 10
13. ix. 50	50° 15′	04° 13′	5
29. v. 56	50° 06′	04° 21′	2
25. vi. 57	Tamar Estuary		T
16. vii. 57	50° 02′	04° 22′	0·5
6. xi. 57	Tamar Estuary		T
14. iii. 58	46° 30′	08° 00′	10, 20, 100, 500
15. iii. 58	47° 20′	07° 22′	0·5, 10, 20, 100, 200
	47° 30′	07° 18′	20, 100
16. iii. 58	47° 40′	07° 13′	0·5, 10, 20
18. iii. 58	47° 46′	07° 05′	20
16. iv. 58	46° 30′	08° 00′	127
19. iv. 58	46° 30′	08° 00′	19
20. iv. 58	47° 19′	07° 23′	9, 18, 303
20. iv. 58	47° 30′	07° 18′	10, 19
20. iv. 58	47° 38′	07° 10′	10, 225
21. iv. 58	47° 46′	07° 05′	10, 19, 125

* Samples brought in by 'Sir Lancelot'.
† Neotype strain (Plymouth no. 27) of *Micromonas pusilla* isolated from this sample.
T Townet sample.

TABLE 2 SEASONAL DISTRIBUTION OF *MICROMONAS PUSILLA* (BUTCHER) MANTON & PARKE

	International Station E 1								Plymouth Laboratory Stations				
									L 6	L 5	L 4	L 3	L 2
Depth (m)... Date	0·5	5	10	15	20	30	50	70	0·5	0·5	0·5	0·5	0·5
17. ix. 57	1	0	0	—	2	—	0	0	4	2	2	2	2
15. x. 57	0	0	0	—	0	—	0	0	0	0	0	1	0
6. xi. 57	1	—	—	—	—	—	—	—	—	—	—	—	—
3. xii. 57	4	5	5	—	2	—	3	4	2	3	3	3	4
21. i. 58	2	2	3	—	3	—	2	0	3	0	0	2	2
18. ii. 58	4	4	5	—	5	—	6	3	5	4	2	4	4
19. iii. 58	5	3	3	—	4	—	4	3	—	—	—	—	—
22. iv. 58	6	5	4	—	6	—	5	5	—	—	—	—	—
20. v. 58	3	4	4	—	5	—	4	4	6	5	4	0	3
10. vi. 58	2	5	3	6	5	—	5	6	3	3	0	0	0
9. vii. 58	6	5	5	4	6	—	6	4	4	3	1	0	0
26. viii. 58	0	0	4	—	2	3	5	4	2	0	0	2	0
1. x. 58	6	6	4	—	4	—	2	2	—	—	—	—	—
22. x. 58	6	3	6	—	4	—	3	1	3	0	0	1	0
18. xi. 58	0	—	2	—	2	—	0	0	0	0	0	0	0
13. xii. 58	1	0	0	—	0	—	0	1	—	—	—	—	—
13. i. 59	2	—	3	—	5	—	3	5	5	2	2	0	2
10. ii. 59	5	—	5	—	3	—	6	5	4	3	3	3	2
12. iii. 59	3	4	3	—	4	—	3	5	2	6	0	2	0
20. iv. 59	2	4	2	—	5	—	3	0	—	—	—	—	—
12. v. 59	4	3	5	—	5	—	1	6	5	4	2	4	4
10. vi. 59	5	3	5	—	3	5	4	3	3	4	3	1	0
11. viii. 59	5	5	4	—	6	—	5	5	6	5	5	2	3
8. ix. 59	2	3	5	2	2	—	4	4	6	3	2	0	2

6, min. no. *M. pusilla* per l. 1000
5, min. no. *M. pusilla* per l. 800
4, min. no. *M. pusilla* per l. 600
3, min. no. *M. pusilla* per l. 400
2, min. no. *M. pusilla* per l. 200
1, min. no. *M. pusilla* per l. 10
0, Absent from sample

E 1	50° 02′ N., 04° 22′ W.
L 6	50° 06′ N., 04° 21′ W.
L 5	50° 11′ N., 04° 13′ W.
L 4	50° 15′ N., 04° 13′ W.
L 3	50° 18′ N., 04° 11′ W.
L 2	50° 20′ N., 04° 10′ W.

FORMAL DIAGNOSES IN LATIN

Micromonas gen.nov.*

Cellula erratica ellipsoïdes vel pyriformis, leniter compressa, parva vel minuta, nuda vel squamis minimis per microscopium luminarium non conspicuis induta; flagellum unicum e latere vel apice oriens, inter nandum retro deflexum; chromatophorum unicum a latere lunulare visum, pyrenoïde magno in sinu sito, amyli granulis nullis, sed testa interdum pyrenoïdi circumdata iodo violascente (non nigrescente); stigma praesens vel deficiens; mitochondrium unicum facieï cavae chromatophori appositum; vacuolum contractile nullum; nucleus subsphaericus prope basim flagelli situs, fibra subtili interdum illi conjunctus. Fissio in statu erratico vel in statu palmelloïde effecta; propagatio sexualis ignota.

Species typica *Micromonas pusilla* (Butcher) comb.nov.

Micromonas pusilla (Butcher) comb.nov., emend. (*Chromulina pusilla* Butcher (1952), *J. mar. biol. Ass. U.K.*, Vol. 31, p. 182.)

Cellula erratica pyriformis, nuda, 1–3 μ longa, 0·7–1 μ lata. Flagellum e latere oriens, vix 1 μ longum, seta tenui terminali ca. 3 μ longa auctum. Amylum per microscopium luminarium non conspicuum, sed stratum tenue pyrenoïdi circumdatum per microscopium electronicum apparens pro testa amylea exili putatum. Stigma nullum.

Habitat in aestuariis ut in ipso mari oras Britannicas alluente. Neotypus die 13 Aprilis 1950 in summo mari lat. bor. 50° 15′, long. occ. 04° 13′ lectus, in Plymouth Angliae sub numero 27 cultus, postea in vivario Cantabrigiensi depositus.

Micromonas squamata sp.nov.

Cellula erratica ovata, apice depressa, 3–5 μ diam.; flagellum ex parte anteriore lateris oriens, cellulae diametro 3–3·5plo longius. Tota cellulae ut flagelli superficies squamis araneaceïs, parce petrificatis vestita. Ciliola lateralia pauca brevia, sat crassa, curva, flagello facile adempta. Testa amylea continua pyrenoïdi circumdata iodo manifesta. Stigma parvum interdum praesens, prope pyrenoïdes facieï exteriori chromatophori appositum.

Habitat in aqua subsalsa. Typus mense Augusto 1951 prope Brancaster Angliae orientalis ab E. A. George lectus, ab eodem sub numero 1965/1 cultus, in vivario Cantabrigiensi depositus.

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* The name *Micromonas* was suggested to one of us (M.P.) by Dr R. W. Butcher.

J. mar. biol. Ass. U.K. (1960) 39, 299–302
Printed in Great Britain

CHEMICAL CHANGES IN SEA WATER OFF PLYMOUTH DURING 1958

By F. A. J. Armstrong and E. I. Butler

The Plymouth Laboratory

(Text-figs. 1–3)

Analyses of sea water collected during 1958 at the International Hydrographic Station E1 (lat. 50° 02′ N., long. 4° 22′ W.) are given here in the same form as in earlier reports (Armstrong, 1954, 1955, 1957, 1958; Armstrong & Butler, 1959). The methods of collection and analysis remain the same. Salinities were determined by the Government Chemist, Department of Scientific and Industrial Research. We wish again to thank Lt.-Cdr. C. A. Hoodless, D.S.C., and the crew of R.V. 'Sarsia', and Capt. W. J. Creese and the crew of R.V. 'Sula' for help at sea.

RESULTS

Temperature and salinity

The vertical distribution of temperature during the year is shown in Fig. 1. The lowest temperature measured at the surface was 8·95° C on 19 March; the highest was 16·45° C on 9 July. A weak thermocline at 15 m was established by 20 May, and it strengthened and persisted with some variation of depth down to 30 m throughout the summer. The water column had become isothermal by 22 October.

Some fluctuations of salinity occurred, as when the mean value of 35·23‰ in January dropped to 35·10 in February and returned to 35·25 in March. These changes were accompanied by the rise and fall in silicate which are shown in Table 1, and suggest a change in water mass at the station.

Phosphate

Vertical distribution is shown in Fig. 2, and integral mean concentrations in Table 1. The winter maximum found was 0·55 μg atom P/l., on 18 February. This was unusually high and in recent years was only exceeded in 1955 (0·59 in February). The lowest concentrations found were 0·07–0·09 μg atom P/l. in the top 10 m layer in June, July and August, and were about as low as are ever encountered at this station. Low values above the thermocline were recorded throughout the summer and until 1 October. By 22 October, with the autumn overturn of the water, phosphate values were uniform through the water column.

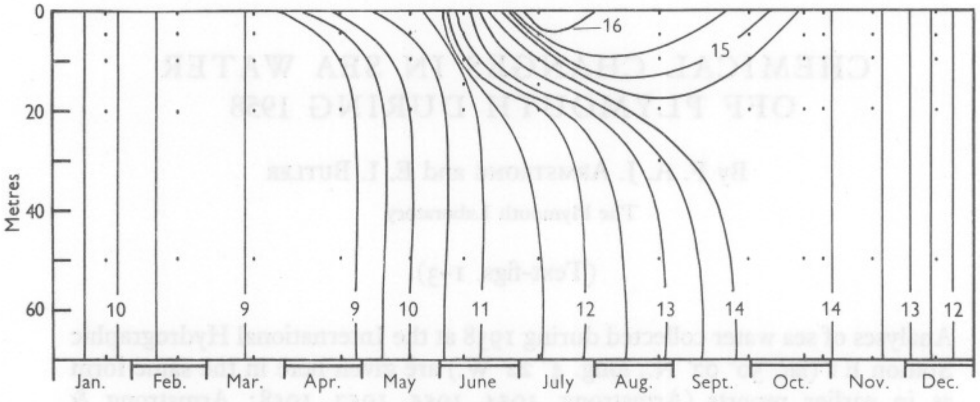

Fig. 1. Vertical temperature distribution at International Hydrographic Station E1, 1958. Contour lines at 0·5° C intervals.

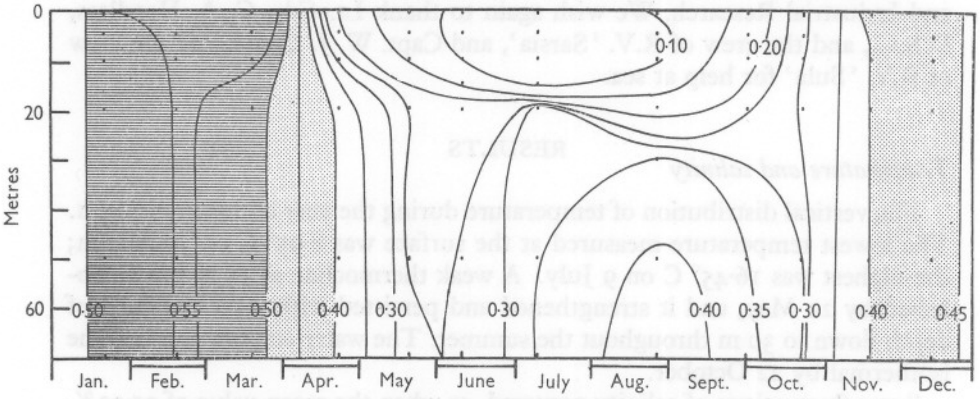

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E1, 1958. Contour lines at 0·05 μg atom P/l. intervals.

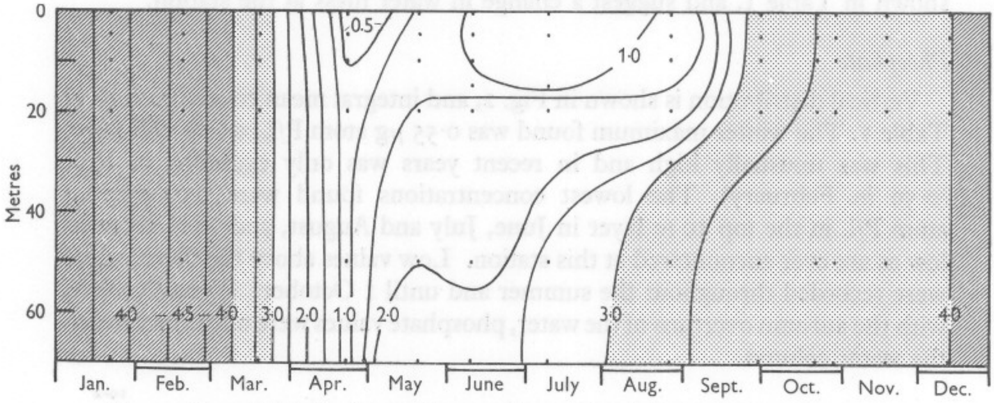

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E.1, 1958. Contour lines at 0·5 μg atom Si/l. intervals.

Total phosphorus

Determinations were made in the early months of the year only, to find the winter maximum, which was 0·75 μg atom P/l. on 22 April, although sensibly similar figures were found in February and March. The value of 1·35 for the ratio of 'total' to 'inorganic' phosphorus is unusually high (Armstrong & Harvey, 1950).

Silicate

Vertical distribution is shown in Fig. 3, and integral mean concentrations in Table 1. The winter maximum value found was 4·67 μg atom Si/l. on 18 February, which was rather high. It was equalled since 1947 only in 1954 (4·70 in January) and went with the high phosphate and low salinity already mentioned.

TABLE 1. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1, 1958

Date	Phosphate (μg atom P/l.)	'Total-P' (μg atom P/l.)	Silicate (μg atom Si/l.)	Ammonia (μg atom N/l.)	Inorganic N (μg atom N/l.)
21 Jan.	0·53	0·69	3·93	—	—
18 Feb.	0·55	0·74	4·67	Less than 0·1	10·5
19 Mar.	0·54	0·73	3·64	Less than 0·1	7·6
22 Apr.	0·37	0·75	0·60	Less than 0·1	10·5
20 May	0·23	0·58	2·16	0·2	8·8
10 June	0·20	—	1·69	1·7	2·1
9 July	0·28	—	1·84	1·4	3·3
26 Aug.	0·30	—	2·61	—	—
1 Oct.	0·28	—	3·62	0·6	6·2
22 Oct.	0·30	—	3·59	—	—
18 Nov.	0·40	—	3·57	0·1	8·7
9 Dec.	0·40	—	3·95	0·2	8·9
12 Dec.	0·41	—	3·61	—	—

Low values of around 0·2 μg atom Si/l. were found in the top 10 m on 22 April, but even in the upper layers concentrations rose again in May and stayed at the 1·0 μg atom Si/l. level throughout the summer, with a temporary fall to 0·3 in July. The vertical distribution of silicate (unlike that of phosphate) had become uniform by 1 October and remained so until the end of the year.

Nitrogen

Integral mean concentrations of ammonia-N and inorganic-N (nitrate + nitrite + ammonia) are given in Table 1. The vertical distribution generally resembled that for phosphate but there are too few observations to allow a diagram to be presented. The winter maximum (of inorganic nitrogen) found was 10·5 μg atom N/l. on 18 February. The ratio N:P was then 19:1 by atoms or 8·6:1 by weight which is similar to that for 1957. On 9 July, nitrogen compounds could not be detected in the upper layers. The methods should detect 0·1 μg atom N/l., and we infer that nitrogen was the limiting nutrient for plant growth, since an appreciable quantity of phosphorus remained available. This may be the rule at this station, in recent years at least, for although we have not the necessary nitrogen analyses, it is notable that phosphate concentrations in summer have never fallen below about 0·05 μg atom P/l., and are usually appreciably higher. We estimate that the method will detect 0·02 μg atom P/l. with certainty, and it is not difficult to reduce the phosphate content of phytoplankton culture solutions below this level, if the nitrogen supply is adequate.

Nitrogen remained low in the upper layers during the summer months, became vertically uniform by 22 October, and increased thereafter until the end of the year.

Integral mean concentrations

Some figures have been discussed. The spring decreases were: phosphate 0·35 μg atom P/l., silicate 4·07 μg atom Si/l., inorganic nitrogen 8·4 μg atom N/l. The ratio N:P consumed was 24:1 by atoms or 10·8:1 by weight.

SUMMARY

The results of analysis of sea-water samples from the International Hydrographic Station E 1 during 1958 are given in graphical form and as integral mean values for the water column of 70 m. The spring decreases of nutrients, conventionally ascribed to consumption by plants were: phosphate 0·35 μg atom P/l., silicate 4·07 μg atom Si/l., inorganic nitrogen 8·4 μg atom N/l.

At the time of winter maximum of nutrients the ratio N:P was 19:1 by atoms or 8·6:1 by weight. The ratio of these elements consumed was 24:1 by atoms or 10·8:1 by weight.

The year was notable for the high phosphorus and silicon concentrations found in February.

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J. mar. biol. Ass. U.K. (1960) 39, 303–317
Printed in Great Britain

THE VIVIPAROUS SCYPHOMEDUSA *STYGIOMEDUSA FABULOSA* RUSSELL

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(Plates I–IV and Text-figures 1–7)

The capture of a remarkable viviparous deep-sea jellyfish, *Stygiomedusa fabulosa*, has already been reported (Russell, 1959). We have now had an opportunity of making a more detailed examination of the specimen, which has been added to the collection of the British Museum as the type specimen under the catalogue number B.M. 1960.4.7.1.

This scyphomedusa was caught in a haul with the Isaacs–Kidd net made on 18 October 1959 from R.V. 'Sarsia' with 3300 m of wire out. The net was shot at 05.53 hr in 43° 51′ N., 3° 55′ W. and reached the surface again at 12.37 h in 44° 04′ N., 3° 39′ W.

The specimen was about 50 cm in diameter across the umbrella and was not easy to handle. When it reached the laboratory it was, however, still practically intact, although it has broken into several pieces since. The form of the whole animal is shown as seen from the subumbrellar side in Pl. I. The surface of the subumbrella is smooth and it is probable that the exumbrella surface is also smooth; the latter cannot be said for certain because the whole surface of the exumbrella is deeply impressed with the outlines of the meshes of the net and most of the epidermis has been rubbed off.

The jelly is thick and firm.[1] That part of the exumbrella overlying the stomach cavity is about 25 cm in diameter and its jelly is 9 mm in thickness. The jelly of the subumbrellar floor of the stomach is about 15 mm in thickness. Beyond the margin of the stomach the jelly of the umbrella is very much thicker, reaching as much as 30 mm. This thick portion extends towards the umbrella margin for 6 or 7 cm after which the jelly again becomes thin and tapers for another 6 or 7 cm to a thin edge at the umbrella margin (Text-fig. 1 A). In the latter thin marginal region of the umbrella the jelly appears to be divided into squares in places. It seems almost certain that this is an artifact caused by the meshes of the net almost cutting through the thin jelly. The margin of the umbrella is not entire; it is much frayed and

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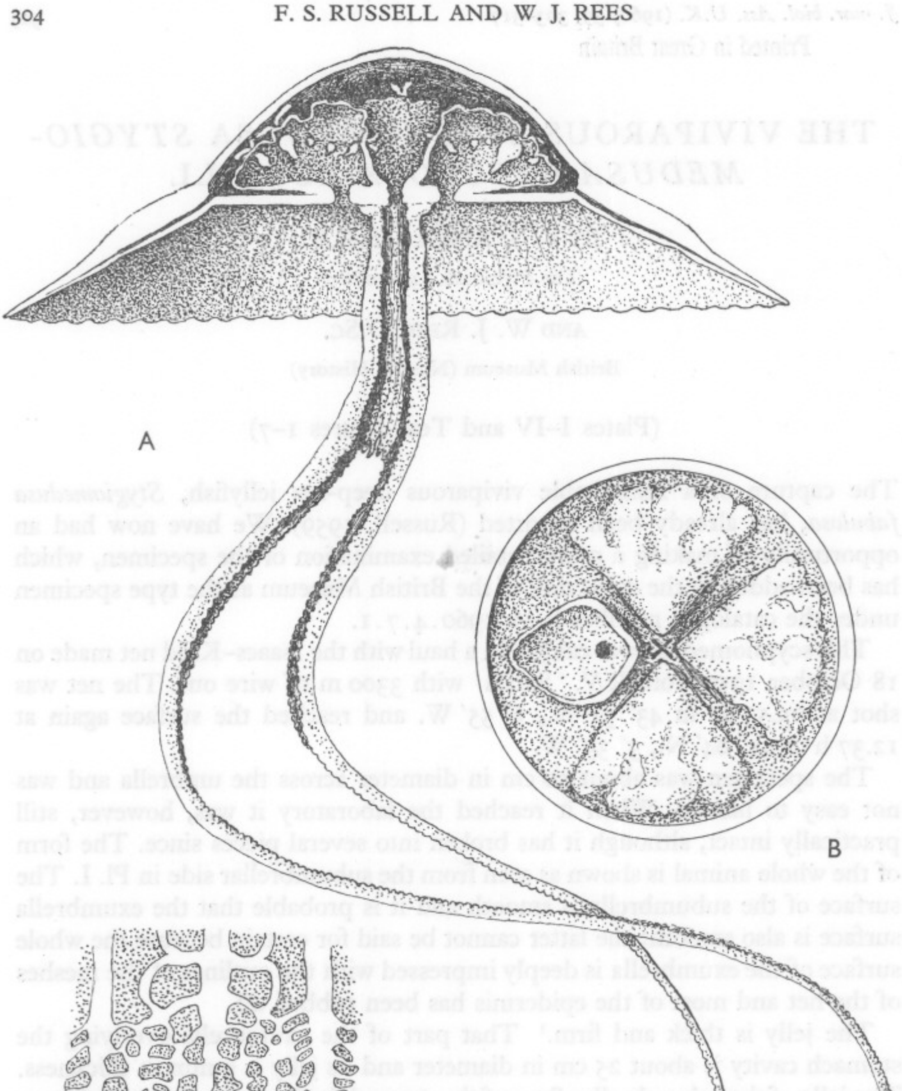
[1] When the medusa was first caught the jelly was very tough but it became brittle after being in formalin and sea water.



Text-fig. 1. *Stygiomedusa fabulosa*: A, half section of complete medusa, the two sectioned brood chambers have been pulled apart to show the one behind; B, vertical view of stomach cavity after removal of exumbrella wall to show arrangement of four brood chambers, one of which has been sectioned near its base to show subumbrellar aperture; C, tracing of enlarged photograph of portion of umbrella margin of young medusa to show gastrovascular canal system (white), marginal lappets and rhopalium. (Del. F. S. R.)

incised, and only in a few places can it be seen that it has shallow rounded lappets. As will be seen later from the description of the young medusa, it is probable that these should have been 60 in number.

There is a weakly developed subumbrellar coronal muscle in the area of the thickened jelly; the muscle fibres are striated.

In the subumbrellar wall of the stomach there are four round interradial apertures each about 15 mm in diameter and situated about 6 cm from the centre of the cross-shaped mouth opening.

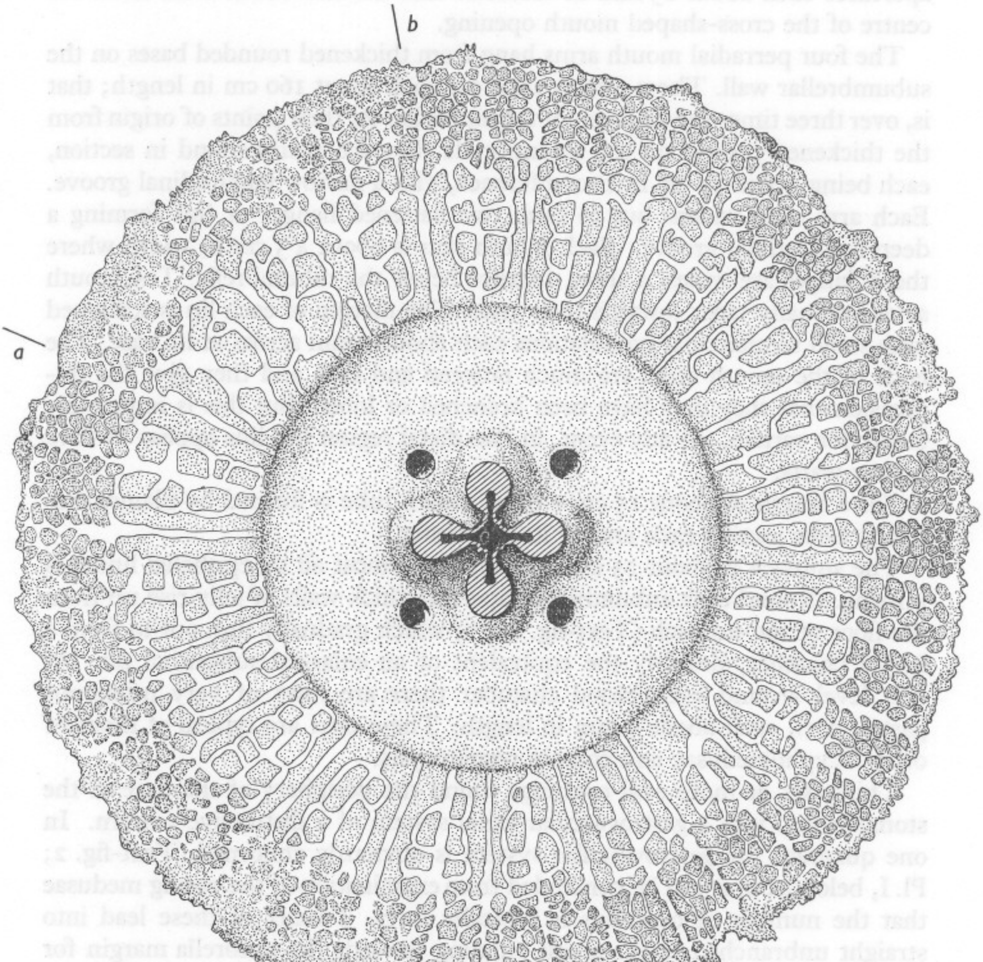
The four perradial mouth arms hang from thickened rounded bases on the subumbrellar wall. These mouth arms are each about 160 cm in length; that is, over three times the diameter of the umbrella. At their points of origin from the thickened pedicel on the subumbrella they are nearly round in section, each being about 11 cm in circumference, with a narrow longitudinal groove. Each arm soon widens out to form two flattened flanges or lips forming a deep longitudinal groove. Each mouth arm is about 4·5 cm in width where these flanges are widest a short distance below the subumbrella. The mouth arms gradually taper towards their ends. The margin of each lip is scalloped with small semicircular crenulations each about 5 mm across at its base. The ends of the mouth arms are much tattered and torn and they give the impression that they may have been branched or lobed, but this is impossible to say for certain. In any event, in this distal region the lips appear to have hollow warts.

For a length of about 15 cm a basal mouth tube is formed by filamentous frilled webs joining each arm to its neighbour.

The stomach is about 25 cm in diameter; almost all its epithelial lining is missing. Round each subumbrellar aperture thick walls of jelly rise up from the floor of the stomach (Text-fig. 1 A, B) which gradually thin out to form a brood chamber, possibly the equivalent of an enlarged subgenital pit. At this level around each brood chamber there are rows of very numerous gastric cirri, each about 5 mm in length. These cirri are typical of those of other Scyphomedusae and contain nematocysts.

Thirty-six or more oval openings round the periphery of the base of the stomach lead into a gastrovascular canal system of a distinctive pattern. In one quadrant the gastrovascular system is obviously abnormal (Text-fig. 2; Pl. I, below), but it can be concluded from examination of the young medusae that the number of openings is typically forty. Twenty of these lead into straight unbranched radial canals running towards the umbrella margin for 6 or 7 cm—that is, across the subumbrellar side of the thickened ring of the umbrella. At the point where the thick jelly thins to form the thinner peripheral portion of the umbrella these straight canals start to give off side branches and they continue to do so, giving off seven or eight branches on either side, until the straight canal enters a continuous circular canal at the subumbrella margin. The side branches themselves branch.

Alternating with these twenty straight canals and also passing across the thick part of the umbrella are twenty straight canals which give off three or four successive branches on each side, each of which re-enters the succeeding branch peripheral to it. In this way a characteristic pattern is produced having the appearance of a number of B's placed back to back. On reaching the outer periphery of the thickened part of the umbrella these canal systems



Text-fig. 2. *S. fabulosa*: subumbrellar view of adult specimen to show gastrovascular canal system (white), subumbrellar apertures, and section of base of mouth tube. The inner half of the gastrovascular canal system is accurately drawn; a portion only of the fine peripheral network of canals is exactly as in the specimen, the majority being filled in to give the general appearance. Note abnormal development between A and B. (×*c.* $\frac{1}{4}$) (Del. F. S. R.)

give rise to a finer branching system like that of the straight canals and all the branches anastomose round the outer 6 or 7 cm of the umbrella. Many of the areas enclosed by this anastomosis are roughly hexagonal in shape. The central canal of each of the 'B' systems of canals finally enters the marginal ring canal, as do some of the branches of the anastomosing system. Most of the actual margin of the umbrella is missing and the marginal ring canal can be seen in only a few places; but its continuity is confirmed by examination of the young medusa. In the zone of thick jelly the canals are about 5 mm in width.

There are apparently no marginal tentacles, and this is confirmed in the young. Only a few marginal rhopalia are present since so much of the umbrella margin is missing. These appear to be small simple statocysts whose stalks receive canals from the ring canal. The rhopalia, on the basis of the young medusa, are twenty in number and are situated at the ends of the 'B' systems of canals, so that these can now be called rhopalar canals as opposed to the unbranched inter-rhopalar canals.

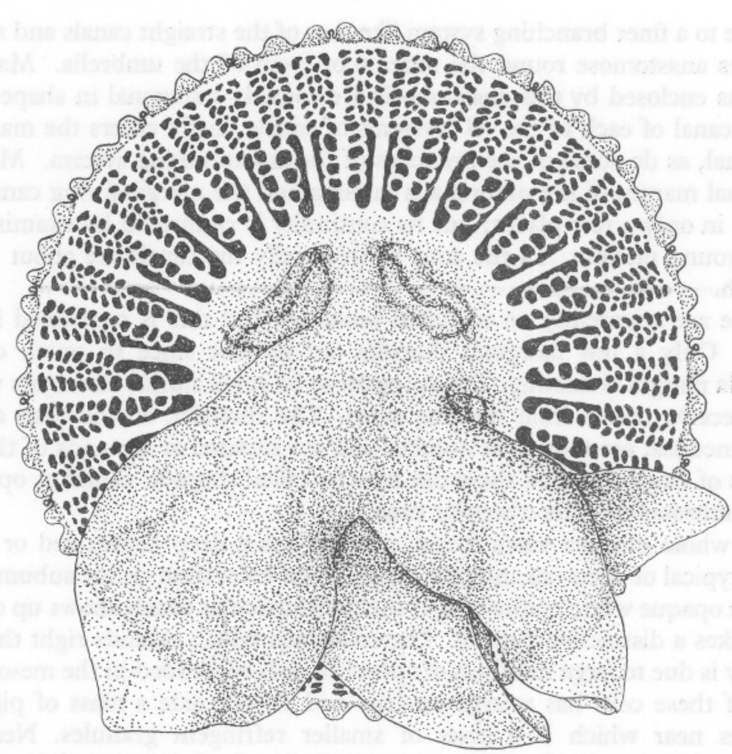
The whole medusa when freshly caught was a deep brown red or plum colour typical of deep-sea animals. Against this coloration on the subumbrella side the opaque white epithelium of the gastrovascular canals shows up clearly and makes a distinctive pattern. The coloration which extends right through the jelly is due to large numbers of spherical cells embedded in the mesogloea. Each of these cells has a large nucleus and on one side a mass of pigment granules near which is a mass of smaller refringent granules. Near the surface of the umbrella there is a thin layer of pigment granules in the mesogloea itself just beneath the surface epithelium.

The colour leaches out, making formalin and sea water pink in colour. Dr G. Y. Kennedy kindly examined the pigment for us, and finds that the bulk of it is a melanin.

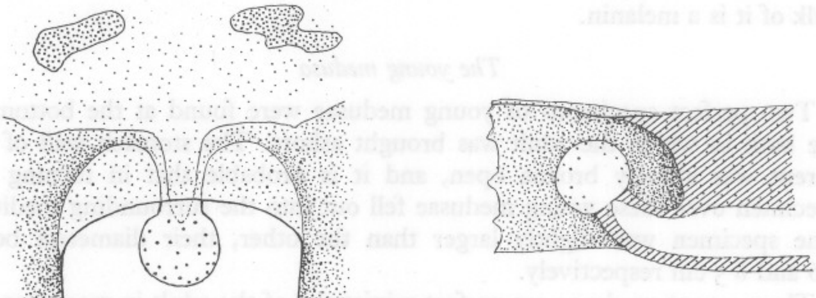
The young medusa

Two perfect specimens of young medusae were found at the bottom of the bath in which the adult was brought ashore. The stomach wall of the parent was already broken open, and it is probable that in turning the specimen over these young medusae fell out into the surrounding medium. One specimen was slightly larger than the other, their diameters being 9·6 and 8·5 cm respectively.

These young medusae are perfect miniatures of the adult in most respects (Text-fig. 3; Pl. III). The jelly is, however, still very thin and membranous and tends to curl inwards at the margins. In each specimen there is a hole about 2 cm in diameter on the exumbrella side over the stomach, presumably where the medusa has broken away from its embryonic attachment, probably prematurely. When lying flat in a dish with the subumbrellar side downwards and drained of surrounding fluid the exumbrella surface shows clearly round



Text-fig. 3. *S. fabulosa*: drawing of young medusa; the gastrovascular system has been drawn semidiagrammatically to indicate the basic pattern. (Nat. size.) (Del. F. S. R.)



Text-fig. 4. *S. fabulosa*: rhopalium of young medusa: A, exumbrellar view; B, semidiagrammatic lateral view half sectioned to show rhopalar canal; the statocyst is not sectioned. (Del. F. S. R.)

its outer half forty radiating ridges corresponding to the septa which lie between the forty main canals of the gastrovascular system. The margin of the umbrella has sixty evenly-rounded lappets and twenty marginal rhopalia. The bases of the two lappets which lie one on each side of a rhopalium together amount to about 8 mm. Between each pair of rhopalar lappets is a single lappet which is situated opposite the end of an inter-rhopalar canal and has a base about 5 mm long. The radial length of each type of lappet is about 3·5 mm. Thus there are forty rhopalar lappets and twenty inter-rhopalar lappets. In the smaller of the two specimens the lappets have not developed to the stage at which they are completely separated to their bases.

The diameter of the stomach is approximately half that of the umbrella. From it radiate forty canals separated by forty clearly seen septa. The gastrovascular canal system is developed exactly as in the adult; there are twenty rhopalar 'B' canals and twenty inter-rhopalar unbranched canals and all run into a complete marginal ring canal after branching to form the peripheral anastomosis of canals.

The mouth arms are very membranous and not yet formed like those of the adult. Their length is not quite as much as the diameter of the umbrella. They are very broad and leaf-shaped, and joined to form a circular basal mouth tube for about half their length.

At the point of origin of each mouth arm from the subumbrella surface the jelly is thickened and this stronger jelly runs radially to the outer margin of the stomach. Between these stiffened areas the subumbrellar wall of the stomach is still very thin and the brood chambers which are already forming push this thin jelly outwards as do the gonads in *Pelagia*. Presumably as the medusa grows the jelly of the stomach wall increases in thickness until only the subumbrellar apertures are left; the condition in *Stygiomedusa* approximates to that indicated by Agassiz & Mayer (1898, plate. viii, fig. 14; pl. x, fig. 23) for *Dactylometra*.

While in external appearance the walls of developing brood chambers give the impression that they might be similar to the gonads of *Pelagia*, a microscopic examination shows no obvious signs of sexual cells. The chamber has a wall of mesogloea from which tapering projections of mesogloea run towards the centre and themselves give rise to branches. The lining epithelium consists mainly of columnar cells, and interspersed at regular intervals are round cells with larger granules, and there are also nematocysts in various stages of development.

There are no marginal tentacles. There are twenty rhopalia, each consisting of a simple statocyst with a short canal entering its stalk from the ring canal. The rhopalia are colourless except for a few scattered pigment cells. The bases of the adjacent marginal lappets join to form a roof over the rhopalium which is itself directed upwards (Text-fig. 4).

The colour of the young medusae is brownish-red, and this coloration extends right through the mesogloea, as in the adult, and is due to numerous spherical cells containing pigment granules. As in the adult also the opaque whitish epithelium of the gastro-vascular system shows up its pattern, and there is also an opaque white line along the axis of each mouth arm.

Reproduction

The four brood chambers protruding into the stomach cavity are covered on the gastric side in this preserved specimen by an epithelium which is folded into narrow ridges. This epithelium consists of columnar cells with nematocysts scattered among them. Around the lower periphery of the brood chamber is a raised convoluted frill along the folds of which the gastric cirri are distributed. The whole forms a band about 20 mm high.

A little above this band, running along the side walls of the brood chamber, is a stripe of modified epithelium which may be called the germinal line (Pl. II, below), as it is from its tissue that the remarkable reproductive bodies develop. In our specimen a whole range of developmental stages can be found.

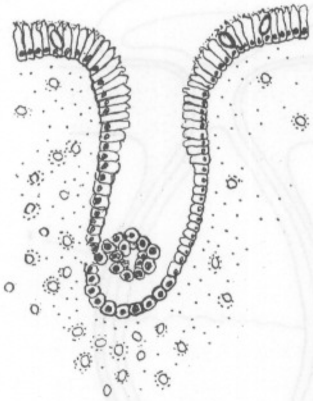
The germinal line forms a shallow groove whose epithelial cells differ from those of the surrounding columnar epithelium in being more cubical and having large rounded nuclei. The cells in the mesogloea beneath are also more numerous than elsewhere. In many places along the line there are small pits in which the cells often show an irregular arrangement. The multiplication of the epithelial cells in some of these pits produces deeper invaginations which are evidently the first stage of the processes leading to the development of the future young medusa. Text-fig. 5 shows a section of such an invagination in which there is a small clump of cells forming a vesicle, presumably the first formation of a cyst. No sexual cells could be found.

The cyst grows into an oval body with a more pointed end on the sub-umbrellar side. As this increases in size it pushes out the wall of the brood chamber so that it projects into the cavity of the chamber. At the same time at the opposite end of the cyst two outgrowths develop which run horizontally in opposite directions so that the cyst now appears T-shaped (Text-fig. 7B). At the stage when the cyst is 8–11 mm in length the tubular outgrowths run along the gastric surface of the chamber wall for 8–10 mm; the outgrowths are 2·0–2·5 mm in width.

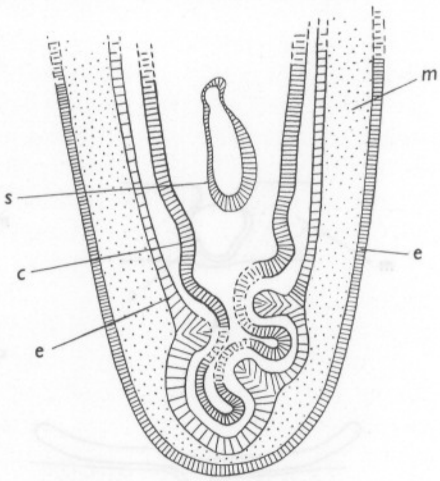
The cyst, continuing to increase in size and protruding farther into the cavity of the brood chamber, carries with it the enveloping brood chamber wall, which becomes more and more attenuated until it forms a thin membrane or capsule surrounding the cyst. At the same time the tubular outgrowths at its base grow away from the gastric wall of the chamber so that they project freely into the stomach (Text-fig. 7C).

At an early stage another body is developing within the cyst. This body we call the scyphistoma and from it a single medusa develops. From this stage onwards the cyst wall can be regarded as a chorion.

The capsule and its contents, from the outside inwards, thus consist of (*a*) an outer wall which is the modified wall of the brood chamber, consisting of two epithelial layers, ectodermal and endodermal in origin, with a thin mesogloea between them; (*b*) the cyst or chorion which consists of a single layer of tall columnar cells with an inner underlying basal membrane; these cells, presumably absorptive and secretory in function, have projections on their free margins and contain very numerous granules; and (*c*) the wall of the scyphistoma which in later stages consists of two layers of epithelium with a thin layer (? mesogloea) between them.



Text-fig. 5



Text-fig. 6

Text-fig. 5. *S. fabulosa*: section through depression on germinal line containing developing cyst. (Del. F. S. R.)

Text-fig. 6. *S. fabulosa*: diagram of longitudinal section of distal end of small capsule 8 mm long. Note the pocketed area and the young scyphistoma lying free in the cavity of the cyst. *c*, cyst; *e*, parent epithelium; *m*, mesogloea; *s*, scyphistoma. (Del. W. J. R.)

Measurements of some of the smaller and medium-sized capsules are given in Table 1.

TABLE 1. SIZE OF CAPSULES

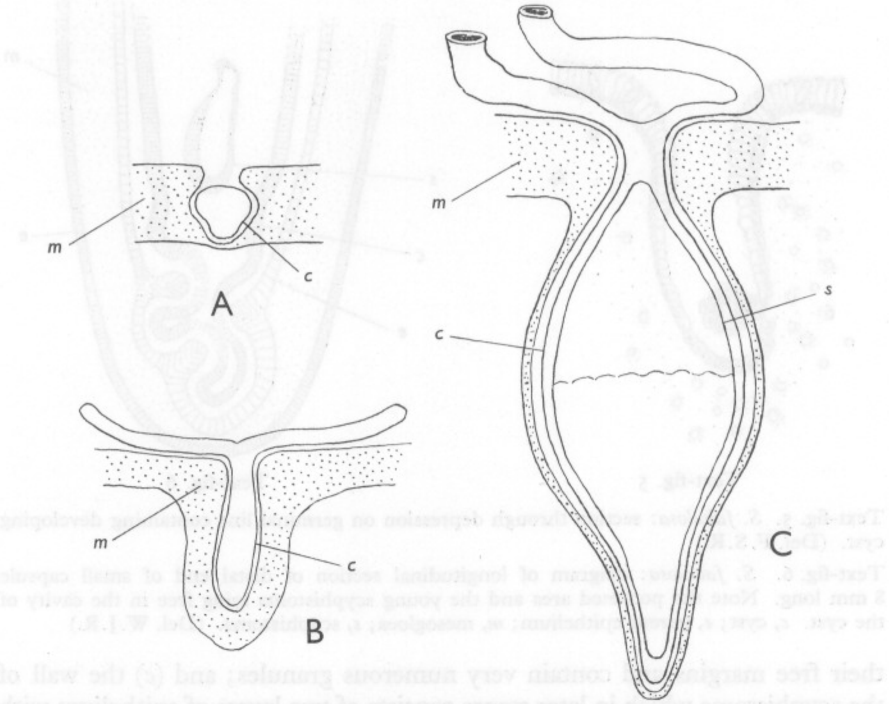
Dimensions of smaller and medium-sized capsules, projecting from the subumbrellar wall of the chamber illustrated on Pl. II (below). The measurements do not include parts embedded in the subumbrellar wall or projecting into the stomach.

	Measurements in mm							
Total length of sub-umbrellar surface of chamber	8·0	8·4	8·6	10·3	31·5	37·6	38·6	45·4
Maximum diameter	3·0	3·0	2·4	4·0	12·0	17·6	17·8	21·3

The larger capsules over 10 mm in length are pinkish-white in colour and become oval in shape with their distal ends narrowing rather suddenly; they are thus somewhat teat-shaped, and their tips are often brown in colour.

The size of a cyst just before it begins to push out the chamber wall is 2·6 mm long and 2·0–2·3 mm in diameter.

The basal outgrowths of the cysts are hollow tubes, closed at their distal ends. They may reach a length of 20 cm, and lengths of 12–17 cm were common. Only the smaller outgrowths up to 3 cm in length are still attached and complete in our specimen. All the others were broken off near the chamber wall and found floating loose in the fluid surrounding the medusa in its container.



Text-fig. 7. *S. fabulosa.* Diagrams of various stages of development of capsules. A, cyst about 2 mm long; B, showing early development of tubular outgrowths at base of cyst; C, fully formed capsule (the ends of the tubular outgrowths are shown as cut off). *c*, cyst or chorion; *m*, mesogloea; *s*, scyphistoma. (Del. F. S. R.)

These tubes have an outer layer of high columnar epithelium the cells of which have numerous granules and projections on their free margins, similar to those of the part of the chorion within the capsule. This is yellowish to orange in colour in the newly captured medusa, and in many instances the epithelium had become stripped from its basal membrane.

Inside some of the small tubes were seen many free, scattered, rounded cells some of which were in process of division. In larger tubes there were, lying free, rounded masses of cells resembling morulae, blastulae and planulae.

In the capsular portion of the chorion differentiation and formation of the scyphistoma begins at an early stage. At a capsule length of 8 mm sections revealed that the inner epithelium of the capsule wall, namely parent tissue, was much developed and pocketed in the distal tip of the capsule and that the chorion tissue was continuous in the pockets and followed their contours (Text-fig. 6). Preservation of the tissue for histological examination was, however, not at all good. Within the chorion sac, lying free in the cavity, there was a young scyphistoma 0·35 mm long. As the scyphistoma increases in size it takes the general shape of the capsule, the distal narrowed end being the developing mouth arms. Although in many of the larger capsules preservation was poor, it was possible to see the umbrella margin and the indications of a gastrovascular canal system in process of formation; but on dissection many of these disintegrated. The most developed capsule, 6·5 cm long and 4·3 cm wide, contained an almost fully developed medusa (Pl. II) complete with gastrovascular system, and mouth arms and the reddish purple coloration typical of the adult.

Some of the capsules had subsidiary capsules developing at their bases (Pl. IV, above).

In some of the capsules differentiation appears to have been abnormal and budding abortive. This feature may be linked with the four abnormal young medusae found (Russell, 1959). In these the medusa had the normal pigmentation but was flattened and pancake-shaped (Pl. IV, below). There were no mouth arms and no stomach, the digestive system being represented by a series of reticulate canals converging on a central point where the mouth should have been.

There remains the question, how does the young medusa escape from the brood chamber? Although the circular subumbrellar aperture connecting the chamber with the exterior is small (15 mm in diameter), it is possible that the young medusa, which is very plastic, might squeeze through. It should, however, be remarked that the only capsule with a very well-developed young medusa in it, although still attached to the subumbrellar wall of the brood chamber, is sticking through an opening in the wall into the gastric cavity so that the young medusa could escape through the mouth. As a few other smaller capsules had also passed through obvious tears in the wall this may not have been natural.

The excised brood chamber shown in Pl. II (below) has ten or so capsules visible to the naked eye. One cannot say how many more very small developing cysts are present. But it is evident that production of medusae is a continuous process and that the number produced by one parent medusa must be at least 50 and may be 100 or more.

Systematic position

In its structural characters *Stygiomedusa* is obviously quite a typical semaeostome scyphomedusa. In its general form and the arrangement of its gastrovascular canal system it agrees with the Ulmaridae, and it differs structurally from them only in the absence of marginal tentacles. We think that the family characters of the Ulmaridae should be enlarged to include species without marginal tentacles and that within the family there should be a new subfamily, the Stygiomedusinae of which *Stygiomedusa* would be the type genus.

DISCUSSION

Stygiomedusa fabulosa is the largest deep-water medusa known; its reddish purple colour and its viviparity are characteristics shared with many other animals living in very deep water. However, viviparity in which a few large medusae with adult characters are produced was hitherto quite unknown in the Scyphomedusae and the brood-caring mechanism by which it is achieved is unique in the history of the Cnidaria.

The brood-caring habit in its various forms is found in many benthic and bathypelagic forms and has been noted for many groups including crinoids (John, 1938), the pelagic octopod *Vitreledonella* (Joubin, 1929, p. 18) and in many gastropods (Thorson, 1950). In many species this is accomplished by the inclusion of many eggs within the single capsule and the successful ones emerge as miniature adults at the expense of the remaining eggs which are usually termed nurse cells.

In *Stygiomedusa* there are no nurse cells, nor have any sexual cells been seen; the uniqueness of its viviparity when compared with the usual methods of brood-caring will be appreciated when it is noted that it is the result of the telescoping of the metagenesis which we find in many Cnidaria and its adaptation for nursing the young medusa.

When we consider the life cycle of a common coastal Ulmarid medusa we find that it has the type of life cycle known to us in the common jellyfish *Aurelia aurita* L. Here the fertilized eggs develop into free-swimming planulae and then into polyps or scyphistomae anchored to suitable substrata in the sublittoral zone; these in turn may reproduce themselves asexually by budding or by the formation of podocysts before transforming themselves into strobilae budding off a large number of ephyrae or larval medusae. These feed on other planktonic organisms and finally acquire the characteristics of the adult. Encystment of the planula also takes place in some scyphomedusae (Rees, 1957*a*, p. 483), although this fact is seldom mentioned in text-books: the encysted stage, which is of variable duration, gives rise to a young scyphistoma.

In a scyphomedusa which has acquired a deep-water habit, continuation of this type of life cycle involving a benthic polyp stage is beset with difficulties.

Even if a suitable substratum could be found, food would probably be scarce both for strobilation and for the growth of the young medusa. The pelagic surface jellyfish *Pelagia perla* (Slabber) has solved this difficulty by having a more direct development in which a single egg gives rise to a single adult and it seems probable that this is what happens also in the bathypelagic medusae *Atolla* and *Periphylla*.

The hydromedusa *Bougainvillia platygaster* Haeckel is in process of becoming an oceanic species and has partly solved the difficulty of finding a suitable substratum by asexual propagation of the life cycle (Kramp, 1957; Rees, 1957*b*). In this species, the immature germinal tissue gives rise directly to stolons or polyps, which, in turn, bud off medusae. Similar phenomona, although differing in detail, have been noted in *Proboscidactyla ornata* and *Phialidium mccradyi*. Thus the familiar pattern of alternation of polyp and medusa may result either from sexual or (more rarely) asexual reproduction of the polyp phase.

Bearing this in mind, we have to consider whether *Stygiomedusa* has acquired an entirely new method of reproduction or whether the familiar Ulmarid type of life cycle has been highly modified to suit the needs of a brood-caring deep-sea species.

The cyst is produced, as has been noted, by asexual budding of parent germinal tissue and this process was hitherto not known to take place in Scyphomedusae. Apart from this, however, the life cycle is clearly a telescoped and much modified Ulmarid pattern. The germinal tissue as already noted forms a stripe of modified epithelium, and it is not possible to decide, from the single medusa available to us, whether this tissue is rudimentary or regressed, or even whether sexual reproduction also may or may not take place at some stage in the life of the medusa. In *Bougainvillia platygaster*, where a parallel case of asexual propagation is known, Kramp (1957) emphasized that 'all the specimens were immature'.

The asexually produced cysts lie in endodermal pockets in the roof of the brood chamber and are analogous with the podocysts of *Chrysaora* and *Cyanea* that may arise either from fertilized eggs or asexually from the bases of scyphistomae. In podocysts of *Chrysaora* and *Cyanea* the contents become organized within the cyst to form ectoderm and endoderm separated by mesogloea so that when the polyp emerges it quickly assumes the form of a scyphistoma. It appears likely that this preliminary differentiation into tissues also takes place in *Stygiomedusa*, but so far as we are aware no obvious primary polyp is formed.

The body within the cyst or chorion sac, which we regard as an atentacular scyphistoma and which is present when the capsule is less than 8 mm in length, results in the budding of a single medusa. This type of monodisk strobilation is also found in the rhizostome medusa *Cotylorhiza tuberculata* (Claus, 1892). The young medusae retain their connexion with the central lumen of their scyphistomae until almost fully formed, and those with a hole in the top of the umbrella found floating freely in the container (see p. 307) had obviously been torn out of their capsules before they were quite ready for liberation.

It is considered that the abnormal medusae found in this species represent some accident or failure in the normal course of development.

Some shallow-water Scyphomedusae protect their young until the planula stage; in *Aurelia* the fertilized eggs are 'retained in small pouches near margins of the free edges of mouth-arms and finally set free in the planula stage' (Mayer, 1910, p. 625). *Cyanea* behaves similarly but nothing more elaborate than this was known, so that *Stygiomedusa* is unique in the complexity of its brood-caring mechanism.

Many deep-water organisms are thought to have been evolved by migration from shallow or surface water, and *Stygiomedusa* is probably no exception. Encystment of the larvae, such as frequently occurs in *Chrysaora* and *Cyanea*, was probably a major factor in enabling the life cycle to take place in the parent medusa. In this way the jellyfish became independent of a substratum for its polypoid phase.

To sum up, the uniqueness of the reproduction of *Stygiomedusa* will be appreciated from the fact that the cyst wall acts as a chorion for the scyphistoma and draws its nourishment directly from the lumen of the parent by means of its tube-like projections.

Our grateful thanks are due especially to Dr J. S. Alexandrowicz who has prepared many sections and helped us considerably in the interpretation of the process of development of the young medusa. We would like also to thank Mrs E. A. Peace for the photographs in Pls. I, II and III, Mr P. J. Green for those in Pl. IV, and Lt.-Cdr. C. A. Hoodless and the crew of R.V. 'Sarsia' for their care in bringing the medusa safely to Plymouth.

SUMMARY

A description is given of the deep-sea scyphomedusa *Stygiomedusa fabulosa* Russell. In general structure this is a typical semaeostome medusa except that it has no marginal tentacles. It is 50 cm in diameter and has the deep reddish colour typical of a deep-sea medusa, due to a melanin.

The medusa is remarkable in that it has an unusual method of asexual reproduction and is viviparous. The young medusae are developed in capsules projecting into the cavities of four brood chambers which protrude into the stomach.

Special cells along a germinal line of the endodermal epithelium of the brood pouch give rise to cysts which have tubular outgrowths into the stomach cavity. Each cyst produces a simple sac lying within it which may be

regarded as a scyphistoma giving rise to a single medusa. The cyst then acts as a chorion passing nourishment to the developing medusa.

The significance of this method of reproduction is discussed.

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EXPLANATION OF PLATES I–IV

PLATE I

Stygiomedusa fabulosa. *Above*, complete specimen; there is a metre rule in front of it. *Below*, portion of umbrella margin to show pattern of gastrovascular canal system; the central section is abnormal. A bit of the brood chamber and capsular tissue is projecting through the subumbrellar aperture.

PLATE II

S. fabulosa. *Above*, the four brood chambers seen from above after removal of the exumbrellar wall of the stomach. In the right-hand top corner there is a capsule containing a nearly fully developed young medusa; this and a few other capsules are protruding into the gastric cavity through openings or tears in the wall of the brood chamber. *Below*, an excised brood chamber seen from the subumbrellar side: the capsule with the young medusa can be seen projecting beyond the centre of the lower margin. The arrow points to the germinal line.

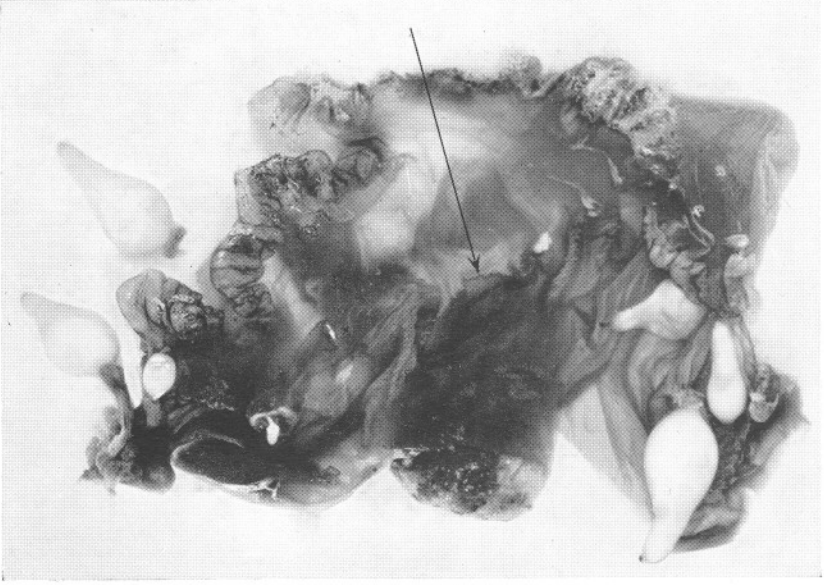
PLATE III

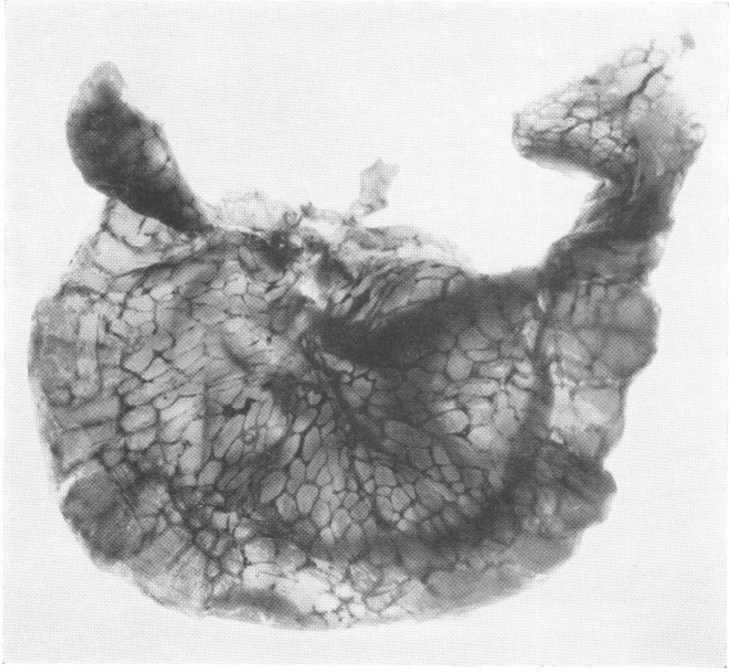
S. fabulosa: two views of one of the young medusae. In the lower photograph a developing brood chamber can be seen at the base of the right-hand mouth arm. (*Ca.* nat. size).

PLATE IV

S. fabulosa. *Above*, enlarged photograph of capsule to show subsidiary capsule at its base. *Below*, abnormal young viewed by transmitted light; the specimen is torn.

(*Facing p.* 318)





J. mar. biol. Ass. U.K. (1960) 39, 319–329
Printed in Great Britain

THE OCCURRENCE OF *INGOLFIELLA* IN THE EDDYSTONE SHELL GRAVEL, WITH DESCRIPTION OF A NEW SPECIES

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(With Text-figs. 1–5)

Among the various small Malacostraca that have lately been found living interstitially in the Eddystone shell gravel (see Spooner, 1959*a*, *b*), one of the more remarkable is a new member of the genus *Ingolfiella*. This genus of small colourless blind amphipods occupies a very isolated position, and is customarily given the rank of a separate suborder. The six species hitherto recognized are listed in Table 1, and their geographic relationships shown in Fig. 5 (p. 328).

TABLE 1. OCCURRENCE OF INGOLFIELLIDS

			Habitat			
Species	Reference	Geographical area	Depth or height	Substratum	No. of specimens examined	Size (length, mm)
Ingolfiella abyssi	Hansen (1903)	North Atlantic, Davis Strait	1870 fm (3420 m)	Globigerina clay	1	2·5
I. littoralis	Hansen (1903)	Gulf of Siam	1 fm (2 m)	Coral sand	1	1·5
I. acherontis	Karaman (1933), Hertzog (1935), Karaman (1954)	Jugoslavia, Skoplje	*c.* 250 m†	Subterranean ground-water	1*	2·5
I. leleupi	Ruffo (1950, 1951)	Belgian Congo, south-east	Above 1000 m†	Cave pools	44	12·5–14·5
I. petkovskii	Karaman (1957)	S. Jugoslavia, at foot of Macedonian mountains	*c.* 50 m†	Subterranean ground-water	Several	Up to 2·0
I. ruffoi	Siewing (1958)	Peru, open coast	Intertidal	Interstices of shingle	100+	1·12–1·52

* Karaman (1957) mentions more recent additional material. This has not been reported on yet.
† Above sea-level.

Of the six species, three were found in marine and three in freshwater habitats. The geographical range could scarcely be more diverse, since it includes abyssal ocean floor (and so a site that was presumably never part of a continent) and uplands on a continental shield (that may never have been under the sea), while the substratum includes both Globigerina ooze settled in quiet oceanic depths[1] and shingle of a wave-beaten shore. The temperature range, as Siewing (1958) has pointed out, is also very wide.

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[1] A detailed analysis of the bottom on which *Ingolfiella abyssi* occurred is given by Boeggild (1900).

The seventh species now to be described has been isolated from two samples of the shell gravel collected with the Forster anchor dredge, at about 25 fm, about 1 mile north-westward of the Eddystone Rock. One sample, collected on 31 March 1959 and cursorily examined, produced two specimens; and another, collected on 9 September 1959, of which 45 litres were examined with care, produced 18.

Ingolfiella britannica sp.nov.

With characters typical of the genus (Hansen, 1903; Siewing, 1958); body elongate, much compressed laterally; segments mostly deeper than long (cf. *I. ruffoi* and *I. acherontis* as contrasted with the more elongate *I. abyssi*, *I. petkovskii* and *I. leleupi*). Length of young adults and larger immature 1·4–1·9 mm. (Fig. 1A).

The front part of the head bears a small but definite lobe, resting in the gap between the two antennae and demarcated from the cephalon proper to which it is attached (Figs. 1A, 4A), as Hansen originally describes for *I. abyssi* and *I. littoralis* but not found by other investigators in the species described subsequently.

Each segment of the body carries a single seta on each side of the median line in the anterior half of the segment, the position being near the centre of the segment in the urosome and progressively more anterior in the front part of the mesosome. There is also a seta on the posterior margin in the lower half of the segment. This simple setation appears to be typical of the genus.

The third urosomite appears to be capable of retraction into the second segment so that as much as nearly half of it may be lost to view (in Fig. 1A it is not quite fully retracted). The rounded telson is similar to that found in other species: on each side it bears one seta and a pair of fine sensory hairs (Fig. 3J).

Antenna 1 (Fig. 1B) bears a flagellum of four and an accessory flagellum of three segments. In the accessory flagellum the 2nd segment is twice the length of the others (Fig. 1D, cf. *I. abyssi*). Aesthetascs are present on the three terminal flagellar segments. In the peduncle segment 1 exceeds the combined length of 2 and 3.

Antenna 2 is typical, with five segments in the flagellum (Fig. 1C).

The mouthparts (Fig. 1E) agree closely with Hansen's (1903) description of *I. abyssi*. The *upper lip* and *mandible* appear not to differ; nor does *maxilla* 2, with five setae on its distal lobe and four on the palp (Fig. 1G). The *maxilla* 1 (Fig. 1F) is essentially similar: a 2-segmented palp with three or four setae terminally, a distal lobe with six toothed spines (each of an individual shape), and a short proximal lobe which appears to bear only a single seta (as in *I. ruffoi*). The simple *maxillipede* (Fig. 1H) bears an elongate endite which is apt to lie hidden behind the basal segment of the 5-segmented palp.

All seven peraeon segments have the coxopodites much reduced and scarcely protruding below the body segment; their margin carries at least one seta posteriorly, and usually a smaller one anteriorly. Only segments 3, 4 and 5 bear gills: these are simple oval structures, of about a third the length of the basal segment of the limb (Fig. 3A–C).

Peraeopods 1 and 2 are modified as gnathopods (Fig. 2), in which, as is characteristic for *Ingolfiella* in contrast with other amphipods, the carpus is enlarged and the functional 'claw' composed of two segments, the propus and dactylus.

In *gnathopod* 1 (Fig. 2A) the basal segment is, as usual, broad; the carpus is elongate, subtriangular, with the 'palm' continuous with the posterior margin. The point of separation of the palm and posterior margin (opposite the tip of the dactylus) is marked by a small blunt spinous projection (*p*), easily overlooked (cf. *I. abyssi*). Distalwards

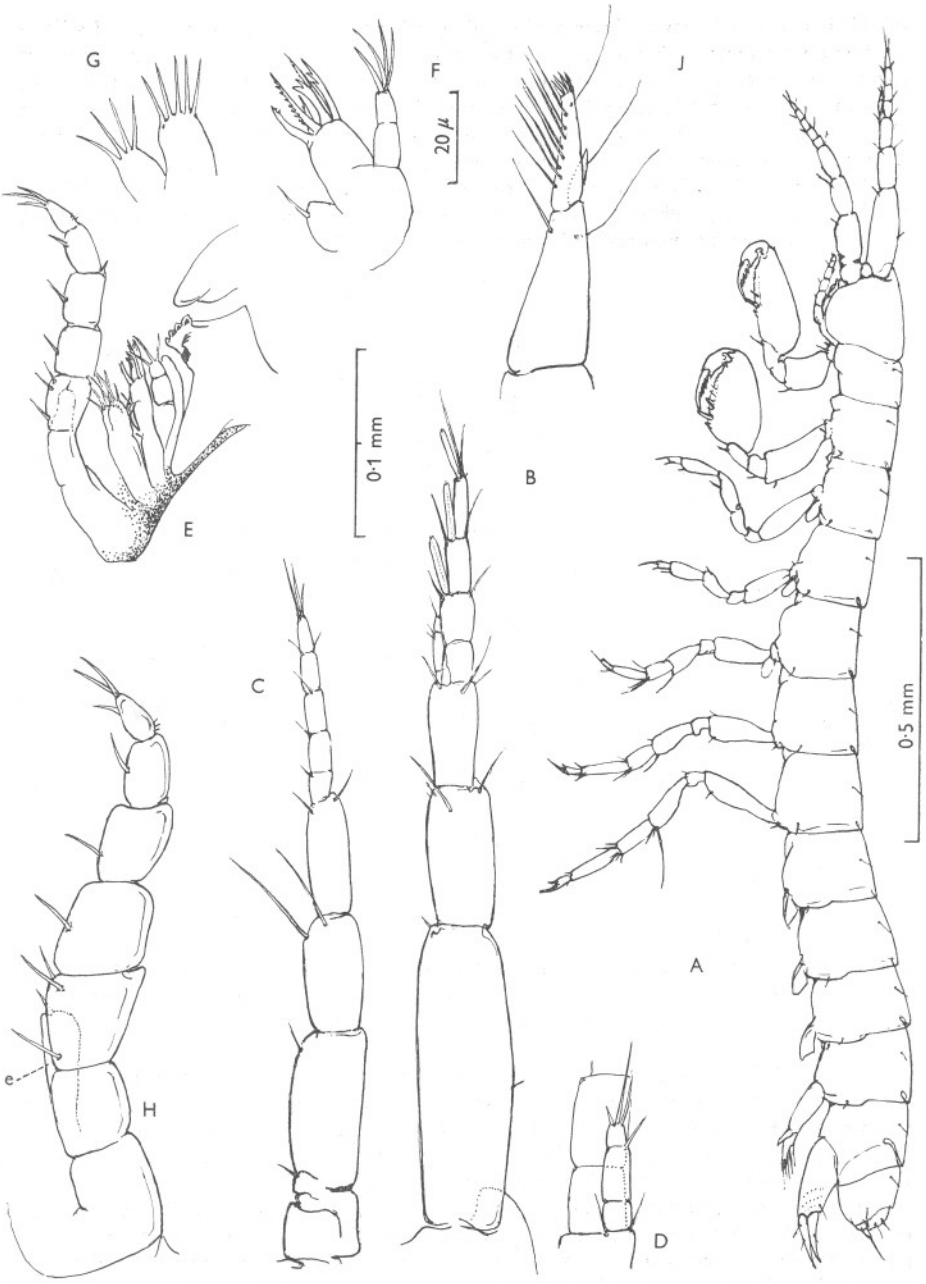

Fig. 1. *I. britannica.* A, Whole animal of 1·71 mm body length (specimen no. 5, chosen as type), probably young male; B, left antenna 1; C, left antenna 2, outer view; D, accessory flagellum of antenna 1 enlarged; E, mouthparts seen from the side; F, maxilla 1, right side, seen from the rear; G, maxilla 2, left side; H, left maxillipede, from rear, *e*, endite; J, right uropod 1 of female seen from inner side, showing long sensory hairs. A, B, C, from specimen 5; D, E, from specimen 11; F, G, H, from specimen 9; J, from specimen 10. The 0·1 mm scale refers only to B, C and J.

of this is a strong linear 'palmar angle' spine, arising on the outer surface, and a little farther on a shorter spine arising on the inner surface. Along the palm a few short setae arise on each margin. The inner side of the propus is straight, but the inner margin of the dactyl is strongly serrate, with four acutely pointed teeth (apart from the elongated tip or 'nail' which might be said to make a fifth tooth). (In *I. abyssi*, *littoralis* and *acherontis* the dactylus of gnathopod 1 is apparently not serrate.)

The carpus of *gnathopod* 2 is broader and possesses a rounded palmar angle which is marked, as in 1, by a short spinous projection (*p*) (this is more strongly developed in *I. abyssi*). Other features are as in gnathopod 1 (see Fig. 2B, C).

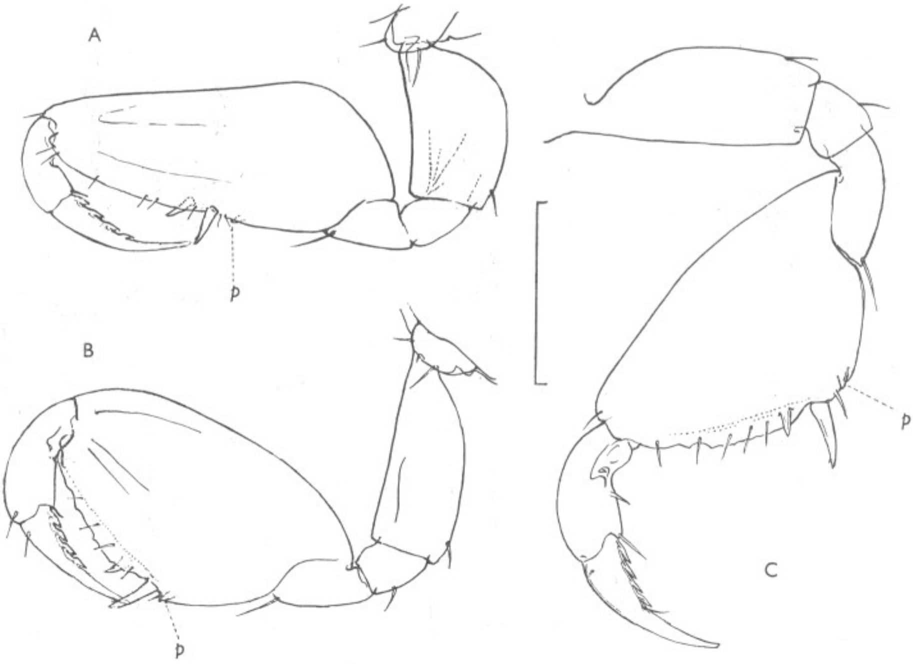

Fig. 2. *I. britannica.* A, Gnathopod 1 of left side, outer view; B, gnathopod 2 of left side, outer view; C, gnathopod 2 of right side, inner view. A and B, from specimen 5; C, from specimen 8. *p*, short spinous projection. The scale represents 0·1 mm.

The remaining five peraeopods (Fig. 3A–E) show progressive changes in shape, 4 and 5 being the shortest, and 7 the longest. As a series these limbs are relatively strong, markedly more so than found in *I. ruffoi* (which, however, they much resemble in shape). The terminal points of the dactyli 5–7 are all long and thin (as in *abyssi*, against *littoralis*). A stout spine arises from the posterior corner of the merus in peraeopods 5 to 7; in 7 it is also elongate, as long as, or longer than, the carpus, and carried in life protruding posteriorly (as shown in Fig. 1). Peraeopod 7 also has a somewhat special armature at the apex of the carpus, where there is a comb of six or seven spines (Fig. 3E): apart from the slender dactylus this limb much resembles that of *I. littoralis*.

The three pairs of *pleopods* (Fig. 4B, C) are broadly triangular and all similar, as in *I. ruffoi* and *I. abyssi*.

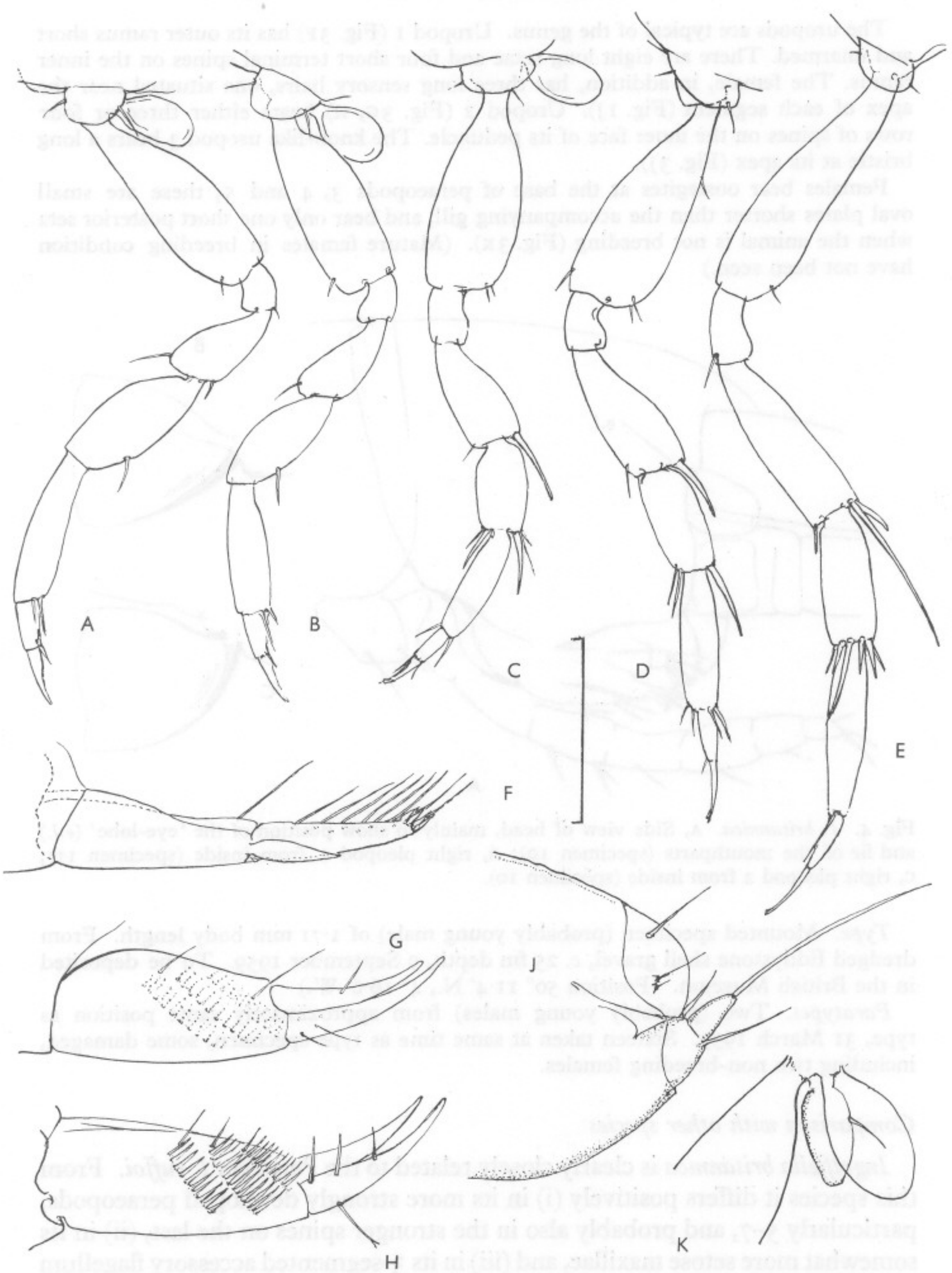

Fig. 3. *I. britannica.* A–E, Peraeopods 3 to 7, left side, outer view; F, G, uropods 1 and 2, left side, outer view (rows of dots represent setal comb showing through); H, uropod 2, right side, inner view; J, telson and uropod 3, seen from left side; K, immature oostegite on base of peraeopod 3. The scale represents 0·1 mm and refers to all but J and K; A–G, from specimen 5; H, from specimen 9; J, from specimen 11; K, from specimen 10.

The uropods are typical of the genus. Uropod 1 (Fig. 3F) has its outer ramus short and unarmed. There are eight long setae and four short terminal spines on the inner ramus. The female, in addition, has three long sensory hairs, one situated near the apex of each segment (Fig. 1J). Uropod 2 (Fig. 3G, H) bears either three or four rows of spines on the inner face of its peduncle. The knob-like uropod 3 bears a long bristle at its apex (Fig. 3J).

Females bear oostegites at the base of peraeopods 3, 4 and 5; these are small oval plates shorter than the accompanying gill, and bear only one short posterior seta when the animal is not breeding (Fig. 3K). (Mature females in breeding condition have not been seen.)

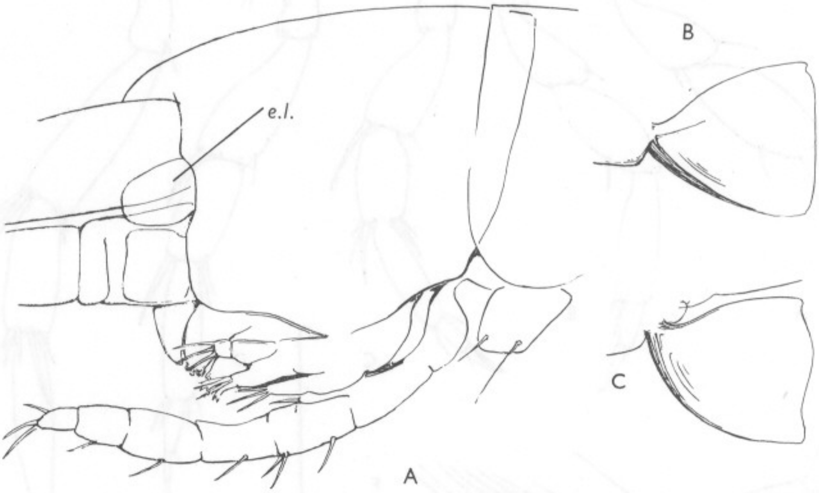

Fig. 4. *I. britannica.* A, Side view of head, mainly to show position of the 'eye-lobe' (*e.l.*) and lie of the mouthparts (specimen 10); B, right pleopod 1, from inside (specimen 11); C, right pleopod 2 from inside (specimen 10).

Type. Mounted specimen (probably young male) of 1·71 mm body length. From dredged Eddystone shell gravel, *c.* 25 fm depth, 9 September 1959. To be deposited in the British Museum. (Position 50° 11·4′ N., 4° 16·6′ W.)

Paratypes. Two (probably young males) from approximately same position as type, 31 March 1959. Sixteen taken at same time as type specimen, some damaged, including two non-breeding females.

Comparison with other species

Ingolfiella britannica is clearly closely related to the Peruvian *I. ruffoi.* From this species it differs positively (i) in its more strongly developed peraeopods, particularly 5–7, and probably also in the stronger spines on the last, (ii) in its somewhat more setose maxillae, and (iii) in its 3-segmented accessory flagellum (2-segmented in *ruffoi*). I cannot be sure that any of the other apparent differences that appear from Siewing's description of *ruffoi* are valid, since small features are easily overlooked. For example the absence, in *ruffoi*, of an 'eye-lobe', a maxillipede endite, and of a small spinous projection delimiting the gnathopod palm, cannot be accepted as certain: all three structures have to be carefully looked for.

From Hansen's original marine species, *I. abyssi* and *I. littoralis*, *I. britannica* differs in having a serrate dactylus on gnathopod 1. *I. abyssi* differs also in its much more attenuate body-form, its more prominent spinose projection at the angle of gnathopod 2, its elongate uropod 1 exopodite, its smaller hind peraeopods, etc. *I. littoralis* has a more oval gnathopod 1, stouter antenna peduncles, and marked differences in certain of the peraeopods.

The two Balkan species show no greater degree of difference although inhabiting fresh water. *I. petkovskii* is at once told from *britannica* by its more shallow body segments and peculiarly modified pleopod 1 (which is linear), but otherwise no very marked divergence is apparent. *I. acherontis* is even closer in its appearance, and, as far as its description goes, only minor differences can be noted, i.e. in lack of more than one tooth on dactylus of gnathopod 1, and in the apparently more pointed shape of its pleopods. It is true that Karaman stated he failed to note an 'eye-lobe' on *acherontis*, and mentions none on *petkovskii*, but this point requires checking.

The remaining species, the larger *I. leleupi* from a cave habitat, shows several special features which distinguish it from the others, and which might justify the erection of a separate genus.

While knowledge of the genus is still so fragmentary, it is much too early to try to assess the degree of relationship between the species known to date. There must be many more awaiting discovery.

Habits

A few of the animals were alive when found, and two at least were fully active at first. They moved by wriggling movements of the body, the compressed form of which seems ideal for progress between gravel particles and in narrow crevices.

A use for the uropod setal combs was shown by one individual which repeatedly tried to clean its gnathopods with them. This behaviour involved bending the body into a loop and pressing the treated limb between the two second uropods.

Habitat

The view may be held that *Ingolfiella britannica*, along with certain other blind colourless forms, is a genuine interstitial animal, and may be expected to be distributed through a depth of the gravel deposit. This is probably not true for most of the many Crustacea to be obtained from the few surface centimetres of the gravel, so that evidence for the above view must be stated.

TABLE 2. NUMBERS OF SMALL MALACOSTRACA PER 45 LITRES OF GRAVEL

9 September 1959

	Agassiz trawl, subsample of 5·7 l. × 45/5·7	Anchor dredge (lower part) full count
(A) A dominant surface species		
Amphipoda		
Leptocheirus pectinatus	34,610	36
(B) Other species numerous at surface		
Amphipoda		
Guernea coalita	726	36
Metopid n.sp.	719	58
Socarnes erythrophthalmus	647	—
Ceradocus semiserratus	632	3
Syrrhoid n.sp.	458	4
Eurystheus lobatus	237	—
Gitana sarsi	205	4
Leptocheirus tricristatus	205	1
Idunella n.sp.	118	3
Megamphopus cornutus	55	4
Maera othonis	47	—
Metaphoxus fultoni	40	1
Liljeborgia kinahani	40	—
Cressa dubia, etc.	16	—
Leucothoë sp., etc.	16	—
Misc. (*Apherusa*, *Nototropis*, *Sympleustes*, *Perierella*, *Normanion*, etc.)	40	3
Isopoda, Tanaidacea, and Cumacea		
Paramunna bilobata	1973	52
Typhlotanais microcheles	324	8
Strongyurella indivisa	205	57
Gnathia oxyurea	189	5
Cumella n.sp.	174	6
Eurycope pygmaea	142	8
Janira maculosa juv.	118	1
Nannastacus spp.	95	5
Paratanais batei	24	1
Microniscid larvae	16	2
Eurydice pulchra, etc.	8	—
Leptognathia sp.	—	1
	7,469	263
(C) Interstitial species distributed through gravel from surface downwards		
Amphipoda		
Bogidiellid n.gen., n.sp.	24	11
Isopoda		
Microcharon harrisi	87	91
	111	102
(D) Interstitial species avoiding the surface		
Amphipoda		
Bogidiella n.sp.	—	10
Ingolfiella britannica	—	18
Tanaidacea		
Strongylura n.sp.	—	7
	0	35
Total per 45 l. of gravel	42,190	436

When the shell gravel has been collected with the Agassiz trawl (now a routine method) which scrapes the surface or at least digs quite shallowly, a density of several hundreds of small Malacostraca is obtained per litre of gravel (evidence from hauls of 15 September 1958, 21 October 1958 and 9 September 1959). Perhaps forty species, of differing abundance, may be got in a haul of 30 l. By contrast, when the more deeply digging Forster 'anchor dredge' is used the equivalent density of Malacostraca is only about 10 per litre of gravel. After an indication of this state of affairs had been got from a haul on 31 March 1959, a careful examination of a large sample (45 l.) taken on 9 September 1959 produced only 436 of these animals. The Agassiz haul, by contrast, collected on the same day, gave a figure of over 42,000 per l. of gravel, as shown in Table 2.

In the 'anchor dredge' sample some species living on or close to the surface are evidently included, but the sample is probably biased towards a depth of between 10 and 20 cm (since it was deliberately taken from the apex of the bag). The composition of this fauna shows a marked preponderance of blind colourless species, and an appreciable proportion of five forms that may be supposed to be genuinely interstitial and surface-avoiding—namely *Microcharon*, two bogidiellids, *Ingolfiella*, and an unknown *Strongylura* with an unusually elongated metasome. Two of these species (group C in Table 2) appear to be equally distributed through the depth of gravel investigated, and the other three, including *Ingolfiella*, seem to avoid the immediate surface of the gravel (group D). None of the group D species have yet occurred in gravel from Agassiz hauls, and for these species at least it can be said that an increase has been found below the surface, albeit the density may remain low even in favourable sites.

DISCUSSION

The recognition of special interstitial forms living in offshore marine deposits raises a further issue. On land, where observation is easier, there is growing evidence of continuity between the faunas of interstitial water, wells, springs, cave pools, underground streams, etc., for the reason that all these habitats are special branches or extensions of the general subterranean water-table through which some species are readily dispersed and others are at least capable of spreading during many generations. There thus arises the notion of a 'hypogean' fauna occupying the not-so-discontinuous medium of subterranean ground-water. May not this be equally true of the terrain below the ocean floor?

Perhaps, indeed, the interstitial fauna of bottom deposits is but the fringe of a more widespread fauna dispersed through rocks below the sea bed, and this supposed 'submarine hypogean' fauna merges with the 'subterrestrial hypogean' of which something is already known. (It may also have broad continuity with the smaller fauna of the dark ocean floor, as does the subterranean fauna with that of deep lake bottoms.) Belief that this indeed may be so is encouraged by the fact that certain malacostracan genera (*Microcharon, Bogidiella*) now found to be interstitial in marine deposits are already familiar from continental sites.

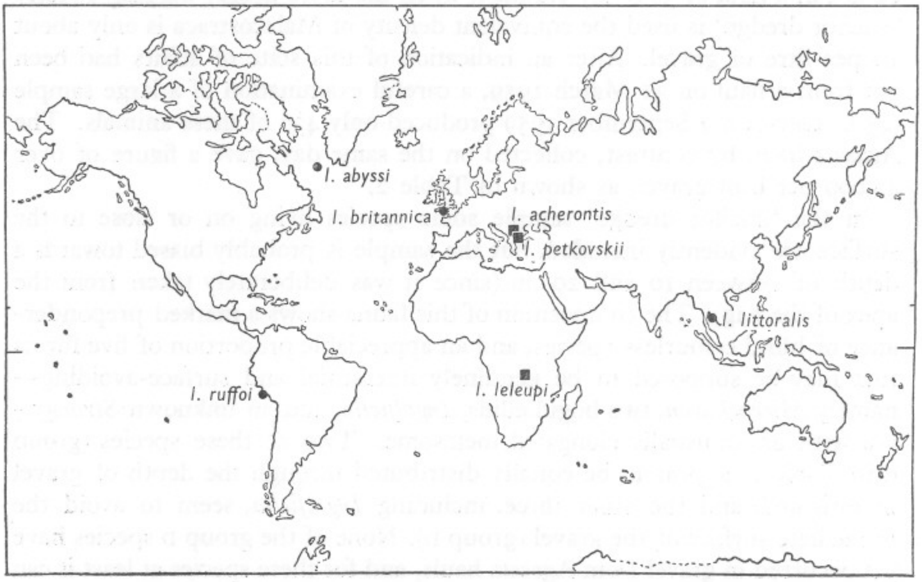

Fig. 5. Distribution of known species of *Ingolfiella* (see Table 1).
●, Marine habitats; ■, freshwater habitats.

The problem presented by what is already known of the distribution of the Ingolfiellidae would now become intelligible. The recorded habitats are just some of the many possible *outposts*, the links between which are not to be found in the seas and surface waters, but in the sub-surface waters that extend beneath both continents and oceans. In this 'hypogean' domain it is supposed that a slow spread and evolution of species has taken place, particularly of a few specialized groups including the ingolfiellids.

On this hypothesis the best chance of finding extensions of range of known species, and the existence of others yet unknown, is to explore hypogean waters. But how to investigate them below the floor of even shallow seas, let alone that at greater depths, presents a formidable oceanographic problem.

SUMMARY

Ingolfiella britannica is described from the Eddystone shell gravel. It is the seventh species of a genus whose distribution has a cosmopolitan aspect, and which occupies an isolated taxonomic position in the Amphipoda.

The species possesses a distinct 'eye-lobe' on the side of the head between the two antennae, as originally described by Hansen for *I. abyssi* and *I. littoralis*, but not seen by subsequent authors in four other species. This is an articulated flap, of very obscure morphological significance.

I. britannica is evidently a true 'interstitial' animal, along with certain other Crustacea occurring with it.

An explanation for the peculiar distribution of *Ingolfiella* is to be sought in the continuity of the 'hypogean' fauna under continents and oceans alike.

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Printed in Great Britain

STUDIES ON MARINE ALGAE OF THE BRITISH ISLES: THE GENUS *CERAMIUM*

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(Text-figs. 1–15)

CONTENTS

INTRODUCTION TO THE SERIES

The British Phycological Society was founded in 1952 to serve as a meeting-ground for phycologists, and to carry out a co-ordinated scheme of work on the algae of this country. The specific projects included the production of a *Flora of British Marine Algae* and the publication of a series of biological studies of individual genera and species.

It had been realized for some time that knowledge of the marine algae which occur on the coasts of the British Isles was very inadequate, and recent activities of the Society have made this increasingly obvious. Morphological data are based largely on static anatomical studies and there is little information available on developmental processes. The significance of the range of external form of the thallus in relation to differing conditions of season and environment has not been fully appreciated so that the limits of many genera and species are extremely ill-defined. There is, moreover, a lack of critical nomenclatural studies, with the result that the names currently applied to taxa are largely the result of tradition, whilst knowledge of their ecology and geographical distribution within the British Isles is very incomplete.

It is hoped that the forthcoming publications of the British Phycological Society will help to resolve some of these problems. Work is progressing on the *Flora of British Marine Algae*. The first of the biological studies of individual genera and species is now being published. It is intended that this series of *Studies on Marine Algae of the British Isles* will provide a *concise* but comprehensive survey of taxonomy, nomenclature, morphology, reproduction, life history, ecology and distribution, with particular reference to the British representatives. Such *Studies* will supplement the descriptions, inevitably abbreviated, in the formal taxonomic treatment of the *Flora of British Marine Algae*. It is hoped that these *Studies* will be published at intervals in this *Journal*.

A schedule, giving the essential requirements for *Studies on Marine Algae of the British Isles*, has been published in the *British Phycological Bulletin*, Vol. 1, No. 7, pp. 78–81. Anyone interested, or willing to assist, in the preparation of these *Studies* should communicate with the Secretary of the British Phycological Society, Mr H. T. Powell, Marine Station, Millport, Isle of Cumbrae, Scotland.

ORIGINAL DESCRIPTION

There is much confusion with regard to the generic name *Ceramium*, not only because of orthographic variation, but also because of the diverse species of algae attributed to the genus by the early phycologists. Wiggers (1780) was the first phycologist to use the current spelling, '*Ceramium*', but the names '*Ceramion*' and '*Keramion*' used by Adanson (1763, pp. 13, (8), 535) are now regarded as orthographic variants of this.

The names *Ceramion* and *Keramion* were proposed by Adanson as a substitute for *Ceramianthemum* Donati (1758), now regarded as a synonym of *Gracilaria* Greville (1830). The diverse species attributed to the genus by later authors are as follows:

Wiggers (1780)	*C. filum* (= *Chorda filum* (L.) Stackh.)
	C. fastigiatum (= *Furcellaria fastigiata* (L.) Lamour.)
	C. furcellatum (= *Furcellaria fastigiata* (L.) Lamour.)
	C. confervoides (= *Gracilaria verrucosa* (Huds.) Papenf.)
Gaertner (1788)	*C. plumosum* (= *Ptilota plumosa* (Huds.) Ag.)
Stackhouse (1797)	*C. saccharinum* (= *Laminaria saccharina* (L.) Lamour.)
	C. bulbosum (= *Saccorhiza polyschides* (Lightf.) Batt.)
	C. digitatum (= *Laminaria digitata* (Huds.) Lamour.)
	C. edule (= *Dilsea carnosa* (Schmidel) Kuntze)
	C. palmatum (= *Rhodymenia palmata* (L.) Grev.)
	C. phyllitis (= *Laminaria saccharina* (L.) Lamour.)
	C. esculentum (= *Alaria esculenta* (L.) Grev.)

Roth (1797) referred various species to the genus *Ceramium* and one of these, *C. virgatum* Roth, is a representative of the genus as now delimited. In addition to *C. virgatum*, Roth included in this, his first, treatment of the genus *Ceramium* species now referred to the genera *Chorda*, *Polysiphonia*, *Ectocarpus* and *Vaucheria*. Silva (1952) has given a full analysis of the early concepts of *Ceramium* and has argued quite rightly in favour of the conservation of *Ceramium* Roth. The existing grounds for conservation of *Ceramium* against *Apona* Adanson (1763) and *Episperma* Rafinesque (1814) were questionable, in that typification of *Apona* is a matter for conjecture whilst *Episperma*, in the absence of specimens or figures, cannot be typified at all. To clarify this situation, Silva proposed, first, that the problematical *Apona* could be suppressed by appropriate typification and by its acceptance as the nomen rejiciendum of *Lemanea*, and, secondly, that *Ceramium* Roth (1797) should be conserved against *Ceramion* Adanson (1763). These two proposals have now been accepted (see Lanjouw, 1956, p. 206).

TYPE SPECIES

A type species for the genus was not designated by Roth. As *Ceramium* Roth (1797) contains but a single species of the genus as now delimited, Silva (1952) has proposed this species, *C. virgatum* Roth, as the lectotype species:

Ceramium virgatum Roth (1797, p. 148; pl. 8, fig. 1)
[non *Ceramium virgatum* Hooker & Harvey (1848, p. 445)]
= *Ceramium rubrum* (Huds.) Agardh (1811, p. 17), fide C. Agardh, loc. cit.

The earlier proposal by Schmitz (1889) of *Ceramium rubrum* as the type species, repeated by Kylin (1956), is incorrect in that *Conferva rubra* Hudson (1762), its basionym, is not listed as such by Roth in his original treatment of the genus.

Roth's herbarium was transferred from Oldenburg to the Botanisches Museum, Berlin, in 1930, and there destroyed by bombing in March 1945 (Pilger, 1953). A few Roth specimens are still in existence in other herbaria, but attempts to locate duplicate material of *C. virgatum* have proved unsuccessful. The figure of *C. virgatum* given by Roth (1797, pl. 8, fig. 1) is not good, but it is sufficiently clear to permit identification; in the absence of a specimen this figure should be designated as the type of *C. virgatum* Roth.

SYNONYMY

Dictiderma Bonnemaison (1822, p. 185)
Hormoceras Kützing (1841,[1] p. 730)
Gongroceras Kützing (1841,[1] p. 730)
Echinoceras Kützing (1841,[1] p. 731)
Acanthoceras Kützing (1841,[1] p. 731)
Chaetoceras Kützing (1847, p. 34)
  nec *Chaetoceros* Ehrenberg (1844, p. 198)
  nec *Chaetoceras* Kützing (1849, p. 138)
Trichoceras Kützing (1849, p. 680)
Celeceras Kützing (1849, p. 683)
Pteroceras Kützing (1849, p. 690)
Ceramothamnion Richards (1901, p. 257)

As Silva (1952) has commented, Bonnemaison (1822) was the first author to distinguish clearly between the species now attributed to the genera *Ceramium* and *Polysiphonia*, placing species of the former in his *Dictiderma*, for which *Conferva rubra* Huds. [= *Ceramium rubrum* (Huds.) Ag.] was designated as the type species. In his

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[1] Kützing's paper '*Ueber* Ceramium *Ag.*' is published in the last part of volume 15 of the journal *Linnaea*, which is dated 1841. Howe (1914, p. 155) has indicated, quite correctly, that Kützing (1849), in *Species Algarum*, consistently cites '1842' as the date of publication of this paper. Because of this, Howe has regarded 1842 as the true date of publication. Setchell & Gardner (1924), on the other hand, have pointed out that in the earlier '*Phycologia Generalis*' (Kützing, 1843), '1841' is cited, equally consistently. Attempts to determine the precise date of publication have not been successful, so that at the present time it would seem best to retain the date of 1841 for this publication until further information is available.

revision of the genus *Ceramium*, Kützing (1841, 1847, 1849), in a series of proposals, suggested that the genus should be divided into nine smaller genera, viz. *Hormoceras*, *Gongroceras*, *Echinoceras*, *Acanthoceras*, *Chaetoceras*, *Trichoceras*, *Celeceras*, *Pteroceras* and *Centroceras*. Of these, only the last, *Centroceras*, has been retained by subsequent authors and this would appear to be well founded. The other proposals made by Kützing were not accepted generally at the time, possibly because of the constant changes of generic circumscription in the various publications and possibly because of the large number of very ill-defined species described by Kützing for these genera. By modern taxonomic standards there is no justification for the generic subdivision proposed by Kützing, other than the separation of *Centroceras*. The genus *Ceramothamnion*, proposed by Richards (1901) for his new species *C. codii*, does not differ from *Ceramium* in any essential feature. Mazoyer (1938) refers *Ceramothamnion codii* to the genus *Ceramium*, rightly stating that there is no justification for the creation of a distinct genus for this species. This opinion has been repeated by this and other authors (Feldmann-Mazoyer, 1940, in Børgesen, 1952; Dixon, 1958), but it should be noted that *Ceramothamnion* was still retained by both Fritsch (1945) and Kylin (1956).

In addition to the synonyms cited above, Børgesen (1953) has recently proposed the new genus *Ceramiella*, for *Ceramium huysmansii* Weber v. Bosse (1923) and has suggested that the *C. maryae* of the same author might also be referable to this genus. Mme Feldmann has commented (in Børgesen, 1953) that in her opinion there is no justification for the creation of a distinct genus for *C. huysmansii* and that this species should be referred to *Centroceras*. At the present time, the morphological information on *Ceramiella huysmansii* is so inadequate that no decision as to the correct taxonomic position of this species can be made. Under the circumstances, Dawson (1954) has adopted the most logical attitude, by retaining both *C. huysmansii* and *C. maryae* in *Ceramium*, pending further study.

DESCRIPTION OF GENUS

Genus of marine and brackish waters.

Thallus of uniaxial construction, erect or prostrate, 0·1–30·0 cm in length, red, brown or purple in colour; axes filiform, 0·1–1·5 mm in diameter, pseudo-dichotomously or irregularly branched, differentiated into axial cells and cortex; axial cells large (up to 1·5 mm in length), ovoid or cylindrical, hyaline or faintly pigmented; cortex formed by the aggregation of the filaments of limited growth, arranged in bands encircling the axial cells and forming a partial or complete investment.

Tetrasporangia borne laterally on filaments of limited growth, partially or completely embedded, tetrahedral or cruciate.

Sexual thalli dioecious, rarely monoecious; spermatangia hyaline, developing superficially from the ultimate cells of the lateral branches of limited growth, forming colourless patches of variable size on the surface of the cortex; carpogonial branches and auxiliary cells developing from the basal cells of the filaments of limited growth near to the apex of an axis; carposporophyte exserted, naked, sessile, subtended by a number of adventitious axes.

MORPHOLOGY AND DEVELOPMENT OF THE THALLUS

The thalli of all Florideae are built up by the aggregation of filaments, which result from the division of apical cells. Some of these filaments are of unlimited growth and form the axes of the thallus; the majority, however, are

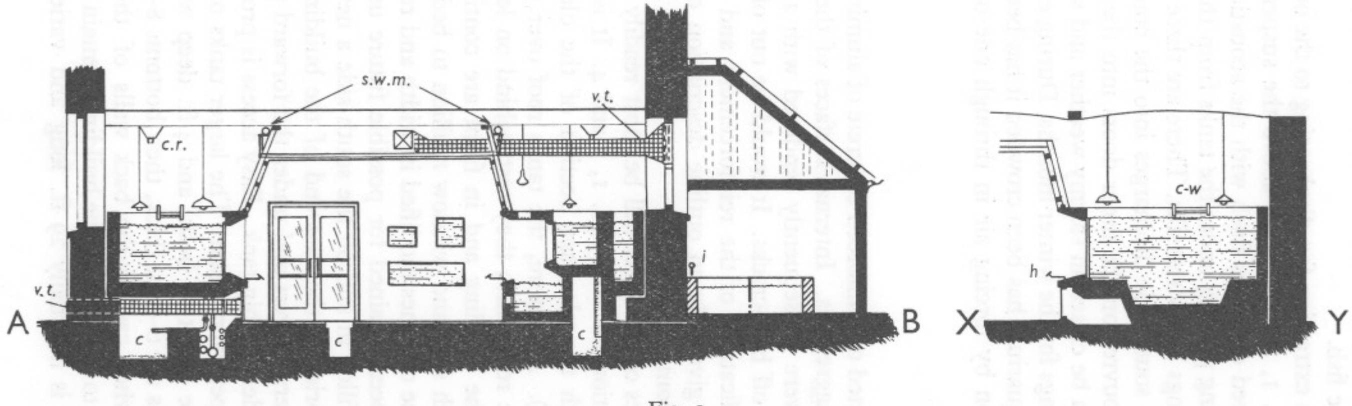


Fig. 2

Text-figs. 1 and 2. Plan and sections of the new aquarium and new outside circulation. Water in the exhibition tanks is indicated by line and dot stippling. *c*, sea-water return culvert; *c.b.*, circulation bench; *c.r.*, overhead conveyor rail (Henderson track); *c-w*, cat-walk; *h*, hand-rail; *i*, inflows; *o*, overflows; *p.b.*, plunger bucket; *s*, sill; *s-w*, swim-ways; *s.w.m.*, sea-water main.

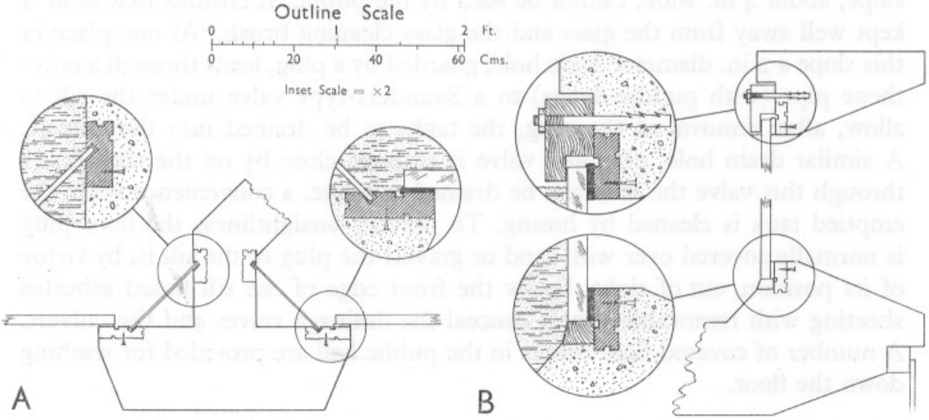
in the sill, about 3 ft. above floor level and nearly 2 ft from the glass, gives some protection to the latter and to the label frames and is a comfortable support to lean on whilst watching the fish.

The hall is ventilated by an extraction fan discharging to the outside at the north-west corner (Text-figs. 1, 2). Trunking above the suspended ceiling draws air through three louvred openings flush with the acoustic tiling. Air enters the hall through trunking passing under the tanks from the outside of the building to louvred openings below the sills. There are three such trunks on each side, but one on the south side discharges into the emergency exit passage, and then through louvres on the inner doors into the public hall. Louvres on the south side can be closed in stormy weather and storm covers are fitted on the outside openings for the winter months. During exceptionally hot calm weather when the aquarium has been crowded it has been necessary to augment normal ventilation by forcing air in through one of the intake trunks on the north side.

Basic construction of the tanks

The new tanks are constructed of reinforced concrete of aluminous cement mixed with local sands and aggregates. Internal surfaces of the back walls and parts of the side walls were subsequently rendered with a waterproof cement and sand mix to seal off hair-cracks. It would be out of place here to give full engineering specifications of the reinforcement and methods of construction; it is feasible to give only an outline description of the tanks as they can be observed in a completed state.

The arrangement and shapes of the tanks will be most readily understood by a study of the plan and sections in Text-figs. 1, 2 and 4. It is instructive to compare these figures with the plan and section of the old aquarium (Wilson, 1952, text-figs. 1, 2). As before, the tanks roof over culverts returning overflow water to the reservoirs; they rest behind on ledges at the bases of the main walls of the building and in front are continuous with concrete pillars extending each stile and window mullion to bedrock below floor level. The culverts are the old ones modified in width and re-asphalted. The old central culvert has been retained for possible future use. The old drainage trenches have been filled in and on the south side a new trench to carry services to the laboratories at the east end of the building has been excavated alongside the southern culvert and under the forward parts of the tanks. These services pass under the big tank. Easy access is provided to all culverts and to the service pipes everywhere. The larger tanks on the north and south sides are 6 ft. wide (front to back) and 4 ft. deep with a water depth of 3 ft. 6 in. Their walls are 6–7 in. thick, their bottoms 8–9 in. thick. Creosoted soft-boards used when casting the back walls of the tanks, to prevent the concrete adhering to the walls of the building, remain in position. The big tank at the east end is internally 29 ft. long and varies in width from about 8 ft. 4 in. at the centre to about 9 ft. 3 in. near each end. The bottom of this tank is about 10 in. thick, and at the north end it drops down to a lower level over an area irregular in shape, thereby increasing the water depth at this place by about 1 ft. 3 in. The small tanks with a water depth of rather less than 2 ft. 6 in. occupy the corners between the ends of the big tank and the north- and south-side series. On the north side at the west end a shallow triangular tank overlaps a floor tank which is divisible into two with a removable partition or, as at present, by built-in rockwork. The floor tank is viewed only through the water surface and is designed for the display of flatfishes on contrasted bottom shingles. Except for this floor tank the water surface in all the tanks is at a uniform height, permitting openings to be made between tanks as described below (p. 402).



Text-fig. 3. A. Plan of a stile between a triangular tank on the right and a larger tank on the left, including a portion of the dividing wall with polythene sheets slid into slate slots to form inflow ducts. Inset are details of slotted slate inserts keyed to the concrete by grooving and rustless-steel screws. In the right inset is shown the edge of a glass pane with sealing compound ('Glasticon', drawn solid black) between it and the slate.

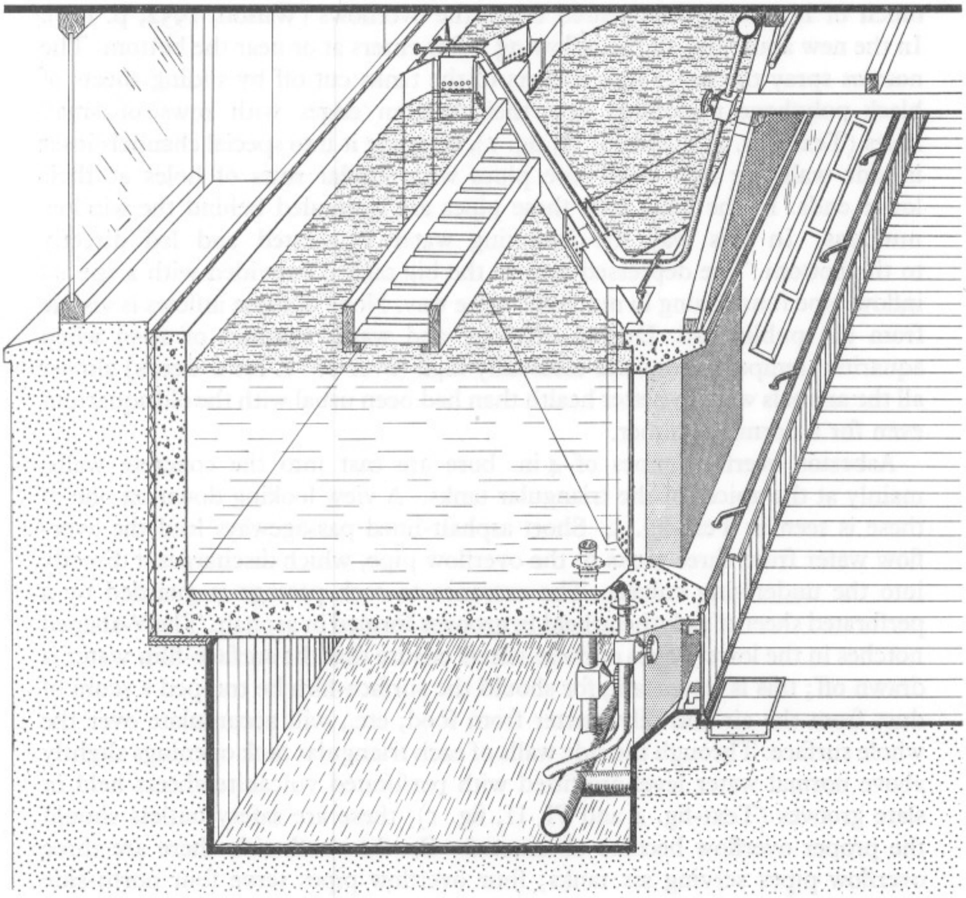
B. Section of a tank front showing lintel walk-way and sill. Inset above are details of teak turnbuckle on rustless-steel rag-bolt, top edge of glass, water level, etc. Inset below shows bottom edge of glass resting on teak block on ledge of sill with details of grooved slate inserts, sealing compound, etc.

Except for the shallower tanks all the window openings are of uniform size, 5 ft. 7½ in. long by 3 ft. high. One advantage of this uniformity is that a single spare pane of glass fits all tanks except the shallow ones. The glass panes, 1 in. thick, overlap the window opening 1½ in. all round. These openings are formed of slate inserts keyed to the concrete (Text-fig. 3). The slates are grooved to give facings exactly 1½ in. wide. This is necessary to achieve uniformity of pressure on the sealing compound and to aid in positioning the glass. The glass is pressed by water pressure against the sealing compound 'Glasticon' ('Glasticord' 304) laid in strip form on the facings (for method of glazing see Wilson, 1952, p. 195). A single teak turnbuckle fixed to the frame above the middle top edge of each pane prevents accidental falling inwards of the glass when the tank is emptied.

The top edges of all window openings are 5 ft. 7 in. above floor level all round the aquarium. The heads or lintels are wide and flat topped, they carry the sloping sides of the suspended ceiling and form convenient walk-ways for servicing the tanks (Pl. II, fig. 1), especially for glass-cleaning. The sills are also wide and carry externally the label frames and support the hand-rail already described. Within each tank the sill provides a ledge $1\frac{1}{2}$ in. wide on which the bottom edge of the glass pane rests, though indirectly with two teak blocks near either end between it and the concrete (Text-fig. 3). From this ledge the sill slopes downwards at 45° to the tank floor (Text-fig. 4). This slope, about 4 in. wide, cannot be seen by the public; it ensures that sand is kept well away from the glass and the glass-cleaning brush. At one place in this slope a 2 in. diameter drain hole, guarded by a plug, leads through a polythene pipe (with puddle-flange) to a Saunders-type valve under the sill to allow, after removal of the plug, the tanks to be drained into the culvert. A similar drain hole, plug and valve is situated close by on the tank floor; through this valve the tank can be drained to waste, a convenience when the emptied tank is cleaned by hosing. To prevent unsightliness the floor plug is normally covered over with sand or gravel: the plug in the sill is, by virtue of its position, out of sight. Below the front edge of the sill fluted asbestos sheeting with removable panels conceal the drainage valves and the culvert. A number of covered floor drains in the public hall are provided for washing down the floor.

Circulation

At the time of writing the same two centrifugal pumps mentioned in a previous paper (Wilson, 1952, p. 204) maintain the circulation, but new pumps of larger capacity will be installed in the near future. The old 4 in. vulcanite main rising from the engine room in the north-west corner (Text-fig. 1) feeds into a new 3 in. black polythene ('Alkathene') pipe which divides into two branches, each controlled by a Saunders valve, one to the north-side tanks and one to the south. These two mains run close to the true ceiling above the corner of the suspended ceiling (Text-figs. 2, 4); there they are readily accessible. Cleaning eyes are provided at bends where needed. From these high-level mains down-dropping $1\frac{1}{2}$ in. pipes, also of black polythene and controlled by Saunders valves, lead through smaller branches to nozzles injecting water into the tanks (Text-figs. 4, 5 and Pl. II, fig. 1). In the old aquarium the mains lay along the tops of the tanks not far above water level and numerous nozzles injected water and air bubbles into the tanks. Not only were these mains an obstruction to servicing but the inflow method was inefficient, for only a portion of the water ever reached tank bottom and



Text-fig. 4. Section through a north-side tank incorporating perspective view facing east and showing portions of three tanks and part of the public hall. Behind the tank is the main wall of the building with a window. The back of the tank rests on a footing of the wall, but indirectly on copper plates forming a sliding bearing to allow for possible movement; the plates are sealed from the sea-water circulation. Between the back wall of the tank and the wall of the building is a layer of creosoted soft-board which during construction prevented the liquid concrete from adhering to the building. Under the tank is an asphalt-lined sea-water return culvert within which is a drain pipe running to waste From this drain pipe there is a connexion, through a valve, to the tank floor and through an open pipe another branch leads to a covered sump in the public hall. A drain in the tank sill, controlled by a valve, can discharge water into the culvert and so back to the reservoirs. At the apex of the triangular tank there is an overflow serving all three tanks, a swim-way between the two larger tanks, and to the latter an inflow each. These structures are shown in greater detail, viewed from above, in Text-fig. 5. A portion of a cat-walk is shown, and in the wall on the nearside a safety overflow from the triangular tank is seen. Still farther forward are two inflows, one of them to the triangular tank. The polythene branch pipe, with Saunders valve, serving the inflows, leads down from the sea-water main at ceiling level. Nearby is the main compressed-air pipe, but no valves or branch connexions to this are shown. In the public hall are seen the handrail with supports inserted in the concrete sill; label frames between it and the glass; and below the sill, fluted asbestos sheeting down to floor level.

much of it quickly disappeared down the overflows (Wilson, 1952, p. 199). In the new aquarium all the inflowing water enters at or near the bottom. The nozzles spray the water into corners of the tanks cut off by sliding sheets of black polythene perforated near their bottom edges with rows of small holes (Text-figs. 4, 5 and Pl. II, fig. 1), or spray it into special channels inset in side walls, or into large-bore pipes with similar rows of holes at their lower ends. In the large tank these pipes are concealed behind the window mullions. In this way the incoming water is aerated and led directly to the bottom. The depressed area in the big tank is provided with a special inflow pipe functioning in much the same way. None of these inflows is visible from the public hall. During the long and warm summer of 1959 when aquarium temperatures were unusually high (over 18° C for 6 weeks) almost all the animals were in better health than had been usual with the old aquarium even for a normal summer.

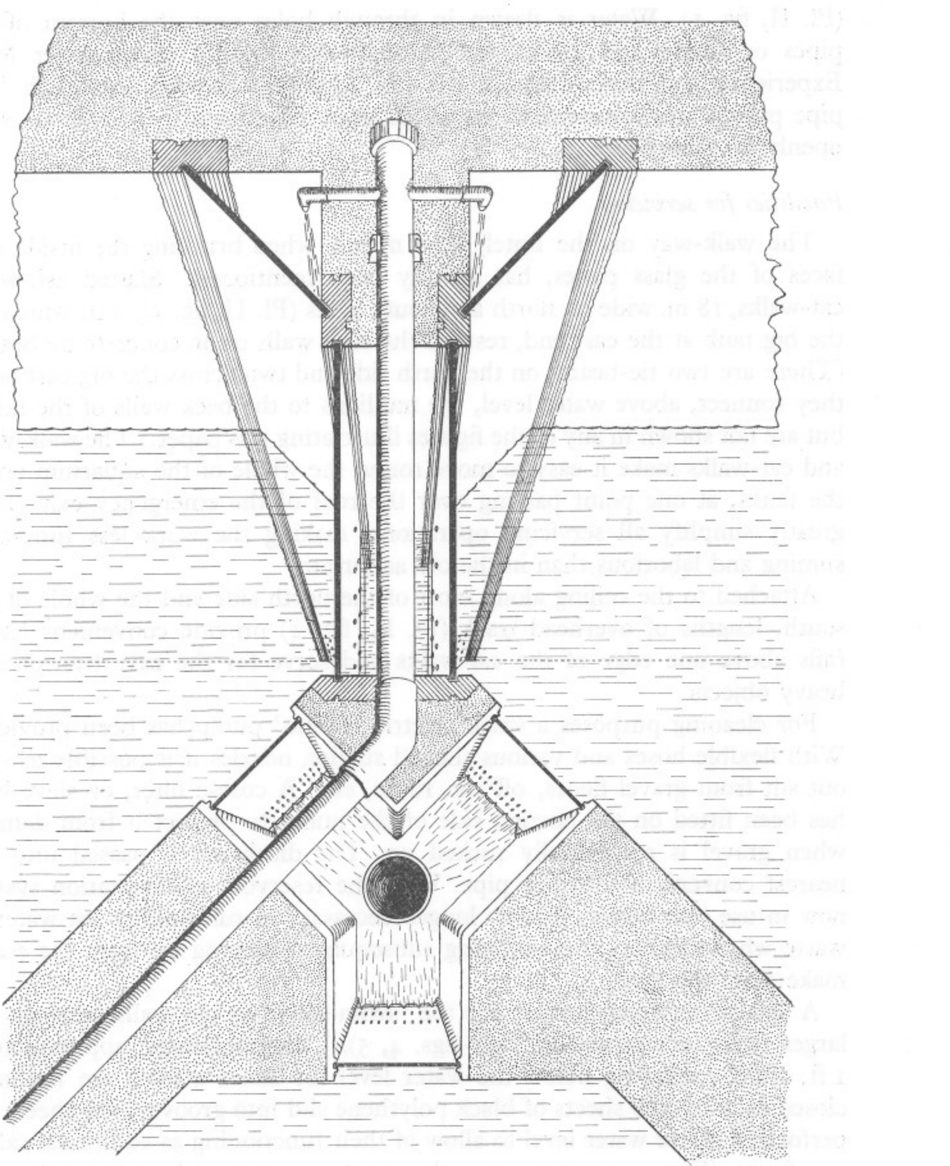
Asbestos overflow pipes of 4 in. bore are cast into the concrete walls, mainly at the apices of the triangular tanks. A view looking down on one of these is seen in Text-fig. 5. Short asphalt-lined passageways lead the overflow water from three tanks to the overflow pipe, which discharges it directly into the underlying culvert. The entrance to each passage is guarded by a perforated sheet of polythene held in grooves formed in asphalt. The V-shaped notches in the lower edges of these sheets ensure that the surface-film water is drawn off; this is important, for should the surface-film be trapped a scum of dust from the air and oily matter from food, etc., will accumulate over the whole surface. Through the side walls of each triangular tank openings slightly above normal water level are fitted with perforated vulcanite sheets held in slate grooves (Text-fig. 4 and Pl. II, fig. 1); these are safety outlets should the proper overflow become obstructed. On the south side there are three overflow pipes serving six tanks; four overflow pipes serve four north-side tanks, the big end tank and the two corner tanks, and all seven tanks can overflow into one another. It is thus impossible for tanks to overfill unless all overflow pipes of a series are simultaneously blocked, which is virtually impossible.

The divisible floor-tank in the north-west corner has two large-bore overflow pipes draining away surface-film water to keep it clear.

Compressed air

In the new aquarium compressed air is used for two purposes only: (1) for lifting water from lower levels to the surface, thereby assisting in maintaining water movement within the tanks; (2) for imparting a rippled surface to bring about a play of light and shade over rocks and gravel, as occurs naturally in shallower regions of the sea.

The air is bubbled up inside pipes of 3 in. bore (concealed behind two window mullions on the north side), or in tank corners behind polythene sheets



Text-fig. 5. Perspective drawing looking down on an overflow serving three tanks, a swim-way between two tanks, and inflows to two tanks. The top faces of the concrete are stippled; of the slate inserts hachured; while the top edges of the sliding polythene sheets are solid black. The top edges of the asphalt lining of the overflow channels are unshaded. Water is shown by dashed lines.

(Pl. II, fig. 1). Water is drawn in through holes near the bottom of the pipes or sheets and gushes out through slits slightly above water level. Experience and experiment in the old aquarium showed that such 'air-pipe pumps' use compressed air much more effectively than diffusers sited openly on tank floors.

Facilities for servicing

The walk-way on the lintel, used mainly when brushing the inside surfaces of the glass panes, has already been mentioned. Slatted ash-wood cat-walks, 18 in. wide on north and south sides (Pl. II, fig. 1), 2 ft. wide over the big tank at the east end, rest on the tank walls or on concrete tie beams. (There are two tie-beams on the north side and two across the big east tank; they connect, above water level, the mullions to the back walls of the tanks, but are not shown in any of the figures illustrating this paper.) The walk-ways and cat-walks make it easy to move round the whole of the aquarium above the tanks, at one point passing over the roof of the emergency exit. They greatly simplify all servicing operations, making the work less time-consuming and laborious than in the old aquarium.

Attached to the ceiling along most of the north side and the whole of the south, lengths of overhead track (Pl. II, fig. 1) provide convenient hand-rails above one edge of the cat-walks and serve for the easy transport of heavy objects.

For cleaning purposes a small electric 'Mono' pump has been provided. With flexible hoses and various shaped suction nozzles it is possible to suck out silt from gravel floors, off the rocks, etc. A coarse filter, or sieve-box, has been fitted on the suction side of the pump to protect it from damage when gravel is accidentally sucked up. The discharge is passed into the nearest convenient overflow pipe. With the reservoir sedimentation system now in use (see below) it is no longer necessary to run muddy sea water to waste when cleaning, necessitating subsequent pumping up from the sea to make good the loss.

A special servicing feature are the 'swim-ways' in the walls between the larger tanks (see especially Text-figs. 4, 5). These openings (approximately 1 ft. wide, extending below the water level for about a foot) are normally closed each by two sheets of black polythene slid into grooves; the sheets are perforated above water level to allow of their functioning as additional safety overflows. These openings, once the sheets are removed, permit fish to be swum from one tank to another as desired. Thus during a major tank-cleaning operation the fish of one tank will be netted and removed to storage tanks in the yard, choosing for netting easily caught and not readily damaged species such as dogfishes and conger eels. The swim-way adjacent having been made watertight (with a bolted-on cover and sealing compound) this tank will be emptied, cleaned and reflooded. The swim-way will then be opened and the fish in the next tank (species such as whiting which are easily damaged by netting) will be driven through into the cleaned tank and shut off there. Their tank in its turn will be emptied and cleaned and made ready for the reception of fish from a tank farther on. Finally, when the whole series has been emptied and cleaned one at a time, the fish will be driven back into their own tanks and the dogfishes and conger eels brought back from the yard. In this way handling of fish will be reduced to a minimum.

In the north-west service area (Text-fig. 1) a number of small asbestos tanks are used to store live food (shrimps, crabs, mysids, worms, etc.) and to accommodate recently caught small animals until such time as they are placed in the exhibition tanks. This corner also houses the 'plunger-bucket' (to work 'plunger-jars' in a laboratory above) which is supplied with water from the north-side series of tanks.

Lighting

It is hardly possible to light an aquarium satisfactorily by daylight. Daylight is too variable in intensity and whatever the orientation of the tanks some will always be more brightly lit than others. When the sun shines strong reflexions of the sunny side will be seen in the darker side unless a curtain, as in the old aquarium, be hung down the middle of the public hall. Too much daylight induces rapid growth of small algae which on dying break up and produce silt; the result is dirty tanks. Back-lighting from windows behind the tanks, a standard feature of many Victorian public aquaria some of which still survive, illuminates the sides of the fish away from the viewer and leaves the backs of the tanks in semi-darkness. A few translucent objects—some sea anemones, ascidians, dogfish eggs, etc.—look well when back-lit but the majority of opaque animals do not. The tanks should be more strongly lit than the public hall, to avoid as far as possible reflexions of people in the glass and to make the tanks appear as a series of bright living pictures within their darker frames.

To exclude daylight the south-side windows have been fitted inside with asbestos sheeting. On the side facing the glass the sheeting is enamelled dark blue, purely as an architectural feature when seen from outside the building. Three windows have been left to open to obtain ventilation while admitting a minimum of daylight (Pl. II, fig. 1). On the north side the windows are sufficiently screened from the sky by the roof over the new outside tanks (see below).

The public hall (Pl. I) is lit mainly by light passing through the tanks aided by a series of recessed lights in the suspended ceiling. It is dim but not completely dark, there being sufficient illumination to see any object on the floor and to allow the Guide Book to be read.

Over the tanks two lines of electric conduit tubing are fixed at main ceiling level, one between the cat-walk and the glass and the other between the cat-walk and the backs of the tanks (Pl. II, fig. 1). At selected points screwed waterproof three-pin sockets are provided from which hang the lights, the heavier ones on chains. Over most tanks there is one main light (usually a 200 W., occasionally 100 W. bulb inside a watertight reflector fitting) 12 in. above water level and 12 in. from the top edge of each glass pane. The back lights are more numerous and more variable; they are mostly 100 W. bulbs in watertight fittings, but fluorescent tubes, protected from damp, are used in places. The back lighting has been arranged to give the most effective illumination of the rock scenery and therefore varies from tank to tank; the front lighting is more constant as it is intended mainly to illuminate the animals. The triangular tanks have only one light, the front one, but special effects can be arranged if needed. Front and back lights are independently fused and switched.

In addition to the main lights, low-wattage bulbs in waterproof plastic bulkhead fittings fixed at a small number of places on the ceiling directly above the tanks (Pl. II, figs. 1) are switched on whenever the main lights are off. These night-lights give sufficient illumination for a number of active fishes to avoid obstructions at night. They probably help the mackerel and some other pelagic fish and they definitely do help Smooth Hounds (*Mustelus mustelus*) and Spur Dogs (*Squalus acanthias*) to avoid bumping their snouts on rocks in the dark. The provision of night-lights was recommended long ago by Saville Kent as a result of his experiences in the former Manchester Aquarium (opened 1874) and their benefit to these same species was noticed independently at Plymouth some years ago.

The floor-tank is lit partly from above by flood-lamps shining down through holes in the canopy over the tank, and partly from lamps behind plate-glass windows in the front wall below water level. The lights are so masked and positioned that they illuminate only the floor of the tank, and none of the surrounds above water level. No lamps or their reflections are visible from normal viewing positions.

At suitable points on the walls behind the tanks three-point 5-amp switch sockets are provided. These are intended for the electric cleaning pump but are available for special or temporary lighting if required.

Rockwork

Few fish are completely at ease in a bare-walled tank. Many invertebrates and some fishes need to be provided with rocky nooks and crannies and with a floor of natural sands or gravels. When an aquarium is intended to attract a paying public the appearance of this rockwork and the treatment of the tank walls is of paramount importance in providing an aesthetically pleasing background against which the animals are viewed. The success or otherwise of the scenic presentation cannot fail to influence receipts at the cash desk.

As the Plymouth aquarium is intended almost entirely for local marine life it was decided to base the scenic presentation on local rocks and of these the beautiful Devonian limestone forming the northern boundary of the Sound was considered most suitable. The rock is very hard and is often bluish white in colour, pink or streaked with pink. Water-worn rocks of various sizes could be picked up from higher tidal levels, and by careful attention to bedding planes could be built into natural-looking cliffs in the tanks. In addition to the use of real rocks rubber-latex moulds were made of small portions of water-worn cliff faces and used to produce artificial rock 'tiles'. One face of each tile exactly reproduces the shape and texture of the natural rock on which the mould was made. The other face, being flat and scored, forms a 'key' for cementing to the back walls, especially of the triangular tanks where it is necessary to keep the thickness of the added rockwork to a minimum. Joints between adjacent rock tiles are filled with cement and sand and modelled to merge the natural mouldings of the various tiles into one apparent solid rock face. A little of the rockwork in one triangular tank is seen in Pl. II, fig. 1. A strong mix (1:3) of sulphate-resisting cement and crushed limestone which had passed a $\frac{1}{4}$ in. sieve was used in making the tiles. Before filling the moulds with the mix the rubber was wetted with a strong solution of 'Teepol' to prevent the adhesion of air bubbles and, after filling, the moulds were vibrated to eliminate all air trapped in the mix. For fixing the tiles to the tank walls a stronger mix (1:2) of sulphate-resisting cement, fine sands and waterproofer was used. Finally, the artificial rock faces were painted to resemble natural rocks. The epoxy resin paints used are non-toxic, are very hard and should withstand repeated cleaning. The final effect is excellent, it being difficult to distinguish artificial rocks from natural and impossible once they are covered with natural growths.

Where the back wall of a tank is left bare it is painted with epoxy resin paint of a moderately dark-green shade to simulate the effect of the greenness seen on looking through many feet of sea water. Near the backs of certain tanks frosted (sand-papered) sheets of Perspex pleasantly diffuse the background to give an appearance of distance; they eliminate shadows which would otherwise show on the walls. Scenic paintings of apparently distant rocks on the walls behind such sheets increases this illusion of remote vistas. The sheets are mostly 6 in. in front of the back wall of the tank, but sometimes are farther away and fish allowed to pass behind. They are held by slotted slates hidden in the rockwork. In arranging such sheets it is essential that side and bottom edges be concealed from view, for if seen the illusion is destroyed.

The angled-out side walls of the larger tanks are painted white (Pl. II, fig. 1), again with epoxy resins. This white surface is, of course, invisible to the public and it helps to reflect back into the tank some light which would otherwise be lost. To conceal the far corners of these tanks, with their inflows and swim-ways, rock cliffs are built against the side walls a little in front of them.

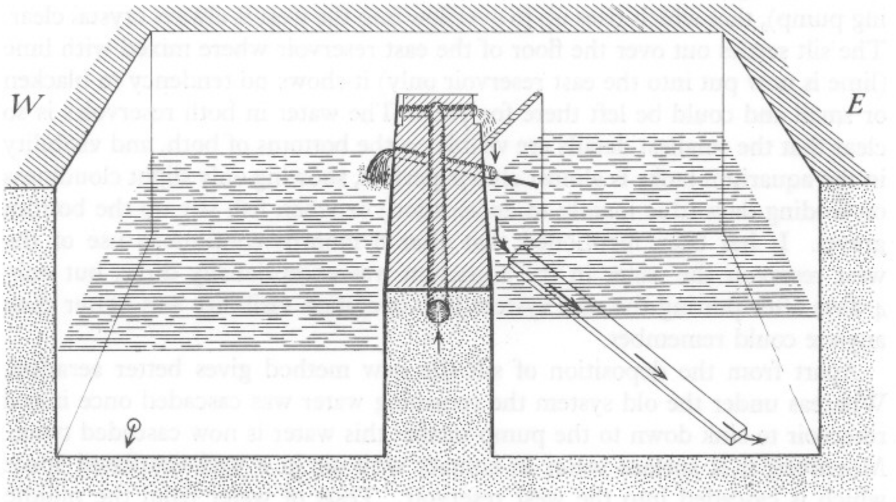
Fish can pass out of sight behind these cliffs but most fishes remain in view. Only lobsters, dogfishes, conger eels and wrasses have been troublesome, often hiding in the concealed corners, and special measures are taken to deal with them. Thus if there are more lobsters in a tank than there are hidden corners some will be forced to occupy holes in full view. Fish swimming into view from behind these cliffs and disappearing again behind them seem to come and go as they would naturally do among rocks in the sea.

After the rockwork was built the bottom of every tank was covered with a layer of sulphate-resisting cement and sand, to which a suitable yellow colouring agent had been added, and rendered to a thickness of an inch. While still wet the rendering was strewn with sand or gravel, gently patted in by hand and given a rippled surface as on a sandy sea shore. Now when fish disturb the loose sand or gravel the rippling helps to retain it in position and where patches of floors are uncovered they match well the sand or gravel and do not look like bare concrete. It is important that the bottom screeding be carried out after the rockwork is in position so that rocks emerge from it as from a natural deposit.

Aquarium reservoirs and water treatments

The provision of clean well-aerated sea water of as near normal chemical and physical constitution as possible is essential to the well-being of an aquarium. Until very recently the water supplied to the tanks of the Plymouth aquarium (from reservoirs for a description of which see Wilson, 1952, p. 204) has always been loaded with varying quantities of silt, although generally satisfactory in other respects. Quite early in the history of the place much effort was expended to free the water from silt, as well as to improve it in other ways. There is frequent reference to these efforts in early Reports of Council and Director's Reports published in early volumes of the *Journal*. Various filters were devised which seem to have functioned for a time but which cannot have proved satisfactory for long. Conditions at one time were evidently so bad that doubts were expressed concerning the efficiency of closed sea-water circulation systems and a single use of water, at least for the laboratory, advocated (*J. mar. biol. Ass. U.K.*, Vol. 4, pp. 77 and 417; Vol. 5, pp. 98–99).

The first major improvement to the condition of the circulating sea water was made when regular treatment with slaked lime (to remove carbon dioxide and restore the pH) was instituted sometime after 1922 (Atkins, 1931). The silt trouble remained and occasions when it was possible to view with some clarity the backs of the largest tanks through 9 ft. of water were regarded as almost noteworthy. Most of the silt was formed in the tanks by the decay of plant growths, the breaking up of faeces, etc., and it was kept in suspension by the stirring activities of the animals, especially bottom fishes. All but the heavier components were carried away in the overflow water and discharged at the surface into one of the two underground reservoirs. From this reservoir water was being drawn off to the pumps at a point about 3 ft. from the bottom, and with it any silt still in suspension. There was thus a steady build-up of suspended particles and the longer the water had been circulating the cloudier it was. The cloudiness of the water in the reservoirs was such that the bottom at a depth of 11 ft. was rarely visible; often it was not possible to see anything at even half that depth. Allowing each reservoir to rest and sediment alternate weeks was only partially successful in clearing the water (see below). The system has been described and criticized in Wilson, 1952, pp. 204 and 209. A method of sedimenting off the silt there suggested has now in modified form been adopted with excellent results.



Text-fig. 6. Diagram of the sea-water reservoirs (not to scale and with roof omitted) to show method of circulation now in use. The direction of water flow is indicated by the arrows.

The method now in use involved no more than minor modifications to the existing reservoirs. These are shown diagrammatically in Text-fig. 6. Water returns from the aquarium along a 1 ft. diameter pipe in the wall dividing east and west reservoirs. At its northern end there is a T-junction where sluices divert the water to one or other of the reservoirs as required; in the old days it would be the reservoir from which water was being pumped, there being then no communication between reservoirs.

During the construction of new underground reservoirs for the new laboratory circulation (see below) the east reservoir had to remain empty for 6 months and only the west reservoir was in use. During this period the water became so dirty that in the aquarium anything farther from the glass than about 2 ft. disappeared from view in a fog of suspended silt. This gives some measure of the partial success of the old method of alternating reservoirs. While the east reservoir was empty a wall was built across its north-west corner and from the bottom of this wall a culvert of brick sides with removable slate top was constructed across the reservoir floor to near its south-east corner. A 6 in. drain pipe was inserted through the dividing wall at the north end, passing under the larger return pipe from the aquarium. With both reservoirs flooded the return water now discharges into the corner cut off by the wall and passes along the culvert to emerge near the south-east corner at the bottom as shown by the arrows in Text-fig. 6. This brings about a continuous overflow of surface water from the east to the west reservoir from whence it is drawn off to the pump through the old suction pipe in the south wall. However dirty the incoming water (as with silt-laden water from the discharge of the cleaning pump), that which rises up to overflow into the west is always crystal clear. The silt settles out over the floor of the east reservoir where mixed with lime (lime is now put into the east reservoir only) it shows no tendency to blacken or smell and could be left there for years. The water in both reservoirs is so clear that the smallest details are visible on the bottoms of both, and visibility in the aquarium tanks is almost always perfect, showing only slight cloudiness on feeding days (due mainly to defaecation) or when fish stir up the bottom gravel. It has been mentioned that after 6 months continuous use of the west reservoir the water in the aquarium was exceptionally dirty, but only 4 days after putting the new system into operation visibility was better than anyone could remember.

Apart from the deposition of silt the new method gives better aeration. Whereas under the old system the returning water was cascaded once into a reservoir to sink down to the pump intake, this water is now cascaded twice. Moreover, it is surface water in contact with air in a well-ventilated space which is cascaded into the west reservoir. Tests of water from the middle depths of the latter have shown close approximations to 100% oxygen saturation.

Means are provided whereby it is easy to revert to the old system of using one reservoir only. This is occasionally necessary for a day or two while one or other of the reservoirs is emptied and cleaned. The method of refilling from the sea was described in Wilson, 1952, p. 205. Sometimes the west reservoir is only partially emptied and the system freshened with new water from the sea pumped into the east reservoir.

The total quantity of sea water held by the reservoirs is about 110,000 gallons when both are completely full, while the total quantity of water in aquarium and service tanks is roughly 17,000 gallons. At the present time the water is circulated at a rate of about 3000 gallons an hour (for description of the pumps see Wilson, 1952, p. 204). This rate is barely adequate, especially in hot weather, and it is desirable to increase the rate to 4500 gallons per hour or even more.

NEW CIRCULATION

An ever-increasing need for more live-specimen storage accommodation, and for research purposes cleaner water less heavily stocked with animal life, led to a decision to build an entirely new circulation system independent of the main aquarium and its ancillaries. Thus, commencing in October 1955 new reservoirs were excavated in the yard between south and north buildings and a new series of outside tanks were built to replace the smaller series illustrated and described in Wilson, 1952, pp. 202–3. The new system was brought into operation for the first time early in September 1957. The contractors for these new reservoirs and new outside tanks were Messrs A. N. Coles (Contractors) Ltd., Plymouth.

New reservoirs

A large hole was excavated in hard limestone to the east of the aquarium reservoirs. In this hole new reservoirs were constructed in concrete (using sulphate-resisting cement) and lined with a rendering of waterproof concrete coated with bituminous paint. They were roofed over at road level with concrete and tarmacadam. The roofing is designed to take a load of 12 tons. At convenient places manholes give access to the reservoirs below. Each reservoir holds about 16,000 gallons of sea water when full and there is a well-ventilated air-space of about 2 ft. between the underside of the roof and the water surface. The dividing wall between the reservoirs has three wide openings 8 ft. 9 in. above reservoir floor level. Water returning from the tanks cascades into a partitioned-off space in the south-east corner of the east reservoir and is there forced to descend to the bottom where silt is deposited. As this east reservoir fills up it overflows the dividing wall through the openings mentioned and cascades into the west reservoir. The depth of the water as it passes over the flat top of the 12 in.-wide wall is very shallow; thus the whole volume of the water as it circulates is at these places brought into close contact with air. From a position 4 ft. above floor level at the west end of the west reservoir the water is sucked away through a black polythene pipe of 3 in. bore to the pumps. The east reservoir is limed weekly through an inspection cover. Provision is made for working from either reservoir only while the other is emptied and cleaned. Each reservoir is provided with a drain hole and plug at its south-west corner and the floor slopes downwards slightly to the drain hole. The 4 in. drain pipe passes under the floor of the new west reservoir and passes through the south end of the old east reservoir of the aquarium circulation to join the main drain. The depth of water in the new reservoirs varies between 8 and 9 ft. when full. The reservoirs are filled through a 4-in. bore iron pipe and through valves connecting with the pumping system used for filling the aquarium reservoirs (Wilson, 1952, p. 205). Compressed air can be supplied to the west reservoir should it ever be needed.

Electric lights in watertight bulkhead fittings are fixed to the roof of each reservoir and are switched from the pump-room in the basement of the south building.

New outside tanks

Under a new roof a new series of outside tanks was used for the first time in September 1957. They comprise (Text-fig. 1 and Pl. II, fig. 2) three blocks of concrete tanks (painted internally with bituminous paint) and nine large (100 gallon) and four small (20 gallon) asbestos tanks on raised plinths (Text-fig. 1). A double tier of slate shelving, built partly against the main building and partly against a wall at right angles to it, forms a circulation unit for bowls and jars. Four of the concrete tanks are divisible by asbestos sheets sliding in grooves; a fifth is bowl-shaped to accommodate squid and cuttlefishes. The water depth of the smaller concrete tanks is roughly 19 in., while the water depth of the large central tank can be varied at will at 23, 31 and 36 in. by placing rubber bungs in the lower overflow holes. All overflow pipes pass down inside the thickness of the tank walls and are fitted with plastic bowl-shaped sieves ('salad-shakers' from a local store) to prevent the ingress of large objects. These overflows discharge into a culvert below ground level which returns overflow water to the reservoirs. The culvert and the lower ends of all overflow pipes are readily accessible through a series of manholes. Inflow pipes are also within the thickness of the walls and discharge into the tanks close to the bottom.

The asbestos tanks are fitted with black polythene piping for inflows and overflows. They can easily be removed and other tanks of different sizes put in their place.

At the time of writing, all tanks east of the circulation benches are supplied from the new reservoirs, while the benches themselves and the tanks west of them are on the aquarium circulation. It is possible for the largest concrete tank and the three asbestos tanks near its western end to be supplied with water from the aquarium circulation should this ever be necessary.

Electric lights for viewing the outside tanks at night are provided under the roofing. It is intended at some future date to fit shutters which in summer will slide up out of the way under the roof, but which in winter can be pulled down to enclose the tank space and protect the system from frost.

New pumps

The new circulation is maintained by paired 'Mono' pumps with stainless-steel impellers inside rubber stators. Driven by 3 h.p. three-phase motors each unit delivers about 3600 gallons an hour. One pump is run for several weeks while the other is serviced and rests as a stand-by. Adjustments to the gearing of the V-belting will enable these pumps to give a greater output should this in future be needed. At present the output is more than ample as it is serving only the outside tanks and those on the first floor of the main laboratory (as described in Wilson, 1952, p. 203,[1] and illustrated in Russell, 1948, pl. XIX).

Circulation efficiency

The total capacity of the outside tanks and those on the first floor is about 2600 gallons; this being less than a twelfth of the reservoir capacity, a much smaller proportion of tank volume to reservoir volume than in the aquarium circulation. The relative rate of flow of the water is also much greater. Even when eventually more experimental tanks in the new block of buildings now being planned are added the new circulation will contain less animal life per unit volume than the aquarium circulation, and be relatively more efficient in every way except temperature stability. There is no regular means of heating or cooling either circulation, and while temperature changes are slow the new circulation is more affected by the weather than is the old. This is because the total volume of water is less than in the aquarium circulation and a greater proportion of it is exposed to air temperature and wind in the yard. When shutters are fitted to close in the outside tanks in winter it will be possible to reduce the rate of loss of heat, though it is doubtful if shutters will help to check rise of water temperature during hot days in summer.

My thanks are due to Mr G. A. W. Battin for making the drawings for this paper and Mr A. C. G. Best for help with the photography.

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[1] Except that the overflow water from these main laboratory tanks no longer runs into exhibition tanks in the aquarium below but is conducted by new piping to the return culvert to the new reservoirs.

EXPLANATION OF PLATES

Plate I

General view of the new aquarium from the public entrance lobby. Note the handrail, label frames, ceiling with inset lights, etc. (A photograph of the old aquarium from almost the same viewpoint is reproduced in Russell, 1948, pl. XXIII, fig. 1.)

Plate II

Fig. 1. View along the tops of the tanks of the south side from the west end. Note especially the shapes of the tanks, the lintel walk-way and cat-walks, the overhead conveyor track, details of inflows and overflows so far as visible, sea-water and compressed-air pipes (one of the latter on tank-back near right foreground), light fittings, etc. Compare especially with Text-figs. 4 and 5.

Fig. 2. View of new outside circulation tanks and circulation bench from the western end. Note in right foreground a pair of concrete tanks painted internally with black bitumen. Further on is the double-tiered circulation bench for bowls, and, in front, four small asbestos tanks on a low circulation table. Behind the circulation bench the outer of three large asbestos tanks, on a raised plinth, is seen. Farther on still is the large and deep concrete tank, then a pair of shallower concrete tanks similar to those in the foreground. Beyond these part of a row of three large asbestos tanks is just visible. (For photographs of the old outside circulation which these tanks replace see Russell, 1948, pl. XXII, fig. 2, and Wilson, 1952, text-fig. 4).

Fig. 1.

Fig. 2.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

BONEY, A. D., CORNER, E. D. S. & SPARROW, B. W. P., 1959. The effects of various poisons on the growth and viability of sporelings of the red alga *Plumaria elegans* (Bonnem.) Schm. *Biochem. Pharmacol.*, Vol. 2, pp. 37–49.

Mercury, silver, copper and arsenic are more toxic than the non-metallic inhibitors hydrocyanic, hydrazoic, iodoacetic, fluoroacetic and malonic acids and 2:4-dinitrophenol to sporelings of *Plumaria elegans* in sea water at pH 8·1. Mercury and silver are more toxic than copper and arsenic, and the toxicities of mercury and arsenic are greatly increased when these poisons are used as lipophilic organic compounds (e.g. phenylmercuric chloride and phenarsazine chloride). All heavy metals are less toxic when used in the presence of reduced glutathione.

The toxicities of an homologous series of primary *n*-alkyl-mercuric chlorides increase to a maximum with that of $n\text{-}C_5H_{11}HgCl$. Lipoid solubilities based on methyl-oleate: sea-water partition coefficients correlate with appropriate toxicity data for the first three members of the series, but those of $n\text{-}C_4H_9HgCl$ and $n\text{-}C_5H_{11}HgCl$ increase without any corresponding rise in toxicity. The 'cut-off' in relative toxicities within the homologous series is not found in complementary experiments with crustaceans.

Mercuric iodide is much more toxic than $HgCl_2$ to *Plumaria* and crustaceans, but whereas various organic compounds of mercury become markedly more toxic to crustaceans when used in the presence of excess KI, their toxicities to *Plumaria* are not increased. E.D.S.C.

BURSA, A. S., 1959. The genus *Prorocentrum* Ehrenberg. Morphodynamics, Protoplasmatic Structures and Taxonomy. *Canad. J. Bot.*, Vol. 37, pp. 1–31.

The morphodynamics of *Prorocentrum* have been studied comparatively in cultures and in plankton. Plankton populations show little morphological variation. In cultures a variety of forms, often similar to other species of *Prorocentrum* which have been described from distant seas, are found. Morphological variation in *Prorocentrum* species depends upon various life phases, individual features of the clones, and various types of cysts. Formation of the morphological aberrants is also affected by ageing of cultures. All protoplasmatic structures, including the cell membrane, possess their own particular features, changing in course of life cycle. Since both physiological and morphodynamic metabolisms are inseparable in their activities, it is useful to complete taxonomic diagnoses with physiological observations. Five new species are described: *Prorocentrum cordiformis*, *P. pomoideum*, *P. pyrenoideum*, *P. redfieldi* and *P. levantinoides*. Morphodynamics in *P. micans* and *P. scutellum* was also studied. Most observations were made *in vivo*. Specific morphological differences in form and structure of protoplasmatic organelles were demonstrated in each species concerned. An attempt was made also to base taxonomic diagnoses upon the apical tooth, trichocysts, and membrane structure. A.S.B.

CARLISLE, DAVID B., 1959. On the neurosecretory system of the brain and associated structures in *Sipunculus nudus*, with a note on the cuticle. *Gunma J. med. Sci., Maebashi*, Vol. 8, pp. 183–94.

In *Sipunculus nudus* a pair of dorsally situated postero-lateral groups of neurosecretory cells in the brain contain each about thirty large cells. The axons run forward to the unpaired sensory organ, a cavity in the brain connected to the mouth region by a ciliated canal. Here the axons make abrupt loops among the sensory cells of this organ and then run into the finger organs, where they terminate in typical neurohaemal endings, vertical to the blood space surrounding the organs. These club-shaped endings are filled with a secretion which has staining properties different from those of the material found more proximally in the axons and cells. The likeness of this system to the hypothalamo-hypophysial system of vertebrates and to the major endocrine systems of crustaceans and insects is emphasized.

The cuticle consists of protein with no trace of chitin or mucopolysaccharides.

D.B.C.

CARLISLE, D. B. & ELLIS, PEGGY E. 1959. La persistance des glandes ventrales céphaliques chez les Criquets solitaires. *C.R. Acad. Sci., Paris*, T. 249, pp. 1059–60.

The ventral glands of locusts, which are homologous to the prothoracic glands of Lepidoptera and probably to the Y-organs of crustacea, normally disappear in the adult insect. In locusts in the solitary phase, however, they may persist in a functional condition.

D.B.C.

COOPER, L. H. N., 1957. Some chemical and physical factors controlling the biological productivity of temperate and tropical oceanic waters. *Proc. 8th Pac. Sci. Cong.* 1953, Vol. IIIA (received by the author 1959).

Differences in conditions of productivity in tropical and temperate latitudes were discussed. A pattern for observation and experiment in tropical seas was proposed. Much of the material in the paper has now only historic interest.

L.H.N.C.

CORNER, E. D. S., 1959. The poisoning of *Maia squinado* (Herbst) by certain compounds of mercury. *Biochem. Pharmacol.*, Vol. 2, pp. 121–32

When *Maia* is immersed in sea water containing added $HgCl_2$ the concentration of the poison in the blood eventually rises above that in the external medium; the concentration in the antennary glands above that in the blood; and the animals excrete small but increasing amounts of mercury in the urine. Most of the poison present in the blood is attached to protein and the concentration of mercury in the blood remains constant for several weeks after poisoned animals are returned to the sea. Mercury also concentrates in various other body tissues, and very large amounts are found on the gills. Similar results are obtained when the poison is administered to the animals by injection. When, however, the poison used is n-$C_5H_{11}HgCl$, although mercury again concentrates at the gills and in various internal organs, the amount detected in the blood is very small and none is found in the urine.

When the animals are immersed for progressively longer times in sea water containing added $HgCl_2$, or are injected with increasing amounts of the poison, the total quantity of amino-N in the urine increases, although that in the blood remains constant. The urine : blood ratio of amino-N also rises when the animals are poisoned with n-$C_5H_{11}HgCl$

although, in this case, the level of amino N in the blood rises as well as that in the urine. Animals poisoned with $HgCl_2$ and then returned to the sea show an abnormally high urine: blood ratio of amino-N several weeks later. By contrast, poisoning with $HgCl_2$ has no effect on the urine: blood ratio of total sulphate. E.D.S.C.

LOWENSTEIN, O. & WERSÄLL, J., 1959. A functional interpretation of the electron-microscopic structure of the sensory hairs in the cristae of the elasmobranch *Raja clavata* in terms of directional sensitivity. *Nature, Lond.*, Vol. 184, pp. 1807–8.

An electronmicroscopic study of the sensory epithelia in the ampullae of the semicircular canals of the labyrinth of *Raja clavata* showed that the hair processes of the sensory cells are compound structures consisting of a number of protoplasmatic filaments, one of which has the typical electron-microscopic structure of the kinocilium, namely nine peripheral plus two central longitudinal fibrillae. This kinocilium is always found on one and the same side of the hair process in a given sensory epithelium and is placed on that side of the sensory hair process which faces in the direction in which the hair process is deflected on excitatory cupula displacement. It appears that this arrangement may be of fundamental functional significance. O.L.

POTTS, W. T. W., 1959. The sodium fluxes in the muscle fibres of a marine and a freshwater lamellibranch. *J. exp. Biol.*, Vol. 26, pp. 676–89.

The efflux of ^{24}Na from the isolated ventricles of *Mytilus* and *Anodonta* has been measured at 15° C and at 5° C. The efflux of sodium in each case is divisible into an extracellular and an intracellular portion except at 15° C in *Anodonta* where the two portions are not clearly distinguishable. The mean rate constant for the efflux of sodium from *Mytilus* ventricle is $2{\cdot}44\ h^{-1}$ at 5° C and $5{\cdot}6\ h^{-1}$ at 15° C. The mean rate constant for *Anodonta* ventricle at 5° C is $4{\cdot}6\ h^{-1}$. The efflux of sodium from the muscle fibres of *Mytilus* ventricle averages 12×10^{-6} mM/cm^2/sec at 5° C and 27×10^{-6} mM/cm^2/sec at 15° C. For *Anodonta* at 5° C it averages $3{\cdot}1 \times 10^{-6}$ mM/cm^2/sec. If the efflux is maintained entirely by an active process then the energy required for the extrusion is 0·26 cal/g/h at 5° C and 0·63 cal/g/h at 15° C for *Mytilus* muscle and 0·046 cal/g/h at 5° C by *Anodonta*. W.T.W.P.

WICKSTEAD, J., 1960. A new record of *Mytilicola intestinalis* Steuer, a parasitic copepod of mussels. *Nature, Lond.*, Vol. 185, p. 258.

Two mature female *Mytilicola intestinalis* Steuer, 7·0 and 8·5 mm long, were recorded from a locality much removed from the limits of their accepted distribution. They were taken free in the plankton in the northern Malacca Strait area, 7° 12′ N., 97° 12′ E. After various considerations, no satisfactory explanation could be given for their capture at such a place in such a manner. J.W.

WICKSTEAD, J. H. & BONE, Q., 1959. Ecology of acraniate larvae. *Nature, Lond.*, Vol. 184, pp. 1849–51.

Several species of acraniate larvae were obtained during a survey of the Indo-Malayan plankton made by the Singapore Regional Fisheries Research Station. Larvae of *Branchiostoma belcheri* Gray were found at a permanent station in the Singapore Strait from mid-October to January. They showed diurnal vertical migratory movements, remaining on the sea-bottom during the day, and rising to the surface at dusk.

Examination of the gut-contents showed that feeding probably only takes place at the bottom. It is suggested that light intensity is the actuating stimulus for the migration (salinity and temperature variations being insignificant), and that it serves both to distribute the species and to enable the larvae to avoid the attacks of nocturnal bottom-feeding predators.

Larvae of *Branchiostoma malayana* Webb, and larvae of the 'amphioxides' type (but belonging to the Branchiostomidae) were obtained at another station, on the surface, at night. This station was over deep water, and examination of the gut contents showed that the larvae fed in mid-water, hence these species are probably truly pelagic, and never live near the bottom. At a third station, 'amphioxides' larvae of *Asymmetron lucayanum* Andrews were collected, which confirms the identification of *Amphioxides pelagicus* Gunther as the larva of *Asymmetron lucayanum*. Q.B.

BOOK REVIEW

DIE WESTKÜSTE SÜDAMERIKAS IM BEREICH DES PERU-STROMS

By E. SCHWEIGGER

Heidelberg-München: Keysersche Verlagsbuchhandlung GmbH, 1959.

This comprehensive work has been written by a German who has spent thirty years studying the Peru current and its manifold influence on the neighbouring land, sea and air. Its greatest value may be as a critical digest of an enormous literature about the west coast, published in periodicals with limited circulation and mostly in Spanish. The task the author set himself was great and many chapters, naturally, do not cut deep. The author's personal interest has been in oceanography, entirely from a descriptive angle. The methods of dynamic oceanography have not been used. 'El Nino', the perturbation of the Peru current which brings death to myriads of fish and sea birds, is examined at length. It seems that much confusion surrounds the term and anyone wishing to use it would be wise to consult this book to find out what it means. The style is friendly and discursive. Anyone in search of a worth-while problem for study may find one on every page. L.H.N.C.

of limited growth and these form the cortical investment to the axes of unlimited growth. In *Ceramium*, the axes each contain a single filament of unlimited growth, that is, they are uniaxial in construction.

Apical segmentation

The basic pattern of segmentation was first outlined by Cramer (1857). Since that date there have been numerous descriptions of apical structure and segmentation.

Each segment formed by the transverse division of the principal apical cell of an axis of unlimited growth divides further to produce from four to nine pericentral cells. The mother-cells remaining after the formation of pericentral cells do not divide again but increase in size to form the axial cells (Fig. 1).

The pericentral cells are formed in a definite sequence, with a fixed orientation. The first pericentral cell formed is cut off on the outer face of each segment; the 'outer face' being determined by the previous pseudo-dichotomy (Fig. 2F). The remaining pericentral cells are cut off successively in pairs to form a ring of cells at the apical pole of each segment (Figs. 1, 2A–E). This orientation of the pericentral cells is of very great importance in that it is associated with the orientation of many other structures, such as spines, tetrasporangia, etc.

The axial cells

The axial cells are formed from the mother-cells remaining after the formation of the pericentral cells. The enlargement of the axial cells is of considerable significance in that it has a profound effect upon the longitudinal growth of the axes. A comparison of the length and volume of newly formed and mature axial cells in various species of *Ceramium* (Table 1) gives a good indication of the degree of enlargement. The enlargement of the axial cells is not related directly to the age of the cell, but shows considerable variation in different parts of the plant. This phenomenon is discussed in greater detail later, with particular reference to its taxonomic implications.

TABLE 1

	Size when formed (μ)	Size when mature (μ)	Increase in length	Increase in volume
C. rubrum	4 × 16 × 16	380 × 316 × 300	95 ×	35,000 ×
C. echionotum	4 × 20 × 20	420 × 240 × 220	105 ×	14,000 ×
C. shuttleworthianum	4 × 12 × 12	220 × 70 × 80	55 ×	2,000 ×

Note. The dimensions, length, depth and breadth, are mean values based on measurements of 400 cells.

The increase in size of the axial cell is associated with the development of a large vacuole. In maturing axial cells there is a peripheral layer of

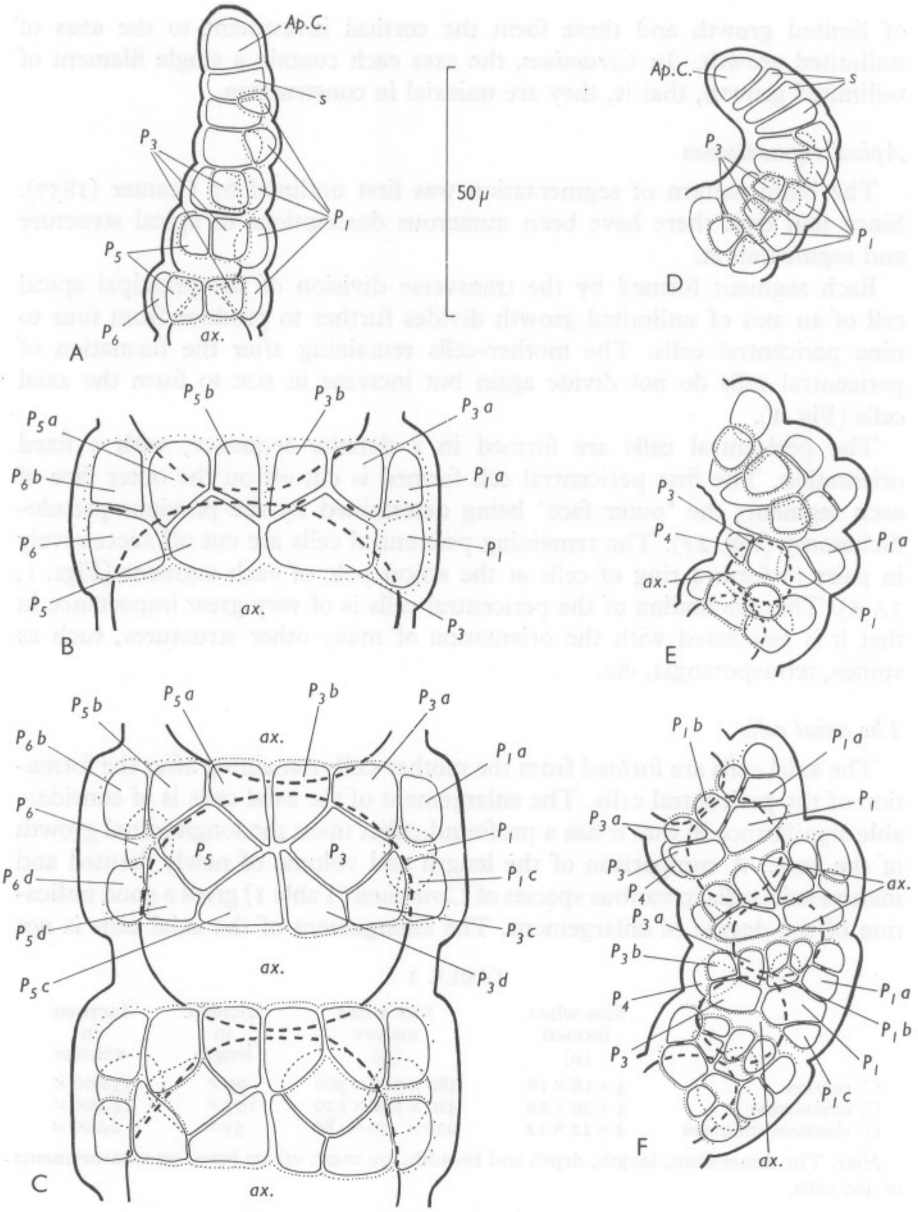

Fig. 1. Apical segmentation and the development of the cortical band in the genus *Ceramium*. The basic pattern of segmentation in straight (A–C) and curved (D–F) apices is fundamentally identical, although there are obvious differences associated with the degree of curvature. *Ap.C.*, Apical cell of an axis; *s.*, segment produced by the transverse division of the apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally directed apical cells of lateral branches of limited growth, produced from P_1; P_1c, P_1d, basipetally directed apical cells of lateral branches of limited growth, produced from P_1.

cytoplasm lining the wall of the cell and a central strand connecting the pit-connexions in the apical and basal walls. Elongate convolute chromatophores are distributed in the peripheral layer of cytoplasm. In those species where the cortex forms a complete investment to the axial cells, the chromatophores, even in the young cells, are only slightly pigmented. As the cells age, the pigmentation disappears completely. The chromatophores are more conspicuous in those species where the axial cell is exposed because of the incomplete cortical investment, but even so degeneration occurs with age.

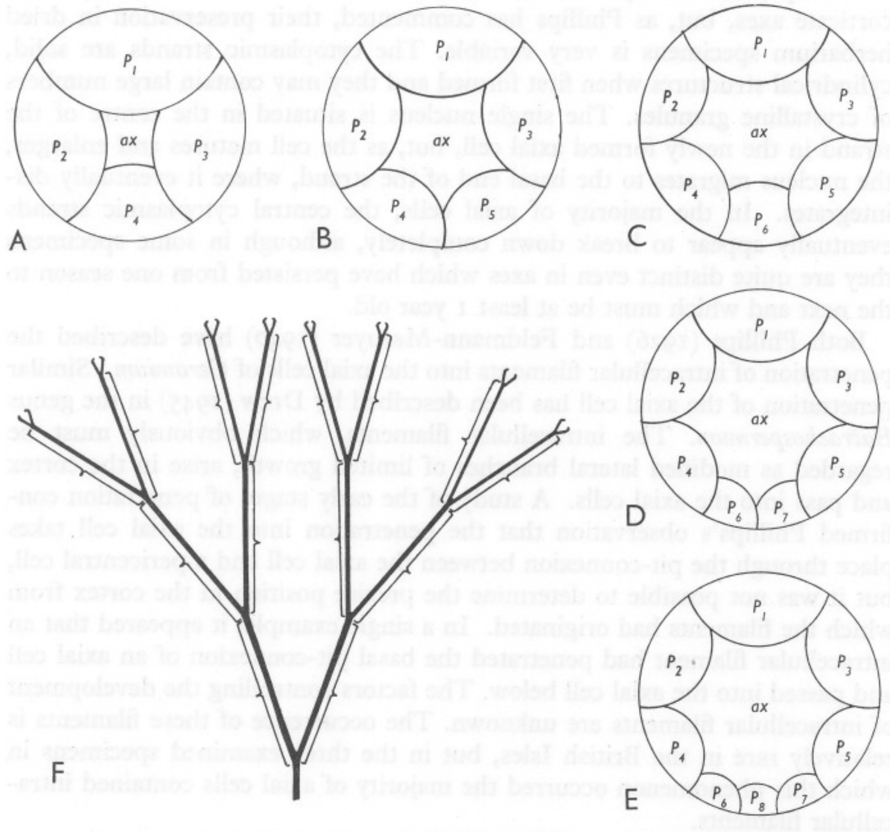

Fig. 2. A–E, Sequence of divisions in segments from which 4, 5, 6, 7 and 8 pericentral cells are formed; F, outwardly directed orientation of the first pericentral cells, in relation to the pseudo-dichotomy of the axes; the positions of the first pericentral cells in each 'sector' are indicated by brackets. *ax.*, Axial cell; P_1, P_2, P_3, etc., pericentral cells, numbered in order of formation.

The presence of a central strand of cytoplasmic material in the axial cells of *Ceramium* has been discussed or figured by various authors (Moore, 1885; Petersen, 1908; Schiller, 1913; Phillips, 1926; Dammann, 1930, 1932; Celan, 1939*a*, *b*; Feldmann-Mazoyer, 1940; Feldmann & Feldmann, 1946; Funk, 1955). Phillips (1926, p. 277) has rightly commented that Moore (1886) mis-interpreted the observations of Hick (1884) on *C. acanthonotum* (= *C. shuttleworthianum*). Hick's observations, which are somewhat obscure, do not refer to the central cytoplasmic strand. These strands, the 'trabeculae' of Phillips, are readily discernible in fresh material, even in completely-corticate axes, but, as Phillips has commented, their preservation in dried herbarium specimens is very variable. The cytoplasmic strands are solid, cylindrical structures when first formed and they may contain large numbers of crystalline granules. The single nucleus is situated in the centre of the strand in the newly formed axial cell, but, as the cell matures and enlarges, the nucleus migrates to the basal end of the strand, where it eventually disintegrates. In the majority of axial cells, the central cytoplasmic strands eventually appear to break down completely, although in some specimens they are quite distinct even in axes which have persisted from one season to the next and which must be at least 1 year old.

Both Phillips (1926) and Feldmann-Mazoyer (1940) have described the penetration of intracellular filaments into the axial cells of *Ceramium*. Similar penetration of the axial cell has been described by Drew (1945) in the genus *Batrachospermum*. The intracellular filaments, which obviously must be regarded as modified lateral branches of limited growth, arise in the cortex and pass into the axial cells. A study of the early stages of penetration confirmed Phillips's observation that the penetration into the axial cell takes place through the pit-connexion between the axial cell and a pericentral cell, but it was not possible to determine the precise position in the cortex from which the filaments had originated. In a single example, it appeared that an intracellular filament had penetrated the basal pit-connexion of an axial cell and passed into the axial cell below. The factors controlling the development of intracellular filaments are unknown. The occurrence of these filaments is relatively rare in the British Isles, but in the three examined specimens in which this phenomenon occurred the majority of axial cells contained intracellular filaments.

Formation of the lateral branches of limited growth

Each of the pericentral cells gives rise to four apical cells, two of which are directed acropetally and two basipetally (Fig. 1). One or more further apical cells may be formed in those species where the cortical band is well developed. The apical cells thus formed segment to produce the much-branched lateral branches of limited growth.

The lateral branches of limited growth derived from a single segment of the principal apical cell of an axis aggregate to form an encircling band of cortex, which is adpressed to the axial cell from which it has arisen. Each cortical band envelops the lower part of the axial cell above, in addition to

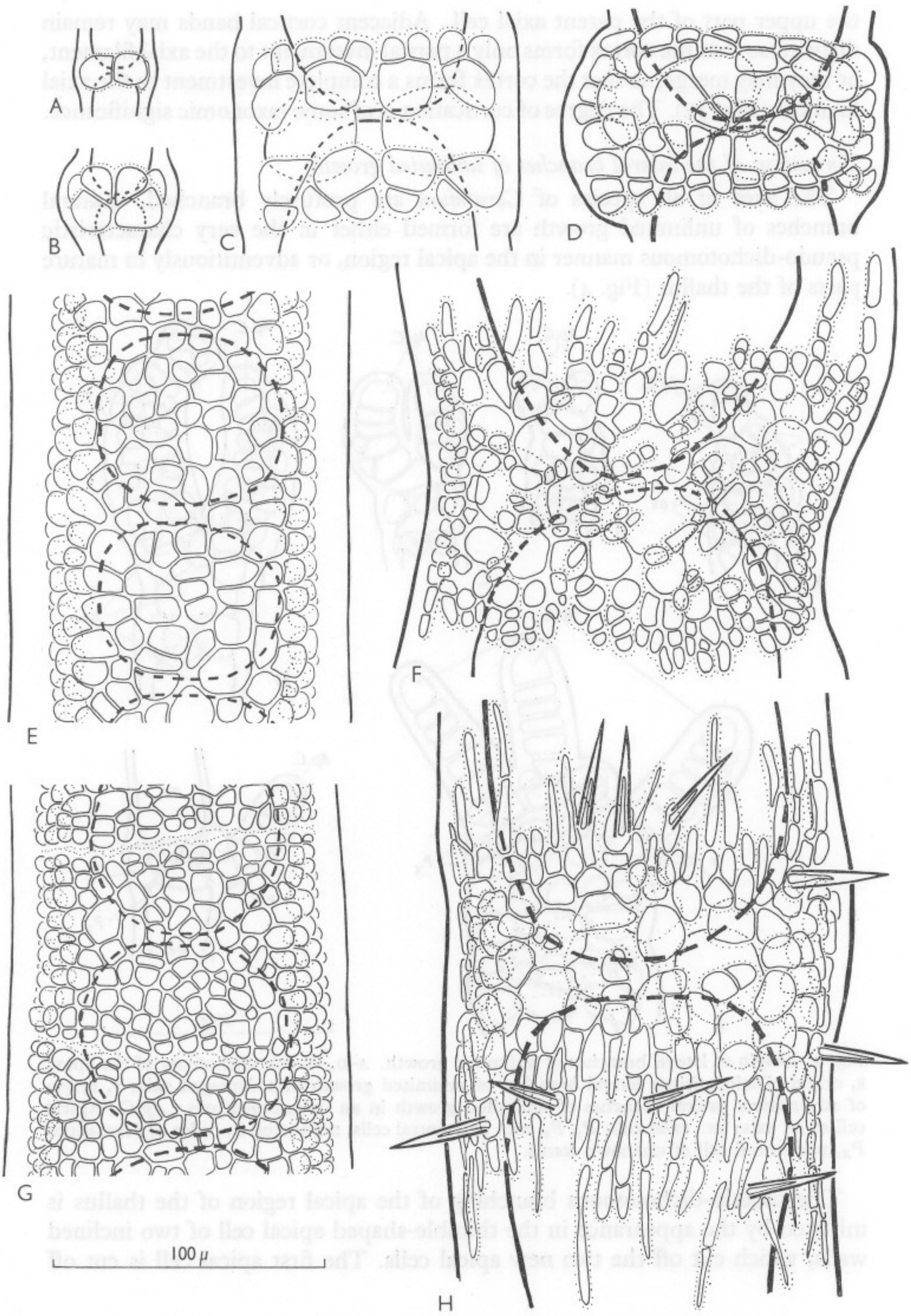

Fig. 3. A–H, Variation in the cortical band in the genus *Ceramium*.

the upper part of the parent axial cell. Adjacent cortical bands may remain distinct, so that the cortex forms only a partial investment to the axial filament, or they may merge, so that the cortex forms a complete investment to the axial filament (Fig. 3E). The degree of cortication is of some taxonomic significance.

Formation of the lateral branches of unlimited growth

The axes of all species of *Ceramium* are profusely branched. Lateral branches of unlimited growth are formed either in the very characteristic pseudo-dichotomous manner in the apical region, or adventitiously in mature parts of the thallus (Fig. 4).

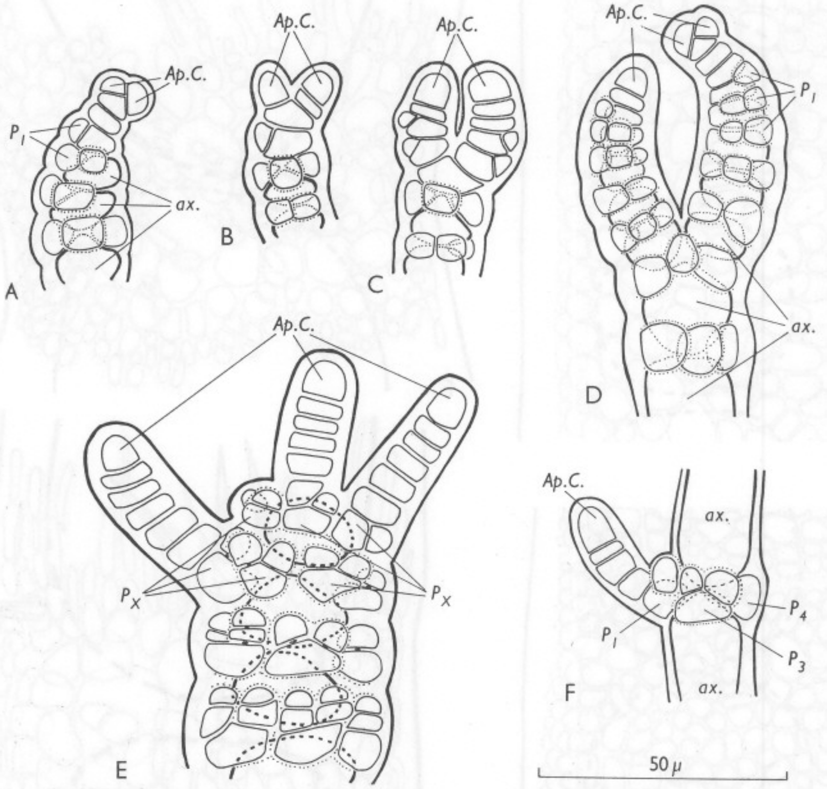

Fig. 4. Origin of lateral branches of unlimited growth. A–D, Pseudo-dichotomy of the apex; E, origin of adventitious lateral branches of unlimited growth in a damaged axis; F, origin of adventitious lateral branches of unlimited growth in an undamaged axis. *Ap.C.*, Apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_X, pericentral cell of unknown status.

The pseudo-dichotomous branching of the apical region of the thallus is initiated by the appearance in the thimble-shaped apical cell of two inclined walls, which cut off the two new apical cells. The first apical cell is cut off eccentrically on the inner face relative to the previous 'dichotomy', whilst the second apical cell is cut off on the outer face, opposite to the first (Fig. 4A, D). As a result of this orientation, the axes of the thallus tend to lie in a single plane, although secondary distortion may disturb the initial arrangement. The two new apical cells segment transversely a number of times before they undergo a further pseudo-dichotomy (Fig. 4A–D). If the growth of the pairs of derivative apical cells is balanced throughout the thallus, then the thallus has a characteristic flabellate appearance, but frequently there are differences in rate of growth between the apical cells of each pair so that the thallus is somewhat racemose.

Adventitious lateral branches of unlimited growth occur frequently in all species of the genus *Ceramium*. They may develop prolifically in apparently normal specimens, although they occur frequently in specimens which have been grazed by animals or damaged in some other way, and in specimens in which tetrasporangia or carposporophytes have developed.

The apical cell of an adventitious lateral branch of unlimited growth is formed by the transformation of the apical cell of a lateral branch of limited growth (Fig. 4E, F). In old, fully developed specimens, after extensive damage, adventitious lateral branches of unlimited growth may arise from any part of the thallus.

The germination of tetraspores *in situ* has been observed on a few occasions, in various species of *Ceramium* (see p. 349), although the phenomenon is not of frequent occurrence, not having been reported by previous investigators. The germlings produced by this 'internal' germination of tetraspores grow out from the parent axis and in this way give rise to a form of 'false branching'. In some examples, the attachment of the germling to the parent is firm and the tissues of the two organisms blend together almost imperceptibly so that it is very difficult to distinguish between an adventitious lateral branch of unlimited growth and the product of 'internal' germination of a tetraspore. In other cases, particularly in those species where the cortical bands form an incomplete investment to the axial filament, the germination of tetraspores *in situ* is very obvious and the attachment is usually very weak so that the germlings are easily detached.

Hairs

Unicellular hairs, similar to those which have been described in numerous species of the Florideae (Berthold, 1882; Möbius, 1892; Rosenvinge, 1911; Feldmann-Mazoyer, 1940) occur frequently in the genus *Ceramium* (Fig. 5A–D). The hairs occur in all parts of the thallus, but normally they are most abundant in the apical regions. A hair may develop from any superficial cell of the thallus. A small uninucleate primordium, with dense granular contents, is cut off from the superficial cell (Fig. 5B, C), which then functions as a basal cell. Rapid elongation takes place, so that when mature the hairs measure up to 100 μ in length. During the process of elongation, the nucleus degenerates and a large vacuole is formed so that the cytoplasm forms a small, meniscus-like mass at the apex of the mature hair. The hairs are thin-walled and very fragile, so that they are easily damaged. Unlike the spines, the hairs cannot withstand desiccation, so that most are destroyed in the preparation of dried herbarium specimens.

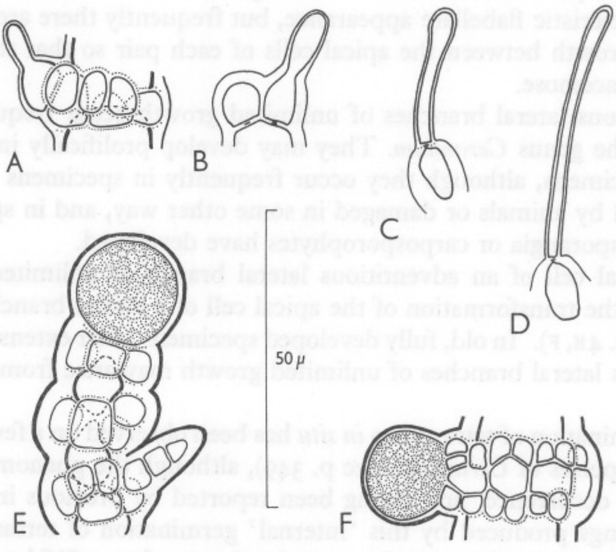

Fig. 5. A–D, Stages in the development of a hair; E, occurrence of *Eurychasmidium tumefaciens* in the apical cell of an axis; F, *E. tumefaciens* in a cell of the cortical band.

Setchell & Gardner (1924, p. 777), in the original description of *C. fimbriatum*, comment on the 'single row of thick, short, unseptate hairs, which are soon deciduous, on the outer curves of the apices'. As figured by these authors (pl. 26, figs. 43, 44), these hairs are much shorter and stouter than the hairs which occur in other species of the genus. Dawson (1954, fig. 55*a*) also gives a figure of this species but it is somewhat crude and little information as to the nature of the hairs can be obtained from it.

Glandular cells

Glandular or vesicular cells ('cellules secretrices', 'Blasenzellen') are widespread in the Ceramiaceae (Kylin, 1915, 1927; Ollivier, 1927, 1928; Feldmann-Mazoyer, 1940). In *Ceramium*, where they were first reported by Reinbold (1906, p. 576), they are formed by the transformation of superficial cortical cells, particularly in the apical regions of the thallus. During development, the cortical cell enlarges slightly, the nucleus and chromatophores degenerate. When mature the contents of the glandular cell are colourless and translucent.

Degeneration takes place very rapidly so that glandular cells tend to be found principally in the apical portions of the axes.

Rhizoids

The thallus is attached to the substrate by unicellular and multicellular rhizoids (Fig. 6). In some species these are formed only at the base of the thallus, but in species of prostrate habit adventitious rhizoids develop from all parts of the plant.

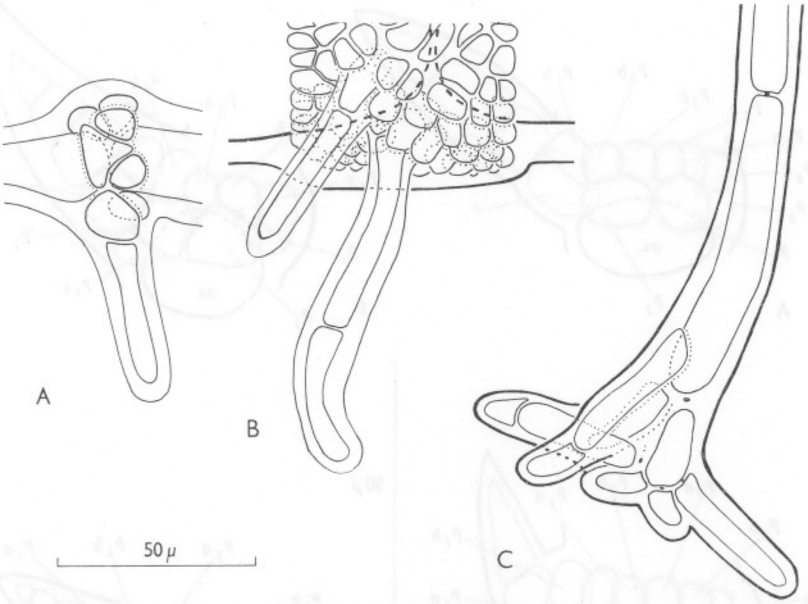

Fig. 6. A–C, Origin and structure of the rhizoids in the genus *Ceramium*.

The rhizoids are formed by the modification of superficial cortical cells. The primordium may remain undivided to form a unicellular rhizoid or it may divide once or twice (Fig. 6B) so that a multicellular rhizoid is formed. Occasionally a number of divisions occur at the apex of a rhizoid giving rise to a multicellular attachment organ (Fig. 6C). Unicellular rhizoids occur more frequently than the multicellular type, but both may be formed from adjacent cortical cells.

The primary basal rhizoid formed in the early stages of development of spore-germlings (see p. 349) frequently penetrates the substrate to which it is attached (Fig. 9D, E), but in most instances the adventitious rhizoids form only a superficial attachment to the substrate. There are some previous reports of the penetration of the substrate by adventitious rhizoids (Feldmann-Mazoyer, 1940), but during the present investigation this has been observed only very infrequently.

Spines

Spine-like structures occur in a number of species of *Ceramium*, of which four occur in the British Isles. In the four British species, spines develop in the meristematic apical regions of the axes, although occasionally they may be formed as adventitious structures in mature fully developed thalli. In order to differentiate between the two types of spine, the former will be referred to as 'primary spines'.

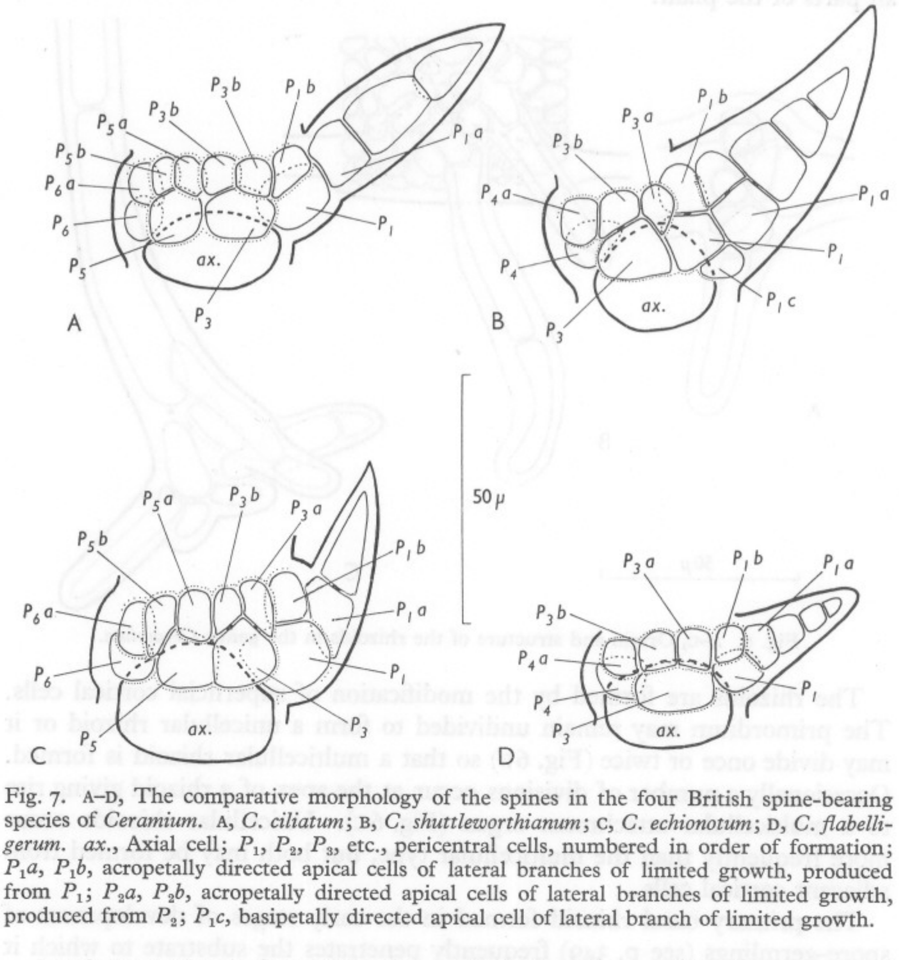

Fig. 7. A–D, The comparative morphology of the spines in the four British spine-bearing species of *Ceramium*. A, *C. ciliatum*; B, *C. shuttleworthianum*; C, *C. echionotum*; D, *C. flabelligerum*. *ax.*, Axial cell; P_1, P_2, P_3, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally directed apical cells of lateral branches of limited growth, produced from P_1; P_2a, P_2b, acropetally directed apical cells of lateral branches of limited growth, produced from P_2; P_1c, basipetally directed apical cell of lateral branch of limited growth.

A primary spine is formed by the modification of one of the two acropetal primordia of lateral branches of limited growth which develop from each pericentral cell. The degree of modification varies from species to species. In all cases, some cells at the base of the lateral branch are incorporated into the cortical band, whilst the terminal cell or cells project to form the spine.

In *C. echionotum* the spine consists only of the terminal cell of the lateral branch of limited growth, whereas in *C. ciliatum*, *C. shuttleworthianum* and *C. flabelligerum*, the spine is formed from a number of cells (Fig. 7A–D). Primordia of lateral branches of limited growth which are to form spines are formed before, and grow very much more quickly than adjacent primordia. Because of this, a spine may be fully developed before the second acropetal primordium of a lateral branch of limited growth is cut off from the parent pericentral cell. The frequency of formation of spines varies considerably in the four species, but, if any spines are formed in a segment, then the first-formed will always occur on the outer face of the axis relative to the previous pseudodichotomy. If more than one primary spine is formed, these will tend to develop from acropetal primordia of adjacent pericentral cells. The conversion into spines of both the acropetal primordia of a given pericentral cell is of very rare occurrence and has been observed only twice by the present author.

Adventitious spines may develop in profusion from any part of the thallus, but they occur usually in the older, more mature parts. In structure the adventitious spines resemble the primary spines, but they are formed by the modification only of the ultimate part of a lateral branch of limited growth. Unlike the primary spines, the orientation of the adventitious spines is not determined and their arrangement is therefore very irregular (Fig. 3H).

Feldmann-Mazoyer (1940, p. 153) has differentiated between the spines found in *C. echionotum* and those of the other species of *Ceramium*, claiming that the spines of *C. echionotum* are modified hairs, whilst those of other species are modified lateral branches of limited growth. The development of the spine in *C. echionotum* will be discussed in detail in a later publication, but it would appear that the incorrect interpretation of the spine structure in *C. echionotum* by Feldmann-Mazoyer results from the failure to study in detail the development of the spine in relation to the development of the cortical band. The spines of *C. echionotum*, like those of *C. ciliatum*, *C. flabelligerum* and *C. shuttleworthianum*, are modified lateral branches of limited growth (Fig. 7A–D).

The occurrence of spines has been reported in a number of other species of *Ceramium*, including: *C. horridum* Setchell & Gardner (1924, p. 777), *C. sinicola* Setchell & Gardner (1924, p. 773), *C. paniculatum* Okamura (1896, p. 36), *C. hamatispinum* Dawson (1950, p. 122), *C. puberulum* Sonder (1845, p. 52), *C. monacanthum* J. Agardh (1894, p. 29), *C. uncinatum* Harvey (1855, p. 257). The spines of *C. monacanthum* are formed by the modification of lateral branches of limited growth, but in other species the information available is so scanty that it is not possible to comment on the origin of the spines. In one or two of the species it would appear from the published figures that the term 'spine' is being used to describe short axes of unlimited growth rather than lateral branches of limited growth; further, detailed investigations of the morphology of the 'spine' in these species are obviously required.

Galls

Superficial gall-like outgrowths, or warts, are of frequent occurrence in the genus *Ceramium*. Chemin (1932) has given an account of the galls found in *C. rubrum*, but apparently he failed to appreciate either the frequency of occurrence of these structures or the taxonomic implications of his observations. Galls have been observed in almost all the British species of the genus during recent investigations (Dixon, unpublished).

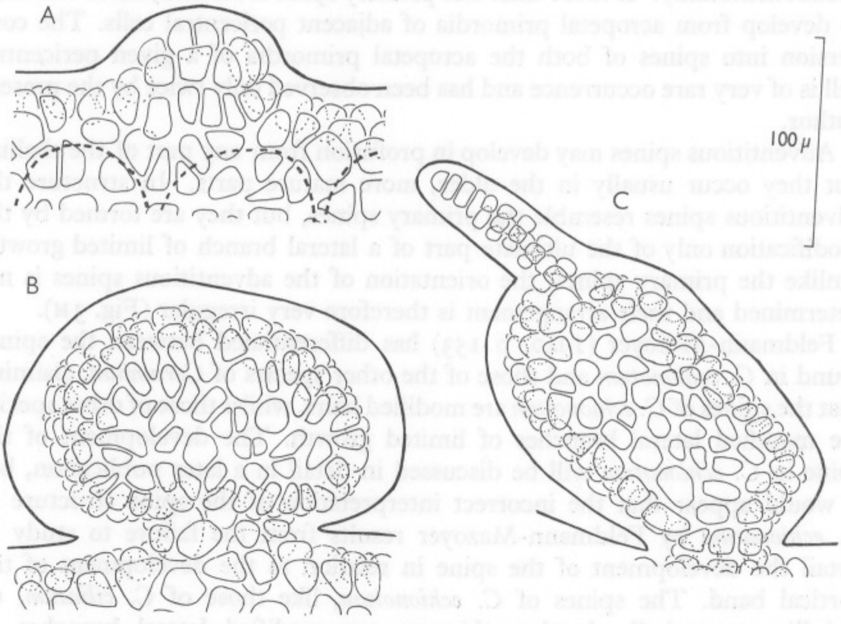

Fig. 8. A, Early stage of development of a gall; B, later stage of development; C, axis differentiating from the tissues of a gall.

Galls occur with varying frequency; some specimens of *Ceramium* may show only a single example, whilst others may be covered with them. All stages of development may occur and it is obvious from a study of their development that these structures are nothing more than proliferations of the outermost cells of the cortex. During the early stages of development (Fig. 8 A) the galls are hemispherical, with a smooth surface, but with age the surface becomes corrugated and in the oldest specimens the proliferations are irregularly lobed. The cells at the periphery of the gall are similar in appearance and size to those of the outermost layers of the cortex, whilst the internal cells are large and often hyaline. In those species of *Ceramium* in which spines are formed, spines may develop also from the surface of the proliferation. This phenomenon appears to have been overlooked by previous investigators, although Kützing (1862, pl. 95*b*, *d*) does give figures of what appear to be galls covered with spines, in *C. monile* (= *C. puberulum*). Hairs, similar to those which develop on the cortical bands, are of frequent occurrence. In one specimen the proliferations were giving rise to structures which resembled normal rhizoids and in another to an axis of unlimited growth (Fig. 8C). The galls are deeply pigmented, red or brown in colour. The largest measure up to 1 mm in diameter and are clearly visible to the naked eye.

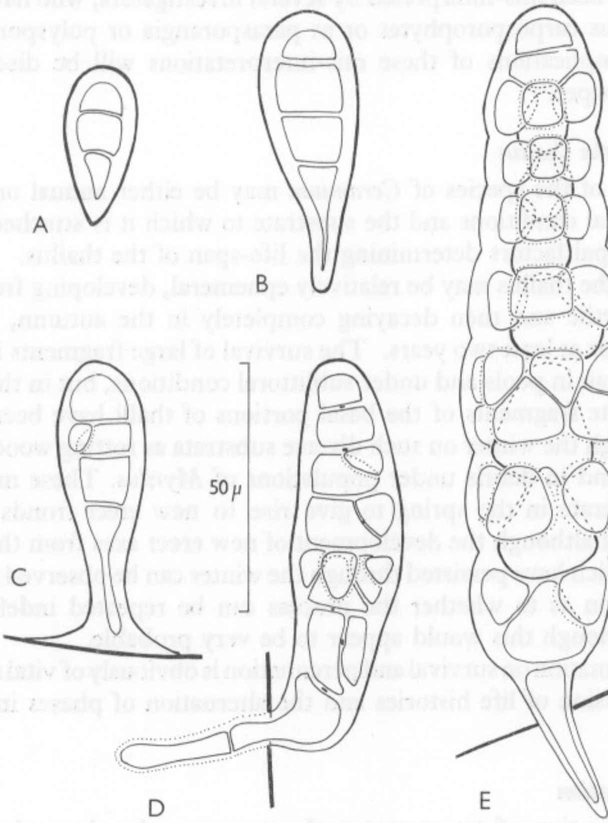

Fig. 9. A–E, Stages in spore germination.

Cantacuzene (1930), as a result of a long investigation of the galls of *Saccorhiza polyschides* and *Chondrus crispus*, has shown that a bacterium occurs in the proliferations of these two species and that similar structures may be produced by inoculation of a culture of this bacterium. Chemin (1932) was unable to offer any explanation for the origin of the proliferations of *C. rubrum*.

It has not been possible to determine the reasons for the development of galls during recent investigations (Dixon, unpublished). No evidence of external damage could be detected even in the youngest examples, neither could the presence of bacteria be detected in fresh or preserved material.

Galls have been mis-interpreted by several investigators, who have regarded them either as carposporophytes or as parasporangia or polysporangia. The taxonomic implications of these mis-interpretations will be discussed in a subsequent paper.

Life-span of the thallus

The thalli of the species of *Ceramium* may be either annual or perennial. Environmental conditions and the substrate to which it is attached appear to be the principal factors determining the life-span of the thallus.

Although the thallus may be relatively ephemeral, developing from a spore, becoming fertile and then decaying completely in the autumn, the thallus may persist for at least two years. The survival of large fragments is relatively rare, other than in pools and under sublittoral conditions, but in the intertidal region, minute fragments of the basal portions of thalli have been shown to persist through the winter on such diverse substrata as rotting wood, concrete, Manx slate and in debris under populations of *Mytilus*. These minute fragments regenerate in the spring to give rise to new erect fronds. It is unfortunate that although the development of new erect axes from these minute fragments which have persisted through the winter can be observed frequently, no information as to whether the process can be repeated indefinitely was obtained, although this would appear to be very probable.

Such information on survival and perennation is obviously of vital importance in any discussion of life histories and the alternation of phases in species of the genus.

Spore germination

The germination of tetraspores and carpospores has been described for various species of *Ceramium* (Derick, 1899; Tobler, 1903; Killian, 1914; Kylin, 1917; Chemin, 1937). All germlings, derived from either carpospores or tetraspores, are of the bipolar type characteristic of the Ceramiaceae. The differences between carpospore and tetraspore germination are insignificant. Little or nothing is known of the germination of the so-called 'polyspores' or 'paraspores'; the only information available is the figure given by Schiller (1913) which is indistinguishable from a similar stage of germination of a carpospore or tetraspore.

In most cases the spore attaches itself to the substrate by a cushion of mucilage and divides to form a principal apical cell and a rhizoid rudiment. The apical cell segments rapidly to form an axis whilst the rhizoid rudiment elongates to form the down-growing basal rhizoid. The rhizoid usually penetrates the mucilage cushion and it frequently grows into the substrate if this is of suitable texture (Fig. 9D, E). The segments produced by the division of the principal apical cell give rise to axial cells and cortical bands in the usual way. Frequently the first-formed cortical bands are slightly aberrent in that development of the band is somewhat restricted, although the pattern of segmentation is normal. In spine-bearing species, the spines may be malformed or even absent in the lowermost segments. The first pseudodichotomy occurs after 12 or even 18 segments have been produced, even in species where only 6 or 7 segments are normally formed between successive 'dichotomies'. At this stage of development, adventitious rhizoids develop from the lowermost cortical bands aiding the attachment to the substrate.

Although not reported by previous investigators, the germination *in situ* of both carpospores and tetraspores has been noted. Previously, it would appear that germination of carpospores *in situ* has been reported only in genera where the carposporangia are enclosed in a compact sterile envelope, i.e. *Bonnemaisonia* (Drew, 1949), *Lemanea* (Mullahy, 1952). In *Ceramium*, where the carposporangia are exposed and the carpospores more easily liberated, such germination *in situ* is surprising, but in a number of examples, the preliminary elongation of the carpospores has been noted and even the formation of the first division wall.

The germination of tetraspores *in situ* occurs more frequently. The mode of division is identical with that of liberated spores, the germlings produced growing epiphytically on the parent axis to produce a type of 'false branching'. The occurrence of such 'false branching' may or may not be very obvious and the rigidity of the attachment of the germling to the parent varies considerably. The occurrence of 'false branching' resulting from the internal germination of tetraspores is easily detected in incompletely corticate thalli, because of the very obvious disturbance of the cell arrangement in the cortical bands. Furthermore, in incompletely corticate thalli the attachment is extremely weak, so that the majority of the germlings are easily detached. In completely corticate thalli, germlings resulting from the germination of tetraspores *in situ* are frequently attached very firmly so that they resemble normal adventitious axes. Occasionally, because of the disturbance of the pattern of segmentation of the parent axis, their origin is obvious, but in most cases detailed microscopic examination is necessary before the product of germination of a tetraspore *in situ* can be distinguished from an adventitious lateral branch of unlimited growth.

In *Ceramium*, the proliferations produced by the internal germination of a tetraspore appear to develop each from a single spore and, without exception, all the examples studied were sterile. Osterhout (1896) has given an account of the *in situ* germination of tetraspores in *Rhabdonia* (= *Agardhiella*) *tenera*, but in this species the germlings are formed, apparently, by the aggregation of the segmentation products of all the four spores of the original tetrasporangium. Furthermore, Osterhout has reported the occurrence on the proliferations in *Rhabdonia* of spermatangia and 'cystocarps' as well as tetrasporangia, in addition to the occurrence of all three types of reproductive structure on the one proliferation; it is obvious that a more detailed examination of *Rhabdonia* is necessary.

The frequency of occurrence of internal tetraspore germination in *Ceramium* varies considerably. A few examples were noted from time to time, but occasionally a plant would be collected in which the majority of tetrasporangia had germinated internally. It is not possible to offer any explanation for this phenomenon.

The germination of tetraspores *in situ* is of considerable importance in any discussion of the occurrence of tetrasporangia and sexual organs on the same thallus. Although Osterhout (1896) commented that 'proliferations resembling those of *Rhabdonia* occur on tetrasporic plants of *Cystoclonium*, *Gracilaria* and other higher Florideae', subsequent investigators appear to have ignored or overlooked the possibility of internal germination of tetraspores in these and other genera of the Florideae.

STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS AND CARPOSPOROPHYTE

Sexual and tetrasporic plants, which are morphologically identical, have been described for most species of *Ceramium*. According to Kniep (1928), most species are dioecious, although Rosenvinge (1924) has reported the occurrence of spermatangia on carpogonial plants of *C. fruticulosum* and a single monoecious plant of *C. pedicillatum* was detected in material collected by Dr J. A. Kitching at Lough Ine, Ireland. The life history is interpreted generally as a regular sequence of sexual, carposporic and tetrasporic phases, but there is little direct evidence to support this assumption (Petersen, 1928; Westbrook, 1935). As in other genera of the Ceramiaceae (Kniep, 1928; Drew, 1944), there have been reports of the occurrence of sexual organs and tetrasporangia on the same thallus, as follows:

C. ciliatum, tetrasporangia and carposporophytes (Woronichin, 1909)
C. circinatum, spermatangia and tetrasporangia (De Toni, 1922)
C. pedicillatum, tetrasporangia and sexual organs (Davis, 1910)
C. rubrum, tetrasporangia and sexual organs (Davis, 1905).

It should be noted that in a number of species tetrasporic plants have a much wider distribution, extending further to the north, than the sexual plants. Accessory methods of reproduction ('polysporangia' and 'parasporangia') occur in a number of species, whilst Chemin (1928) and other authors have described vegetative propagation.

Tetrasporangia

The tetrasporangia of *Ceramium* are produced in the cortical bands, developing laterally from cells of the lateral branches of limited growth. The number of tetrasporangia formed in a given cortical band varies considerably. In those cortical bands where a single tetrasporangium develops, it is formed always in the second position, that is, on the outer face of the axis relative to the previous 'dichotomy'. In most species, however, a number of tetrasporangia are produced in each cortical band, distributed in a whorl, or, where the number is excessively large, irregularly arranged (Fig. 10).

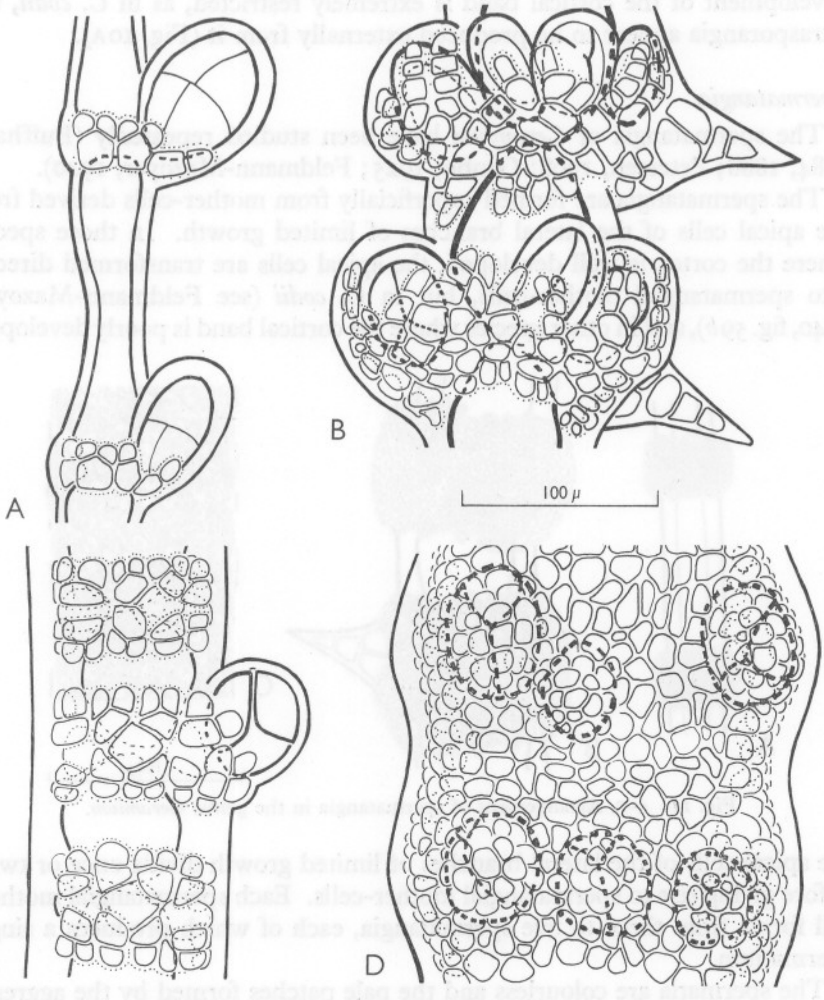

Fig. 10. A–D, Arrangement of tetrasporangia in the genus *Ceramium*.

The primordia of tetrasporangia are relatively small, but when mature the tetrasporangia measure 30–110 × 20–60 μ. The division is usually tetrahedral, although a cruciate arrangement of tetraspores has been reported in a number of species (cf. Rosenvinge, 1924, p. 373). In the British Isles, the cruciate arrangement occurs frequently in certain species (Fig. 10A).

The degree of emergence of the mature tetrasporangium from the cortical band is determined by the size of the sporangium and the extent of development of the band (Fig. 10A–D). In those species with continuous cortication, the tetrasporangia tend to be immersed completely (Fig. 10D), whilst in those species with interrupted cortication, they are partially emergent. Where the development of the cortical band is extremely restricted, as in *C. codii*, the tetrasporangia appear to be produced externally from it (Fig. 10A).

Spermatangia

The spermatangia of *Ceramium* have been studied repeatedly (Buffham, 1884, 1888; Petersen, 1908; Grubb, 1925; Feldmann-Mazoyer, 1940).

The spermatangia are formed superficially from mother-cells derived from the apical cells of the lateral branches of limited growth. In those species where the cortex is well developed, the apical cells are transformed directly into spermatangial mother-cells, but in *C. codii* (see Feldmann-Mazoyer, 1940, fig. 59*b*), and in other species where the cortical band is poorly developed, the apical cells of the lateral branches of limited growth divide once or twice before giving rise to spermatangial mother-cells. Each spermatangial mother-cell forms from three to five spermatangia, each of which produces a single spermatium.

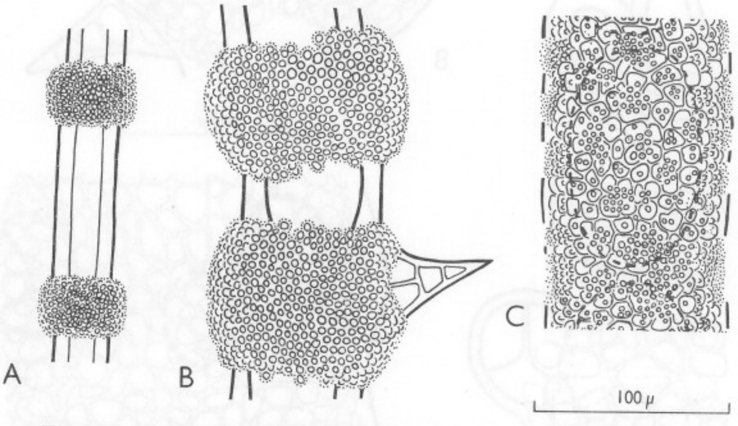

Fig. 11. A–C, Arrangement of spermatangia in the genus *Ceramium*.

The spermatia are colourless and the pale patches formed by the aggregation of spermatangia are very characteristic. Where the cortical bands are distinct, the entire surface of each band is covered with spermatangia, but where the cortical bands are confluent, the spermatia tend to form patches of irregular outline (Fig. 11).

The carpogonial branch and the development of the carposporophyte

Although the carpogonial branch and carposporophyte of *Ceramium* have been investigated repeatedly (Janczewski, 1876; Phillips, 1897; Kylin, 1923; Rosenvinge, 1924; Miranda, 1929*a*, *b*; Dammann, 1930) the details of their development given by the different authors are somewhat contradictory. Many of the accounts are fragmentary and it may be that the confusion results from the inadequate examination of a number of different species. A full investigation of the structure and development of the carpogonial branch and carposporophyte throughout the genus *Ceramium* is urgently required.

In all investigated species of *Ceramium*, a pericentral cell functions as the supporting cell of the carpogonial branch. As far as can be ascertained, the supporting cell is always derived from the first-formed pericentral cell of a segment, so that the carpogonial branch develops in the second position, that is on the outer face of the axis relative to the previous 'dichotomy'. In sexual thalli, the carpogonial branches are produced intermittently. Frequently, the first-formed pericentral cells from a number of adjacent segments in an axis are converted into supporting cells; such fertile regions occur at intervals along the axes separated by sterile regions. The number of supporting cells produced in depauperate specimens is reduced considerably, so that carpogonial branches occur only at infrequent intervals.

As in all Ceramiaceae, the carpogonial branch is four-celled. The carpogonium is relatively small, but the trichogyne reaches a length of up to 50 μ. The cells of the carpogonial branch are smaller than the adjacent cells of the cortical band. The conversion of the first-formed pericentral cell into the supporting cell and the formation of one or more carpogonial branches disrupts the regular pattern of development of the cortical band. A supporting cell is larger than the normal first-formed pericentral cell from which it is derived and only one or two of the four lateral branches of limited growth normally formed from a pericentral cell are produced by a supporting cell. As a result of the disturbance of the pattern of segmentation, the position of a carpogonial branch can be detected relatively easily. It should be noted that the hairs, which may bear a superficial resemblance to trichogynes, are merely added to the normal vegetative structure, with no disturbance at all.

According to Kylin (1923, p. 63) a single carpogonial branch is formed from each supporting cell in *C. rubrum*, although in material of this species from the Channel Islands (Dixon, unpublished), the formation of two carpogonial branches from the same supporting cell was observed in a number of specimens. Janczewski, Phillips and Rosenvinge have reported the occasional formation of two carpogonial branches in other species of the genus.

A detailed study has been made of the development of the carpogonial branch in a species of the *C. diaphanum/strictum* complex (sensu Feldmann-Mazoyer, 1940), collected near Prah Sands, Cornwall. In this material, the formation of two carpogonial branches from a supporting cell occurred frequently (Fig. 12B), but such supporting cells were intermixed with others from which only a single carpogonial branch had developed (Fig. 12C, D). No explanation can be offered to account for this phenomenon.

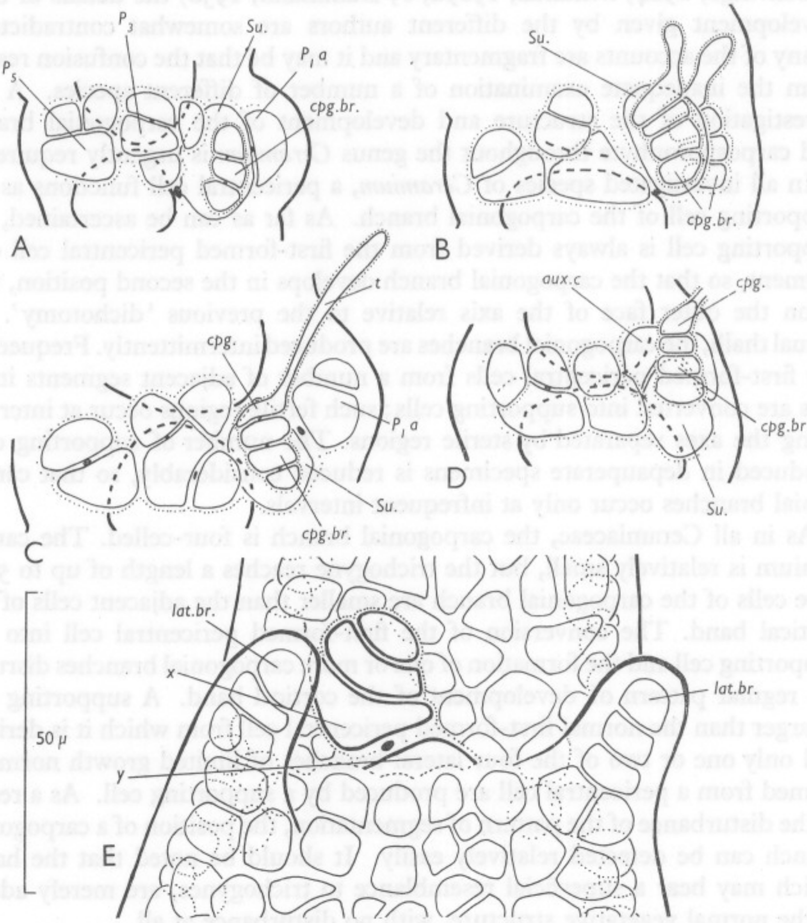

Fig. 12. A, B, Development of the carpogonial branch; C, mature carpogonial branch; D, early post-fertilization stage; E, initial stage in the development of the carposporophyte. *aux.c.*, Auxiliary cell; *cpg.*, carpogonium; *cpg.br.*, carpogonial branch; *lat.br.*, adventitious lateral branch of unlimited growth; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, acropetally directed apical cell of lateral branch of limited growth, produced from P_1; *Su.*, supporting cell, formed by the modification of the first-formed pericentral cell; *t.*, trichogyne; *x.*, *y.*, cells at the base of the carposporophyte, whose origin cannot be stated with certainty.

As in all Ceramiaceae, the auxiliary cell is cut off from the supporting cell subsequent to fertilization (Fig. 12D).

Details of the development of the carposporophyte are a little confused. Various authors have given a few observations on stages of development in certain species, but the absence of an over-all survey of carposporophyte development throughout the genus is a serious deficiency. Taking into account both personal observations and the descriptions of previous authors, it is possible to summarize the information available in a general way. It is thought that communication is established between the carpogonium and the auxiliary cell, and that subsequently one or more primordia are formed from the auxiliary cell. There are differences of opinion (cf. Kylin, 1923; Miranda, 1929*b*) as to whether the auxiliary cell divides into two cells before the formation of primordia. The further development of the carposporophyte results from the segmentation of these primordia. Fusions between certain cells have been reported by most previous investigators, but it must be stated that there is some evidence from personal observations to indicate that the fusions are not obligatory and that the cells involved are not always determined specifically. It is obvious that careful and detailed investigations are necessary for the solution of these problems.

The young carposporophyte forms a cluster of cells on the surface of the thallus (Fig. 12E). Because of the orientation of the carpogonial branches, the carposporophyte frequently lies on the outer side of the axis relative to the previous 'dichotomy'. The carposporophyte is situated usually in a small depression in the side of the axis (Figs. 12E, 13A, B), resulting from the diminished enlargement of the adjacent axial cells and the absence of some of the lateral branches of limited growth from the pericentral cell which developed into the supporting cell. As the carposporophyte enlarges, adventitious lateral branches of unlimited growth are formed from filaments of limited growth of the segment below it. The number of adventitious axes thus formed is often very characteristic, for instance in *C. shuttleworthianum* a single adventitious axis is produced, whilst in other species up to five or even seven such axes may be formed. The growth of these axes is restricted so that they rarely exceed 2 mm in length. When fully mature, the carposporophyte is encircled by these axes which form a loose, incomplete involucre.

Accessory methods of reproduction

Sporangia containing more than four spores, to which the terms 'polysporangium' and 'parasporangium' have been applied, have been reported in several species of *Ceramium*. Throughout the Florideae, the application of these terms is extremely confused. Schiller (1913) attempted to differentiate between the two types of sporangium, but in *Ceramium*, the system suggested by him proved to be inapplicable (cf. Rosenvinge, 1924, p. 399). Drew (1937, 1939), as a result of detailed cytological and morphological studies of selected examples of sporangia, has suggested that in the Florideae the sporangia containing more than four spores are of two categories, (*a*) those which are *not* homologous with tetrasporangia and which are purely accessory, e.g. the 'parasporangia' of *Plumaria elegans* (Drew, 1939), (*b*) those which *are* homologous with tetrasporangia, e.g. the 'polysporangia' of *Spermothamnion snyderae* (Drew, 1937) and other Florideae (Westbrook, 1930), but the lack of data has prevented the general acceptance of this scheme and the terms 'polysporangium' and 'parasporangium' are still applied indiscriminately by different authors to the same structure. In the genus *Ceramium* the position is complicated by certain authors failing to recognize gall-like proliferations which have been misidentified and described as 'parasporangia' or 'polysporangia'. In the following account a number of descriptions have had to be discounted because of the possibility of such confusion in the absence of an illustration (e.g. Kylin, 1907).

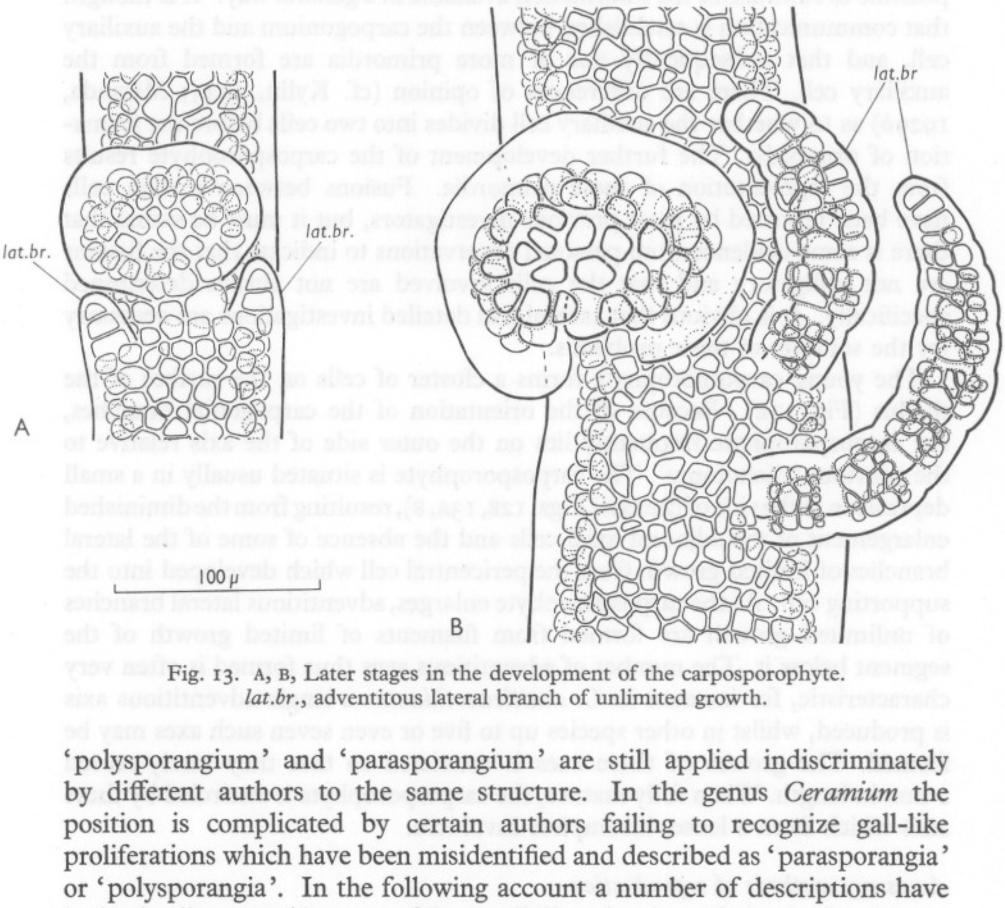

Fig. 13. A, B, Later stages in the development of the carposporophyte. *lat.br.*, adventitous lateral branch of unlimited growth.

There are two types of accessory reproductive structure in species of the genus *Ceramium*. These differ in structure, position and development.

Lateral sporangia, which contain from five to twelve spores, and which bear a close resemblance to tetrasporangia, have been figured in a number of species, including *C. diaphanum* (Petersen, 1908, figs. II and IV), *C. strictum*

(Lakowitz, 1929, fig. 491), '*C. deslongchampsii*' (Rosenvinge, 1924, fig. 321) and *C. vertebrale* (Rosenvinge, 1924, fig. 325). There are no reports of the occurrence of these sporangia in the British Isles, and despite a widespread search during the past seven years, no indication of their occurrence could be found. Although little is known about the development of these lateral sporangia, from the figure given by Rosenvinge (1924, fig. 313) it would appear very probable that these sporangia should be interpreted as modified tetrasporangia and the term 'polysporangia' applied to them. A detailed cytological study of their development is urgently required. It should be noted that there is one difference between the lateral sporangia and tetrasporangia in that tetrasporangia are embedded in the cortical band, whilst the lateral sporangia are formed superficially. No information is available on the mode of germination of the 'polyspores' or of their significance in relation to the life-histories of the species in which they occur.

There have been numerous confusions between galls and the lateral 'polysporangia'. The figure of *Gongroceras agardhianum* given by Kützing (1862, pl. 77) has been a constant source of confusion. A study of the specimen on which this figure is based (now in the Rijksherbarium, Leiden) proves beyond doubt that the structures illustrated by Kützing are galls, but the figure has been copied repeatedly by subsequent authors (Lakowitz, 1929, fig. 485; Kylin, 1937, fig. 117D, 1956, fig. 28D; Oltmanns, 1904, fig. 425.4, 1922, fig. 563.4; Schiller, 1913, fig. 1), the galls being described variously as 'polysporangia' or 'parasporangia'. The report by Phillips (1926) of the occurrence of 'parasporangia' in a specimen of *Ceramium* collected in Anglesey is also based upon a misinterpretation of galls, whilst it would appear that both van Goor (1923) and Feldmann-Mazoyer (1940) have made the same error in their interpretation of *C. deslongchampsii*. The figure of *C. tenuissimum* with 'parasporangia', given by Feldmann-Mazoyer (1940, fig. 113 p) is almost certainly based upon a gall.

It is to be regretted that the failure to detect any of these structures during extensive collecting of species of the genus *Ceramium*, undertaken throughout the British Isles during the last seven years, has prevented any detailed investigation of their structure, development and significance. In view of the many confusions between the galls and lateral 'polysporangia', the similarity between the few figures of the early stages of development of 'polysporangia' and the initiation of a gall and the lack of information on the development and germination of 'polyspores', the possibility that all supposed 'polysporangia' are nothing more than galls cannot be rejected.

The second type of structure, which consists of an irregularly shaped mass of spores, is formed only in an apical position. The first report of the occurrence of these structures was made by Kützing (1863, p. 1, pl. 1) in his account of *Hormoceras acrocarpum*, whilst Schiller (1913) has given a detailed account of their structure and development in *Ceramium strictum*. According to Schiller, the specimens occurred in an area of the Adriatic Sea where there was heavy pollution by sewage. Feldmann-Mazoyer (1940) has given a report of similar structures in *C. diaphanum*, but in the ecological notes she makes no mention of organic pollution. This type of structure does not appear to have been reported outside the Mediterranean. Nothing is known of the early stages of development, but the origin of the spore-masses by the modification of a tetrasporangium would appear to be very improbable. Schiller (1913, fig. 18) has given a figure of a young stage of germination of a spore from one of these spore-masses but the subsequent development of the germlings is unknown. Although nothing is known of their cytology or of their significance in relation to the life histories of the species in which they occur, the application of the term 'parasporangium' to these spore-masses would appear to be justified, pending a more detailed cytological and cultural investigation.

Finally, Richard (1901), in the original description of *Ceramothamnion codii* (= *Ceramium codii* (Richards) Mazoyer), described, in addition to male and tetrasporic plants, a third type of thallus in which occurred spore-masses of a type very different from those described by Schiller. The spore-masses of *Ceramium codii* are subtended when mature by a group of adventitious axes, and, because of this, they bear a close resemblance to carposporophytes. The early stages of development of these spore-masses (Richards, 1901, pl. 22, figs. 17, 18) are not very clear and Richards, in the absence of any indication of a carpogonium, regarded the spore-masses as 'polysporangia'. Collins & Hervey (1917, p. 134) admit that the supposed 'polysporangia' are 'quite indistinguishable from cystocarps' but state that the failure to detect the procarp is a strong argument against such an identification, although Howe (1918), commenting on the 'alleged polysporangia of non-sexual origin where one would naturally expect cystocarps of sexual origin', has suggested that the 'alleged polysporangia...are in reality cystocarps'. *C. codii* has been reported in the British Isles (Dixon, 1958), but only in a sterile condition, so that further investigation of the spore-masses, which is obviously desirable, has not been possible.

Petersen (1908, p. 14) comments briefly on the occurrence of 'monospores' in *C. diaphanum*, but the basis for this report is not at all clear. As Rosenvinge (1924, p. 374) has commented, the citation by Petersen of a figure by Gobi (1877, fig. 8) is particularly baffling. It must be admitted that Gobi's figure is not particularly well drawn, but the structures are described by him as 'Tetrasporen', and, as Rosenvinge has commented, the structures in question are tetrasporangia, the division of which is not shown.

Vegetative propagation

There is considerable experimental evidence in various species of *Ceramium* to show that new thalli can arise from detached fragments of the axes (Oltmanns, 1895; Massart, 1898; Tobler, 1906; Chemin, 1928). Rhizoids develop adventitiously from the cells of the cortical bands so that the fragment becomes attached to the substrate, and then new apices regenerate in the manner already described (see p. 341).

FUNGAL INFECTIONS

There are numerous records of fungal infections in species of *Ceramium*, but little is known of the occurrence of these fungi in the British Isles. The nomenclature adopted in the following account is based essentially on that of Sparrow (1943).

Eurychasmidium tumefaciens (Magnus) Sparrow. Magnus (1872, 1875) described and figured *Chytridium tumefaciens* occurring in the axes and rhizoids of *Ceramium acanthonotum* (= *C. shuttleworthianum*) and *C. flabelligerum*. Subsequently transferred to the genera *Olpidium* (Wright, 1879) and *Pleotrachelus* (Petersen, 1905), the species was ultimately made the type species of a new genus *Eurychasmidium*, by Sparrow (1936), because of the biflagellate zoospores. The organism studied by Sparrow occurred in the cells of the cortical band and in the apical cells of *Ceramium diaphanum*, but was absent from the rhizoids. It has been suggested subsequently by Feldmann & Feldmann (1956) that two distinct fungi had been confused by Magnus (1872, 1875) in his original description of *Chytridium tumefaciens*. According to these authors, one organism (that studied by Sparrow) was restricted to the apical cell and the cells of the cortical band, whilst the other occurred only in the rhizoids. The latter entity was described as a new species under the name *Olpidiopsis magnusii*. Because of possible confusion between these two organisms, previous reports of the occurrence of *Eurychasmidium tumefaciens* must be regarded with caution, but it would appear that there have been no reports of the occurrence of this species in the British Isles since the early Irish record of Wright (1879). This is surprising in view of the frequency with which it has been collected on various species of *Ceramium* from many different localities (Dixon, unpublished). The fungal thallus develops within a superficial cell of a cortical band, or in an apical cell. The infected cell increases in size so that it forms, on the surface of the thallus, a spherical or hemispherical protuberance, which is extremely prominent due to its highly refractive contents, its thick wall and its size (Fig. 5E, F). Following infection of a cell of the cortical band, the development of adventitious lateral branches of unlimited growth was noted only in a few examples, but Sparrow (1936, 1943) comments that in the material of *C. diaphanum* examined by him, the development of adventitious lateral branches of unlimited growth, subsequent to infection, is of very frequent occurrence, and that, as a result, the axes of the host species have a characteristic 'bushy' appearance, which is a useful indication of the site of infection. Sparrow mentions the infection of the apical cell of the host species but states that this causes little hypertrophy. In the

British material examined, the infection of the apical cell occurred very frequently with considerable effect on the appearance of the host. Cessation of apical growth of the axes was followed, in most cases, by the development of adventitious lateral branches of unlimited growth, such as are formed whenever the apical cell of an axis is damaged or destroyed. Feldmann & Feldmann (1956) suggest that the sites of infection of *Eurychasmidium tumefaciens* and *Olpidiopsis magnusii* are quite distinct, but from a superficial examination of the British material collected personally it would appear that this suggestion may not be fully justified. A more detailed investigation of the two supposed species and their characteristics is obviously required.

Chytridium megastomum Sparrow. Described originally by Sparrow (1934) as a parasite on *Striaria attenuata*, this fungus was detected subsequently at Woods Hole (Sparrow, 1936) as a parasite on *Ceramium diaphanum*. There is no evidence of its occurrence in the British Isles.

Pontisma lagenidioides Petersen. This fungus is restricted to species of *Ceramium*, occurring usually in the axial cells or the innermost cells of the cortical bands. *Pontisma lagenidioides* is widely distributed, occurring in various species of *Ceramium*: Denmark (Petersen, 1905), in *C. rubrum*, *C. strictum* and *C. fruticulosum*; Sweden, Gullmar Fjord (Aleem, 1955), in *C. diaphanum*; Germany, Kiel Bay (Höhnk, 1940), in '*Ceramium* sp.'; France, Banyuls (Aleem, 1950), in *C. diaphanum*; France, Roscoff (Feldmann, 1954; Feldmann & Feldmann, 1956), in *C. tenuissimum*; U.S.A., Woods Hole (Sparrow, 1936), in *C. diaphanum*. According to Sparrow (1943), *Pontisma lagenidioides* is found most commonly in dead or decaying material. In the British Isles it has been detected on two occasions, in a decaying specimen of *Ceramium strictum* collected in the drift at Port Erin, Isle of Man, and in a specimen of *C. diaphanum* collected *in situ* by Dr J. A. Kitching, at Lough Ine, Ireland.

Rhizophidium discinctum Petersen. Described originally from Scandinavia on various Chlorophyta, this species was detected subsequently on *Ceramium diaphanum* maintained in a laboratory aquarium for several days (Sparrow, 1936). There is no evidence of its occurrence in the British Isles.

Thrausochytrium proliferum Sparrow. Described originally by Sparrow (1936), as a saprophyte in *Bryopsis plumosa* and *Ceramium diaphanum*, there are no indications of the occurrence of this species in the British Isles.

Chytridium polysiphoniae Cohn. Cohn (1865) described this fungus as a parasite on *Polysiphonia violacea*; subsequently it has been detected on various marine algae, including *Ceramium*: Denmark, in *C. rubrum*, *C. strictum* (see Petersen, 1905); *C. fruticulosum* (see Sparrow, 1934); U.S.A., Woods Hole (Sparrow, 1936), in *C. rubrum*. Specimens probably referable to this species have been detected in the British Isles (Dixon, unpublished) on other host species, but not on species of *Ceramium*. According to Sparrow (1943), *Chytridium polysiphoniae* is undoubtedly a 'composite' species in need of detailed investigation.

Petersenia pollagaster (Petersen) Sparrow. Reported originally in Denmark by Petersen (1905), in *Ceramium rubrum*, and again by Sparrow (1934) in '*Ceramium* sp.', it is very probable (teste Aleem, 1955) that this species is not distinct from *Petersenia lobata* (Petersen) Sparrow, which has been collected from a variety of host species in Denmark (Petersen, 1905; Sparrow, 1934), the United States (Sparrow, 1936) and Sweden (Aleem, 1955). Neither entity has been detected in the British Isles.

Olpidiopsis andreei (Lagerhaim) Sparrow. There is some doubt concerning the occurrence of this fungus in *Ceramium*. Sparrow (1934, 1936, 1943) has reported the occurrence of a '*Pleotrachelus*-like' fungus in *Ceramium diaphanum*, which is probably referable to *Olpidiopsis andreei*, whilst Aleem (1950) has identified as *O. andreei* a fungus collected in *Ceramium diaphanum* at Banyuls. As this species occurs most frequently in genera of the Chlorophyta and Phaeophyta, the reports of its occurrence in *Ceramium* should be treated with caution.

Olpidiopsis magnusii Feldmann & Feldmann. It has been suggested by Feldmann and Feldmann that the previous reports of *Eurychasmidium tumefaciens* refer to two different organisms (see p. 359). These authors have separated what they consider to be the two forms and have described *Olpidiopsis magnusii*, as occurring in the rhizoids of *Ceramium flabelligerum* at Roscoff (Feldmann, 1954; Feldmann & Feldmann, 1956). An organism similar to that described by these authors has been collected on two occasions in specimens of *C. flabelligerum*, but in addition to the infection of the rhizoids, cells of the cortical bands of these specimens were also infected, with the fungus similar to *Eurychasmidium tumefaciens*. Unfortunately, the specimens had been fixed before examination so that detailed study was impossible, but it is obvious that a detailed investigation of the two species and their supposed characteristics is urgently required.

Pythium marinum Sparrow. *P. marinum* was described originally by Sparrow (1934), occurring saprophytically on *Ceramium rubrum* in Denmark. There is no indication for its occurrence in the British Isles.

Pythium maritimum Höhnk. Höhnk (1940) collected at Kiel a species of *Pythium*, growing saprophytically on '*Ceramium* sp.'. From the illustration given by Höhnk (1940, fig. 4) the host species cannot be determined with certainty, but it would appear to be a species of the *diaphanum/strictum* complex (sensu Feldmann-Mazoyer, 1940). Höhnk claimed that this species of *Pythium* differed in certain respects from *P. marinum* Sparrow and it was therefore described as a new species under the name *P. maritimum*. There are no reports of the occurrence of *P. maritimum* in the British Isles. The differences between *P. marinum* and *P. maritimum* do not appear to be very significant and it is to be regretted that an authoritative opinion as to the status of these two entities is not available, as the description of *P. maritimum* would appear to have been overlooked in the most recent monograph of the genus (Middleton, 1943).

Aleem (1955, p. 25) has given a brief account of an organism of uncertain affinity, found in the cortical cells of *Ceramium rubrum*, near Kristineberg, Sweden, which he compared with *Pyrrhosorus marinus*, described by Juel (1901) from material of *Cystoclonium purpureum* from the same area. The observations of Aleem are extremely brief, being based upon a single collection, and in view of the possible complexity of the life history of this organism, the report should be treated with caution until more detailed observations are available.

THE VALIDITY OF CRITERIA USED FOR SPECIFIC AND VARIETAL SEPARATION

At the present time, the taxonomy of the genus *Ceramium* is in a state of chaos. This is the result of the failure of phycologists to refer back at all times to original authentic material and the failure to recognize and interpret seasonal and environmental modifications of the external form of the thallus. The search for nomenclatural type specimens is frequently a long and laborious task but, with patience, it is usually possible to locate the authentic material. In order to overcome the second difficulty, the value of the features used for the separation of species must be assessed critically. Frequently, the characters by which different supposed taxa are reputedly distinguished prove on detailed examination to have no real significance. It is obvious that a critical survey of the validity of the criteria used for specific and varietal separation is essential if these difficulties are to be overcome.

The morphological features used by previous authors for the separation of species and varieties in the genus *Ceramium* are as follows: (1) the number of pericentral cells, (2) the development of the cortical band, (3) the dimensions of the axial cells, (4) the 'index of cortication', (5) the occurrence of adventitious lateral branches of unlimited growth, (6) the distance between pseudo-dichotomies, (7) the curvature of the apices, (8) the spines. Each of these morphological features will now be discussed in detail.

The number of pericentral cells

From four to ten pericentral cells are formed from each segment of the apical cell of an axis of unlimited growth. The number of pericentral cells produced varies from species to species, but it is relatively constant for each species. This feature has been used by some previous investigators, but it must be applied with care, because of the slight variation which does occur. A species with seven pericentral cells, where segments with six and eight pericentral cells occur occasionally, can be distinguished readily from a second species where four pericentral cells occur constantly.

As Phillips (1926) has stated, the number of pericentral cells can be estimated accurately only by tracing the pit-connexions with the axial cell. Usually the number of pericentral cells can be counted in a transverse section with a fair degree of accuracy, even if the pit-connexions are not located, but in old material errors may be introduced by this technique, as it is possible for a cell derived from a pericentral cell to intercalate itself into the ring of pericentral cells. Although the pericentral cells are often visible in a side-view of an axis, attempts to count them in this position are unlikely to be successful, particularly with the larger numbers.

The development of the cortical band

The appearance of the cortical band is the principal diagnostic feature in the genus *Ceramium*. Despite its importance, there have been no critical studies of the features controlling the development of the band and little regard for the modifying effects of season and environment. The different types of cortical construction exhibited by the various species of *Ceramium* can all be related to the patterns of cell division and cell enlargement occurring in the branches of limited and unlimited growth. The cortical band itself may be regarded as a cylindrical structure formed by the aggregation of the filaments of limited growth which are orientated radially as well as acropetally and basipetally.

The radial dimensions of the cortical band are determined by the degree of enlargement of the pericentral cells and their immediate derivatives, together with the extent of growth of the radially orientated filaments of limited growth. Of these two factors the former is by far the more important. The enlargement of the pericentral cells and their immediate derivatives occurs quite independently of the enlargement of the axial cells. As a result, the outline of the axes may be regularly cylindrical if the enlargement of the axial cells and the radial growth of the cortical band is balanced, or the axes may be constricted or inflated at the cortical bands if there is any marked difference between the enlargement of the one and the radial growth of the other.

The length of the cortical band produced at each segment of an axis is determined by two factors: (1) the number of divisions of the apical cells of the lateral branches of limited growth, (2) the degree of enlargement of the cells of the lateral branches of limited growth. Variation in the length of the cortical band results from variation of one or both of these factors.

In certain species, the apical cells of the lateral branches of limited growth may cease to divide at a very early stage of development, so that any increase in the length of the cortical band is caused entirely by increase in cell size. This is in fact relatively restricted, so that in these species there is very little variation in the dimensions of the cortical bands as the thallus ages. In those species where the apical cells of the lateral branches of limited growth continue to divide throughout the life of the thallus, there may be considerable variation in the dimensions of the cortical bands. Where the apical cells of the lateral branches of limited growth continue to divide throughout the life of the thallus, the acropetal and basipetal margins of the cortical bands are either sharply defined and parallel to one another (Fig. 3 G) or very diffuse and ill-defined (Fig. 3 H), according to whether the divisions of the apical cells take place synchronously or irregularly. Finally there may be marked differences between the growth of the acropetal and basipetal faces of a cortical band resulting from differences in the rates of cell division and cell enlargement.

It should be noted that in those species where the cortex forms a continuous investment to the axial filament, it is often difficult to ascertain the limits of the cortical bands as the lateral branches of limited growth of adjacent segments merge with one another.

In conclusion it may be stated that the appearance of the cortical band is perfectly adequate as a diagnostic character, providing that the patterns of cell division and cell enlargement are interpreted correctly.

The dimensions of the axial cells

An axial cell is derived from each segment of a principal apical cell; after the formation of pericentral cells, no further divisions occur and the resulting axial cell merely increases in size. The ultimate dimensions of an axial cell are determined by its position in the thallus and the pattern of cell enlargement is extremely complex. The dimensions of the axial cells are of obvious importance in that they determine the dimensions of the frond. In order to investigate the pattern of cell-size variation, measurements were made of every axial cell in plants of various species collected from a wide range of environments from different parts of the British Isles. Although there are considerable fluctuations in the dimensions of the axial cells, both between species, and even in the same species, the same general pattern of variation was detected in all the thalli examined.

The over-all range of size of the axial cells is shown by a comparison of the average length and volume of these cells in successive sectors of the thallus, from base to apex. In this connexion, the term 'sector' is applied to the portion of the thallus between successive 'dichotomies'. If the average length of the axial cells in each sector is calculated, the average length per sector increases from a minimum value immediately behind an apex to reach a maximum value either at or near the base of the thallus. The rate of increase of the average length of the axial cells per sector and the maximum value attained vary enormously and it is obvious that they are affected to a very great extent by the environmental conditions. The average measurements of the axial cells of the basal, first-formed, sectors of a plant are often slightly lower than the maximum size, but this decrease in size does not occur in all examples.

Measurements of the average size of the axial cell per sector, made in this way, do not show the very characteristic pattern of variation of cell-size within each sector. In any sector of the thallus, apart from those sectors immediately behind the principal apical cells, where *all* axial cells are enlarging actively, the axial cells show considerable variation in length, the smallest axial cell occurring at the basal end of the sector, that is, immediately after a 'dichotomy', whilst the largest occurs towards the opposite end of the sector (Fig. 14). In mature thalli, the largest axial cell in a sector is about twice the length, or about three times the volume of the smallest. This pattern of variation is complicated by other factors, for instance, the formation of tetrasporangia or the development of adventitious lateral branches of unlimited growth may inhibit to a certain extent the enlargement of the associated axial cell. As a result, there may be small irregularities in the pattern of axial cell size, but these have no major effects on the general pattern of variation within each sector.

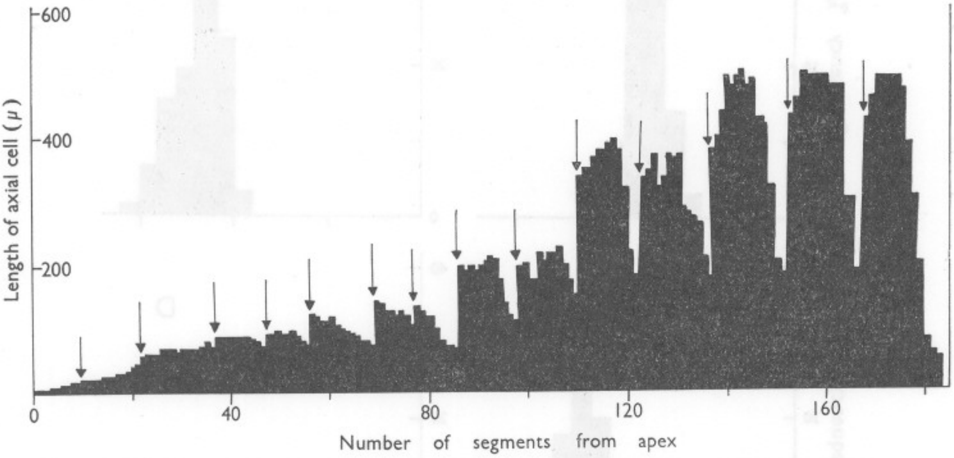

Fig. 14. Histogram showing the pattern of variation in size of the axial cells in relation to distance from the apex and the positions of pseudo-dichotomies; the position of each pseudo-dichotomy is indicated by an arrow.

The interaction of the two patterns of variation of axial cell size, that is, between the sectors of a thallus and within each individual sector, is most complex (Fig. 14). It will be obvious from this that any measurements of axial cell size must be cited in relation to a particular part of a thallus, and that 'average' measurements must be based upon sufficiently large samples (> 300 cells).

The 'index of cortication'

In those species where the axes are incompletely corticated, the ratio of the length of the cortical band to the length of the adjacent non-corticated portion of the axial cell has been used as a taxonomic criterion.

Those investigators who have used this ratio do not appear to have given any consideration to the significance of this feature. As has been shown previously, the factors affecting the length of the cortical band are very complex, whilst the patterns of variation of axial cell size are extremely complicated.

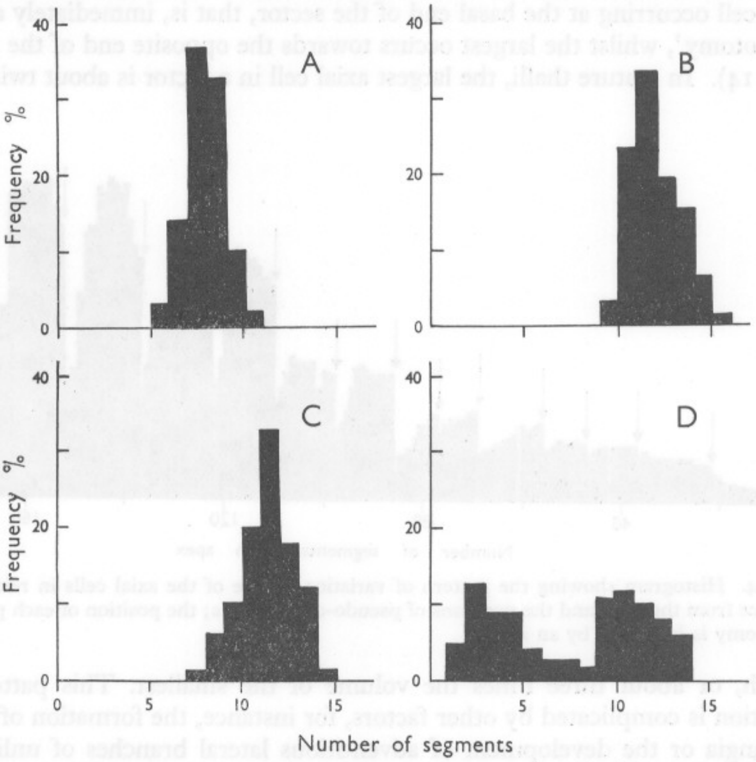

Fig. 15. A–D, Histograms showing the number of segments produced between successive pseudo-dichotomies in three species of *Ceramium*. A, *C. shuttleworthianum*; B, *C. echionotum*; C, *C. ciliatum*, excluding adventitious lateral branches; D, *C. ciliatum*, including these branches.

Furthermore, the 'index of cortication' does not represent the direct ratio of the dimensions of the cortical band and the axial cell, as the length of the non-corticated portion of the axial cell is actually the *difference* of the lengths of the axial cell and cortical band. Hence, the 'index of cortication' may be represented as follows:

$$\text{Index of cortication} = \frac{\text{length of axial cell non-corticated}}{\text{length of cortical band}}$$

$$= \frac{(\text{length of axial cell}) \text{ minus } (\text{length of cortical band})}{\text{length of cortical band}}$$

$$= \frac{\text{length of axial cell}}{\text{length of cortical band}} - 1.$$

The interaction of the two patterns of variation is so very complex that significant differences in the 'index of cortication' occur in the same species, or even in the same specimen, according to the position on the thallus at which measurements are taken. As a taxonomic criterion, the 'index of cortication' is of very dubious validity.

The occurrence of adventitious lateral branches of unlimited growth

The formation of adventitious lateral branches of unlimited growth has been described previously (see p. 341), but no explanation can be offerred to account for the occurrence of these structures. Although most frequent in damaged specimens, they may develop prolifically in axes which are apparently normal. Adventitious lateral branches of unlimited growth are formed also in tetrasporic and 'cystocarpic' specimens after the shedding of spores has commenced and immediately beneath a developing carposporophyte. Although used frequently by previous investigators, the occurrence of adventitious lateral branches of unlimited growth is of very little taxonomic significance.

The distance between pseudo-dichotomies

In certain members of the Ceramiaceae, the formation of lateral branches of unlimited growth takes place with some regularity (cf. Chadefaud, 1954), but there is considerable variation in the genus *Ceramium* in the number of segments produced between successive pseudo-dichotomies. The measurement of the number of segments produced between successive pseudo-dichotomies (cf. Newton, 1931) is of very little significance even if the formation of adventitious lateral branches of unlimited growth is eliminated. If no distinction is made between lateral branches of unlimited growth of adventitious origin and those which have arisen by the pseudo-dichotomy of the apex, and in old specimens this is often impossible, the number of segments occurring between successive lateral branches has no taxonomic significance whatsoever.

The curvature of the apices

In some species of *Ceramium*, the apical portions of the axes are incurved strongly, whilst in others, the axes are straight throughout. The degree of curvature of the apical parts of the axes has been used by some previous investigators as a taxonomic criterion, particularly at the subspecific level.

The degree of curvature of the apical regions of an axis depends upon the relative rates of development of the lateral branches of limited growth in each segment. As stated previously, the first pericentral cell is formed in the secund position, that is, on the outer face of the axis relative to the previous pseudo-dichotomy. In those species in which the apices are strongly incurved, the apical cells of the lateral branches of limited growth are produced by the first-formed pericentral cell immediately after its formation. In this way, the cortical band is well established on the outer face of the axis by the time the final pericentral cell is cut off on the inner side (Fig. 1D–F). As a result, when the final pericentral cell has been formed, each cortical band is wedge-shaped in longitudinal section, with the apices of the wedges pointing inwards, relative to the previous pseudo-dichotomy. The axes are formed by the aggregation of these wedge-shaped cortical bands and they are therefore strongly incurved. As the axes age, the eccentric development of the inner and outer faces of the cortical bands becomes less marked so that the degree of curvature diminishes until, in mature thalli, the axes are straight or almost so.

In those species of *Ceramium* in which the apices are straight or only very slightly incurved, the pericentral cells are cut off in rapid succession, and the further development of the filaments of limited growth does not take place until after the complete ring of cells has been formed (Fig. 1A–C). The development of the cortical band is thus completely symmetrical in these species.

The degree of curvature of the apical region of an axis appears to be almost constant and is sufficiently stable to serve as a valid taxonomic criterion.

The spines

The comparative morphology of the spines in the British species of *Ceramium* has been discussed in detail (see p. 344). Although the spines of all the British species must be regarded as modified lateral branches of limited growth (Fig. 7A–D), the spines are very different one from another, both in structure and development. Previous confusion with regard to the morphology of the spines is the result, essentially, of the failure to study the patterns of development by which spines are formed. In the European species, the patterns of development of the different types of spine are constant and sufficiently stable to serve as a valid taxonomic criterion.

DISTRIBUTION

According to Kylin (1956), there would appear to be about sixty species of *Ceramium*, of which twenty are reputed to occur in the British Isles (Parke, 1953). Such computations are of little significance as the taxonomy of *Ceramium* is in a chaotic state at the present time.

Much of this chaos has come about as a result of the failure to take notice of, and interpret, the modifying effects of season and environment upon exceedingly plastic material. The position has been made worse by the failure of many workers to refer back at all times to original or authentic material. As a result there have been numerous misidentifications, epithets have been misapplied by the majority of investigators and frequently the same entity has been described repeatedly under 'new' names by successive authors.

In this treatment of the genus *Ceramium* and its species, the determination of specific limits will be based entirely on morphological and ecological circumscription.

KEY TO THE BRITISH SPECIES

It is proposed to consider the British species of *Ceramium* in two groups. This treatment does not imply that the groupings are considered to be of fundamental importance; the species are arranged in this way merely for convenience.

Group A. Species in which the mature axes are either completely or incompletely corticate, but where the cortical bands give rise to spines.

Group B. Species in which the mature axes are either completely or incompletely corticate, but where spines are absent.

KEY TO THE SPECIES OF GROUP A

1. Spines single-celled. *C. echionotum*
   Spines two-, three- or four-celled. 2
2. Each spine consisting of a linear row of cells, sharply delimited from the cortical band. 3
   Each spine multicellular at the base, merging with the cortical band. *C. shuttleworthianum*
3. Basal cell of spine large ($>30\ \mu$ in length), hyaline or faintly pigmented. Spines usually in whorls, very conspicuous. Pericentral cells 6 or more. *C. ciliatum*
   Basal cell of spine less than $25\ \mu$ in length, deeply pigmented. Spines sparse, inconspicuous. Pericentral cells 4. *C. flabelligerum*

Note. A key to the species of group B is in preparation.

ACKNOWLEDGEMENTS

I am indebted to Dr M. T. Martin for her assistance and encouragement during the preparation of this paper; to Prof. N. A. Burges, Dr E. M. Burrows and Dr M. W. Parke for advice and helpful criticism; to Mr R. Ross for assistance with nomenclatural problems and to Mrs Y. Butler, Miss C. I. Dickenson and Dr J. Th. Koster for help with literature and specimens. I would like to thank the Joint Committee on Research of the University of Liverpool for financial help towards the cost of visiting herbaria and libraries and the Directors and Curators of the following herbaria for permission to examine specimens: British Museum (Natural History); Royal Botanic Gardens, Kew; Rijksherbarium, Leiden.

The British Phycological Society has made a grant to the Marine Biological Association towards the cost of publication of these Studies.

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J. mar. biol. Ass. U.K. (1960) 39, 375–390
Printed in Great Britain

STUDIES ON MARINE ALGAE OF THE BRITISH ISLES: *CERAMIUM SHUTTLEWORTHIANUM* (KÜTZ.) SILVA

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(Text-figs. 1–7)

CONTENTS

ORIGINAL DESCRIPTION

The species was first distinguished by Carmichael, as *Ceramium acanthonotum*, in his unpublished *Algae Appinensis*, the manuscript of which is now preserved at the Herbarium of the Royal Botanic Gardens, Kew. Harvey (in Hooker, 1833), in publishing Carmichael's description, regarded the species merely as a variety of *C. ciliatum*. Agardh (1844) raised the variety to specific status, and it is as *C. acanthonotum* that the species has been known generally. Kützing (1841),[1] in a revision of the genus *Ceramium*, had described the entity independently as *Acanthoceras shuttleworthianum*; the specific epithet *shuttleworthianum* has priority over *acanthonotum* [see Article 60 of the International Code of Botanical Nomenclature (Lanjouw, 1956)]. The priority of the epithet *shuttleworthianum* was indicated, independently, by both Silva (1959) and Dixon (1959); of the two publications, that by Silva is the earlier.

The original material of *A. shuttleworthianum* is preserved at the Rijksherbarium, Leiden. According to Kützing (1841, p. 739), the species was described on the basis of material 'an der irischen Küsten: Shuttleworth'. In the Kützing herbarium there is a single Irish specimen of *A. shuttleworthianum* attached to a small mussel (*Mytilus*);

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[1] For comments as to the precise date of publication, see Dixon (1960, p. 333)

this has been designated as the type specimen (Herb. Lugd. Bat. 940.265.127). The specimen is labelled only as 'Irland' and no further information is available as to the locality from which it was collected.

SYNONYMY

Ceramium ciliatum β acanthonotum Carm. ex. Harv. (in Hooker, 1833, p. 236).
Ceramium acanthonotum (Carm. ex Harv.) J. Agardh (1844, p. 26).

For details of the type material of this entity, see Appendix (p. 388).

DESCRIPTION OF THE SPECIES

Frond lax, 0·5–4·0 cm in length, red or reddish brown in colour; axes filiform, 0·1–1·0 mm. broad, usually entangled or intertwined; branching regularly pseudo-dichotomous in the apical region, highly irregular in the older parts due to damage and subsequent regeneration by the development of adventitious lateral branches of unlimited growth; cortex bearing spines; cortical bands always distinct, even in the apical region; spines conical, secund or in whorls, multicellular at the base; cells of spine small ($< 25\,\mu$ diameter) with pigmented chromatophores.

Tetrasporangia secund or in whorls, emergent from the cortical band when mature.

Spermatangia forming colourless patches over each cortical band.

Carposporophytes spherical, usually lateral, sessile, subtended when mature by a single adventitious lateral branch of unlimited growth.

STRUCTURE AND DEVELOPMENT OF THE THALLUS

The principal apical cells of the axes of *Ceramium shuttleworthianum* are smaller than those of most other species of *Ceramium*, but the pattern of segmentation conforms to the general description already given (Dixon, 1960).

Each segment cut off by the principal apical cells of an axis gives rise to four pericentral cells (Figs. 1E, 2H–K). There is no variation in the number of pericentral cells produced. The filaments of limited growth arise from the pericentral cells, and their development is restricted so that the length of the cortical bands rarely exceeds $120\,\mu$ (Fig. 3A–C). The enlargement of the axial cells varies enormously, so that the 'index of cortication' is extremely variable. Kützing (1862, p. 29) described *Acanthoceras shuttleworthianum β longiarticulatum*, characterized by the extreme length of the non-corticated axial cells in mature parts of the thallus. The taxonomic status of this entity will be discussed later.

From six to ten segments are produced by the principal apical cells between each pseudo-dichotomy. Mature thalli of this species are of very irregular appearance and only rarely do they exhibit the characteristic pseudo-dichotomous structure found in other species of the genus. Most specimens suffer severe damage either by animal grazing or as a result of the extreme exposure of the environment in which they occur. In addition, infection of the principal apical cells of the axes by *Eurychasmidium tumefaciens* (see p. 383) occurs frequently (Fig. 6A). The subsequent regeneration of adventitious lateral branches of unlimited growth (Fig. 1 D) results in a tangled mass of irregularly branched axes.

Glandular cells occur frequently in *Ceramium shuttleworthianum*, although not reported in this species by previous investigators. Development occurs as in other species of the genus, by the direct modification of a superficial cell of the thallus.

The spines of *C. shuttleworthianum* are of very characteristic appearance. During the formation of a spine (Fig. 2 A–K), the apical cell of a lateral branch of limited growth divides rapidly to form a projecting filament of

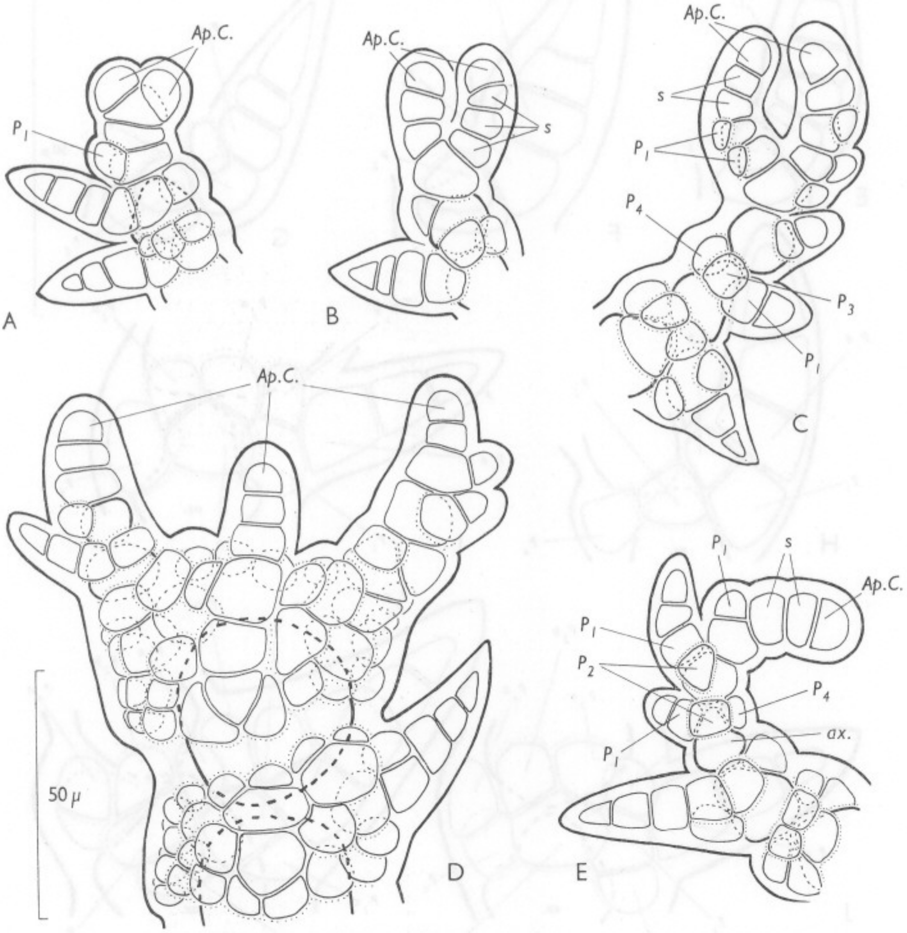

Fig. 1. The apex and the origin of lateral branches of unlimited growth in *C. shuttleworthianum*. A–C, Pseudo-dichotomy of the apex; D, origin of adventitious lateral branches of unlimited growth in a damaged axis; E, the apex of an axis, showing the general pattern of segmentation. *Ap.C.*, apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; *s.*, segment, produced by the transverse division of the apical cell of an axis.

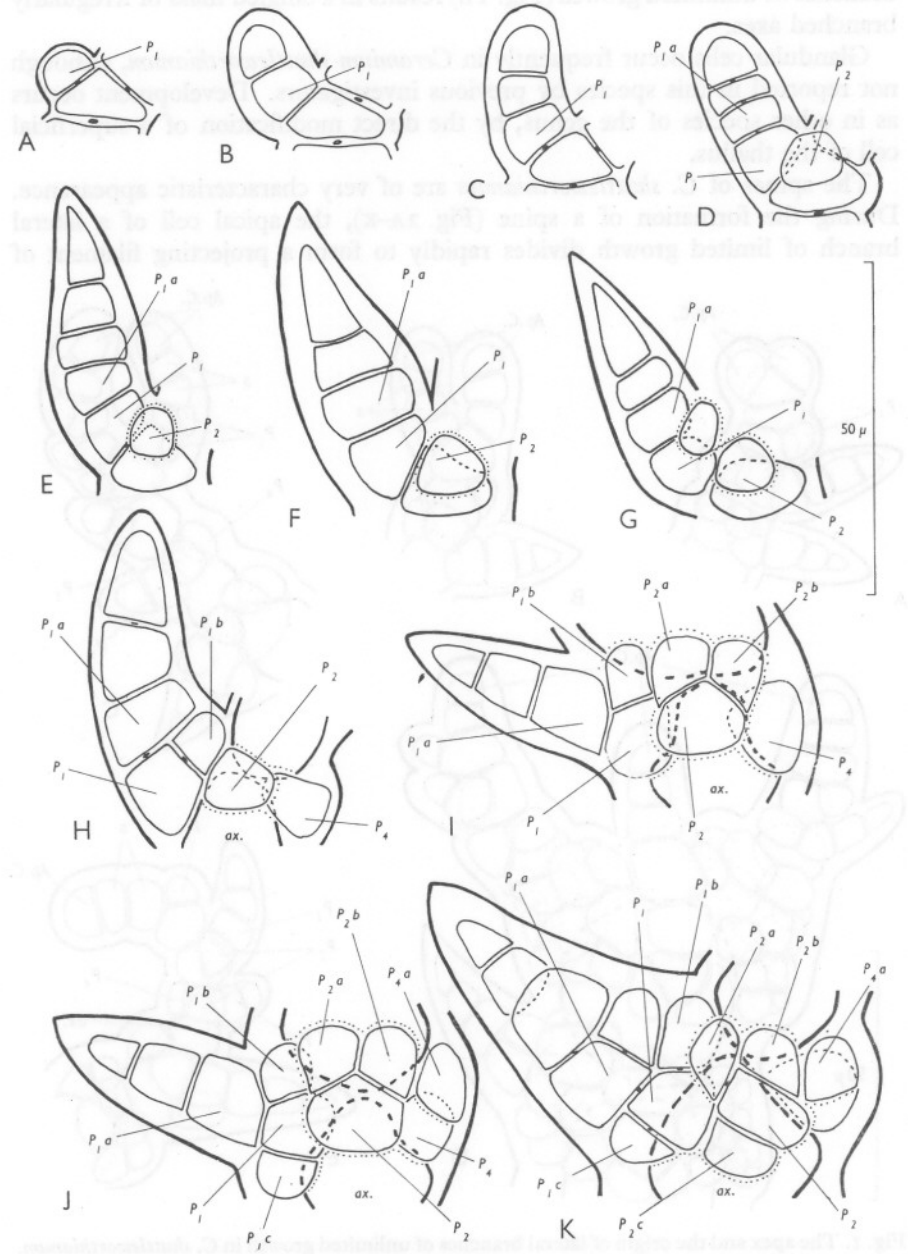

Fig. 2. A–K, Details of the stages in the development of the cortical band, in *C. shuttleworthianum*. *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally-directed apical cells of lateral branches of limited growth, produced from P_1; P_1c, P_1d, basipetally directed apical cells of lateral branches of limited growth, produced from P_1, etc.

three to five cells. The rapid development of the spines is indicated by the occurrence of fully developed spines within one or two segments of the apex of an axis. The lowermost cells of the filament divide transversely to form part of the cortical band, whilst the other cells of the filament, that is, those cells which project to form the spine, may divide transversely also, so that the spine is conical in shape, with a broad multicellular base. The cells of the spine do not enlarge excessively, as in some other spine-bearing species of *Ceramium*. Moreover, the chromatophores and cytoplasmic contents are retained so that the cells of the spine resemble the cells of the cortical bands. As a result, the boundary between spine and cortical band is not sharply defined, as in many of the spine-bearing species of *Ceramium*, and the spines merge with the cortical bands in *C. shuttleworthianum* (Fig. 3).

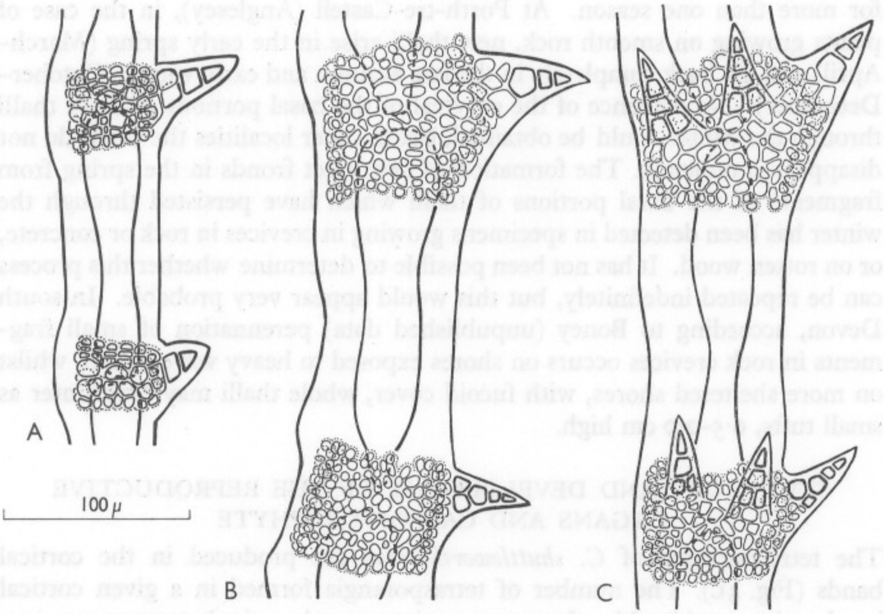

Fig. 3. A–C, Range of form of the axes in *C. shuttleworthianum.*

Adventitious spines may develop occasionally from the cortical bands of old mature axes. Such spines, which resemble the primary spines in appearance, occur most frequently in specimens which have been grazed by animals or damaged in some other way.

The number of spines occurring at each cortical band is not constant. In every cortical band, a single spine is formed in relation to the first pericentral cell, but other spines may develop in relation to the other pericentral cells, or arise in an adventitious manner. In the extreme case, a whorled arrangement of spines may result (= var. *coronata* Kleen, 1874). The taxonomic significance of these observations will be discussed later (see p. 386).

The life-span of the thalli of *C. shuttleworthianum* is extremely variable. At certain localities in the west of Ireland it would appear that many of the thalli are perennial; Boney (unpublished data) has reported the perennation of large thalli in south Devon. From herbarium collections, it is obvious that in France thalli can survive through the winter. In northern England and Wales, on the other hand, the erect system of the thallus survives only rarely for more than one season. At Porth-tre-Castell (Anglesey), in the case of plants growing on smooth rock, new thalli arise in the early spring (March–April) and die back completely in the late autumn and early winter (October–December). No evidence of the survival of the basal portions of these thalli through the winter could be obtained, but in other localities the thalli do not disappear completely. The formation of new erect fronds in the spring from fragments of the basal portions of thalli which have persisted through the winter has been detected in specimens growing in crevices in rock or concrete, or on rotten wood. It has not been possible to determine whether this process can be repeated indefinitely, but this would appear very probable. In south Devon, according to Boney (unpublished data) perennation of small fragments in rock crevices occurs on shores exposed to heavy wave action, whilst on more sheltered shores, with fucoid cover, whole thalli may overwinter as small tufts, 0·5–2·0 cm high.

STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS AND CARPOSPOROPHYTE

The tetrasporangia of *C. shuttleworthianum* are produced in the cortical bands (Fig. 4C). The number of tetrasporangia formed in a given cortical band varies considerably. In many specimens, only a single tetrasporangium develops in each band, on the outer side of the axis relative to the previous pseudo-dichotomy. Frequently several tetrasporangia develop in each band, and in the extreme condition a whorled arrangement results. The mature tetrasporangia measure 50–100 × 20–40 μ and when fully developed they are usually only partially immersed in the cortical band (Fig. 4C). The cortical bands of *C. shuttleworthianum* are relatively small and the internal development of the tetrasporangia causes extensive distortion, so that the orientation of the spines is changed considerably.

Spermatangia are produced superficially from mother-cells derived from the apical cells of the lateral branches of limited growth. Frequently the whole surface of the cortical band is covered with spermatangia (Fig. 4B) and when a large number of cortical bands is involved then the thallus develops a very characteristic indefinite outline which is readily identifiable.

No detailed studies have been made previously of the structure and development of the carpogonial branch and carposporophyte of *C. shuttleworthianum*, although Miranda (1929*b*) has stated that the carpogonial branch and carposporophyte resemble those of *C. flabelligerum* (Miranda, 1929*a*). Despite the abundance of carposporophytic material of *C. shuttleworthianum* in Ireland, the Channel Islands and the Isle of Man, the collection of specimens of this species with carpogonial branches and young stages of carposporophyte development was found to be particularly difficult. In seven years, only a single suitable specimen was collected. From this one specimen it would appear that the carpogonial branch is of the characteristic four-celled structure and that the supporting cell is formed by the modification of a first-formed pericentral cell. The lack of suitable material has prevented any detailed study of the carposporophyte development. The mature carposporophyte is

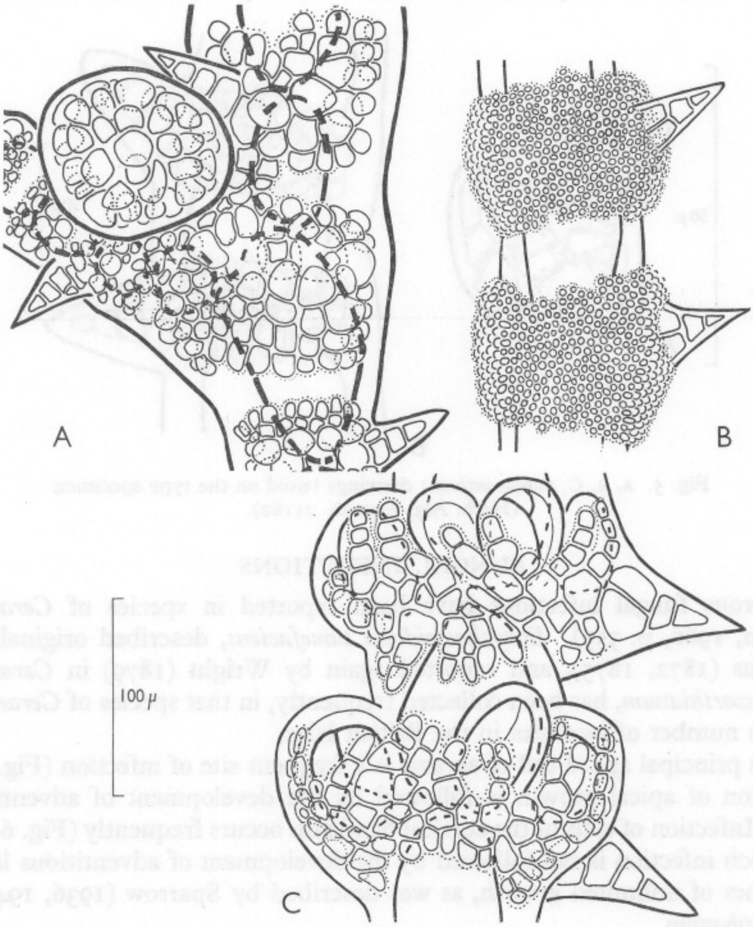

Fig. 4. A–C, Reproductive structures in *C. shuttleworthianum*.

typical (Fig. 7A), but it differs from that of many other species of the genus in that it is subtended by only a single adventitious lateral branch of unlimited growth. In most species of *Ceramium* the mature carposporophyte is a lateral structure which is enveloped by a cluster of encircling adventitious axes, but in *C. shuttleworthianum* it appears to lie in a dichotomy of which one arm is formed by the parent axis and the other by the adventitious axis.

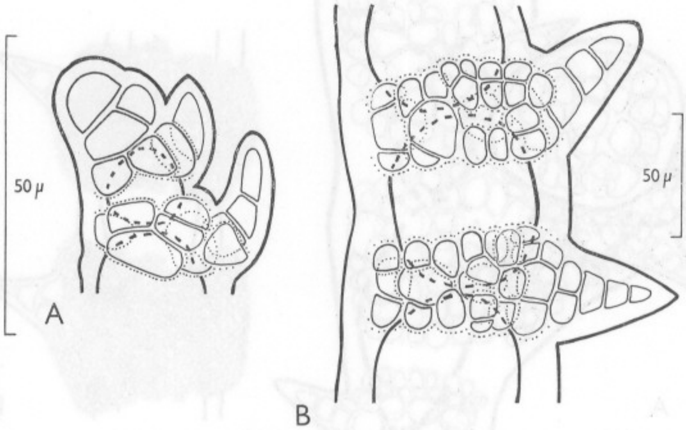

Fig. 5. A, B, *C. monacanthum*; drawings based on the type specimen (Herb. Alg. Agardh. 21162).

FUNGAL INFECTIONS

Numerous fungal infections have been reported in species of *Ceramium* (Dixon, 1960, p. 359). *Eurychasmidium tumefaciens*, described originally by Magnus (1872, 1875), and reported again by Wright (1879) in *Ceramium shuttleworthianum*, has been collected frequently, in that species of *Ceramium*, from a number of localities in the British Isles.

The principal apical cell of an axis is a frequent site of infection (Fig. 6A); cessation of apical growth is followed by the development of adventitious axes. Infection of cells of the cortical band also occurs frequently (Fig. 6B, C), but such infection is not followed by the development of adventitious lateral branches of unlimited growth, as was described by Sparrow (1936, 1943) in *C. diaphanum*.

DISTRIBUTION

Many previous records are incorrect because of confusion with other species of the genus. The following data are based upon examined specimens only.

British Isles

C. shuttleworthianum is generally distributed throughout the British Isles. Specimens from the following counties have been examined: Cornwall, Devon, Somerset, Dorset, Hampshire, Kent, Essex, York, Northumberland, Cumberland; Isle of Man; Glamorgan, Carmarthen, Pembroke, Cardigan, Merioneth, Caernarvon, Anglesey, Denbigh; Wigtown, Ayr, Bute, Renfrew, Argyll, Inverness, Ross and Cromarty, Sutherland, Caithness, Moray, Banff, Aberdeen, Fife, West Lothian, Midlothian, East Lothian, Berwick; Orkney, Shetland; Donegal, Sligo, Mayo, Galway, Clare, Kerry, Cork; Channel Islands.

Previous reports of the occurrence of this species in Norfolk, Durham and Cheshire have not been confirmed.

World

Iceland, Faroes, northern, central and southern Norway, and the Atlantic coast of France.

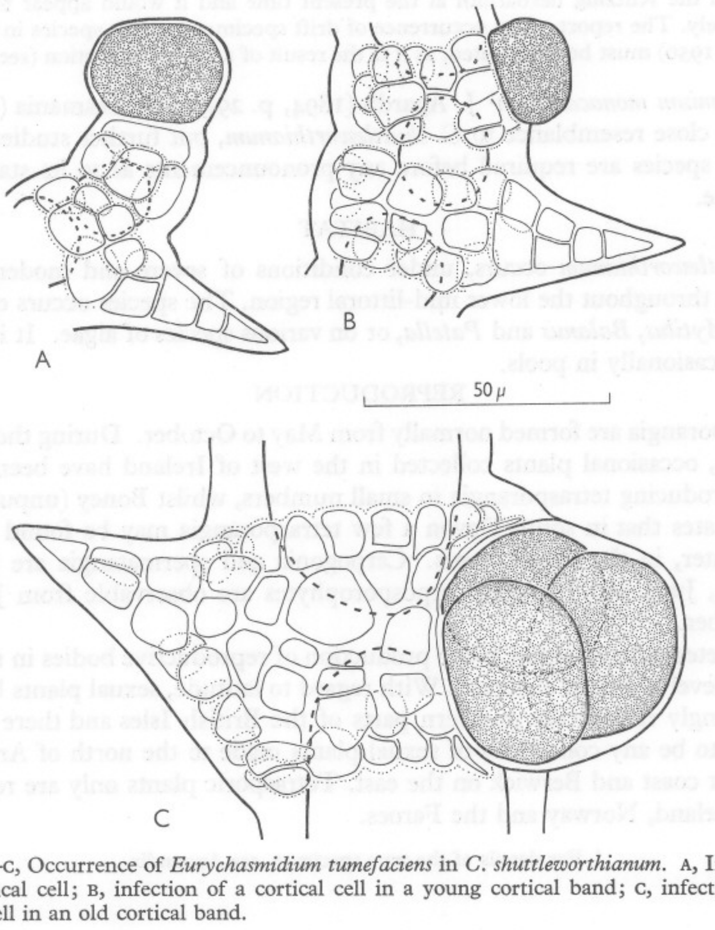

Fig. 6. A–C, Occurrence of *Eurychasmidium tumefaciens* in *C. shuttleworthianum*. A, Infection of the apical cell; B, infection of a cortical cell in a young cortical band; C, infection of a cortical cell in an old cortical band.

The southern limit of the species cannot be stated with certainty. Miranda (1929*b*) has claimed that the species occurs on the north coast of Spain, but this report must be treated with caution as no illustration is given by Miranda and it has not been possible to locate any specimens of *C. shuttleworthianum* from the area cited by this author. According to Børgesen (1930), the report of the occurrence of this species in the Canary Islands, by Sauvageau (1912, p. 184), is based on a misidentification; the specimens on re-examination proved to be a mixture of *C. ciliatum* and *C. flabelligerum*.

With regard to the northern limit of the species, it is obvious, from a study of the description and figure given by Sinova (1912), that the reported occurrence of this species in the Murmansk area is also based upon a misidentification.

It would appear that *C. shuttleworthianum* does not occur on the coasts of Germany (Migula, 1909) or Denmark (Rosenvinge, 1924), although it should be noted that Kützing (1845, p. 293) records the species from the island of Föhr, in the North Friesian archipelago. This record is based, according to Kützing, on a specimen collected by Frölich and identified by him as '*Ceramium diaphanum*'. This specimen is not in the Kützing herbarium at the present time and it would appear to be lost completely. The report of the occurrence of drift specimens of this species in Holland (Lucas, 1950) must be discounted, as it is the result of a misidentification (see p. 387).

Ceramium monacanthum[1] J. Agardh (1894, p. 29), from Tasmania (Fig. 5), bears a close resemblance to *C. shuttleworthianum*, but further studies of the former species are required before any pronouncements as to its status can be made.

HABITAT

C. shuttleworthianum occurs, under conditions of severe and moderate exposure, throughout the lower mid-littoral region. The species occurs on rock, or on *Mytilus*, *Balanus* and *Patella*, or on various species of algae. It is found only occasionally in pools.

REPRODUCTION

Tetrasporangia are formed normally from May to October. During the winter months, occasional plants collected in the west of Ireland have been found to be producing tetrasporangia in small numbers, whilst Boney (unpublished data) states that in south Devon a few tetrasporangia may be found during the winter, in the larger plants. Carpogonia and spermatangia are formed in May, June and July and carposporophytes are observable from June to December.

No detectable variation in the production of reproductive bodies in relation to tide level has been observed. With regard to latitude, sexual plants become increasingly rare in the northern parts of the British Isles and there do not appear to be any collections of sexual plants made to the north of Argyll on the west coast and Berwick on the east. Tetrasporic plants only are reported from Iceland, Norway and the Faroes.

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[1] For details of the type specimen, see Appendix.

LIFE HISTORY

Little is known of the life history of *C. shuttleworthianum.* From personal observations, equal proportions of sexual and tetrasporic plants have been detected in a number of localities on the west coast of Ireland, southern England and the Channel Islands, although, in the same locality, variations in the proportions of sexual and tetrasporic plants have been noticed from year to year. The observations of Boney (unpublished data) in south Devon, on the other hand, indicate a preponderance of tetrasporic plants in that region. In north Wales, northern England, the Isle of Man and parts of Scotland sexual plants are relatively rare, whilst they are unknown in northern Scotland, Norway, Faroes and Iceland. The occurrence of sexual and tetrasporic plants in equal proportions suggests that the life history is of the '*Polysiphonia*-type', with a regular alternation of sexual, carposporic and tetrasporic phases, but from the data presented above it would appear very probable that the sequence of phases in the life history may vary considerably over the range of the species.

The regeneration of new thalli from small fragments of the basal portions of old thalli of *C. shuttleworthianum* has been demonstrated. In certain localities, such regeneration occurs frequently, whilst in others it would appear to be relatively rare. The occasional occurrence of extensive perennation in any locality could have a profound effect upon the frequency of occurrence of sexual and tetrasporic phases, in that it could obscure the actual sequence of phases in a life history, or introduce deviations from the proportions of sexual and tetrasporic phases to be expected in a life history of the '*Polysiphonia*-type'.

FORM RANGE

Ceramium shuttleworthianum is one of the least polymorphic species of the genus. In the British Isles the dimensions of the thalli vary considerably, but the variation appears to result more from the effects of damage and the subsequent regeneration than from any other cause, although the degree of enlargement of the axial cells has some effect upon the size of the thallus. The species occurs throughout the lower mid-littoral region, but there is no detectable range of form in relation to tide level and it would appear very probable that this results from the extensive damage, which occurs at all levels, obscuring any effect of tide level on the form of the thallus. The species is found in pools only rarely. The specimens from pools are larger and more regularly branched than other specimens growing out of water at the same tide level.

Most specimens of *C. shuttleworthianum* collected in the British Isles develop a single spine at each cortical band (Fig. 3A, B), but occasionally a number of spines occur, forming a partial or complete whorl (Fig. 3C).

Kleen (1874, p. 19) proposed that such specimens should be separated as *C. acanthonotum* var. *coronata*. Kjellman (1883, p. 172), after a re-examination of Kleen's original material,[1] reduced the status of this variety to forma *coronata*, with the following remarks: 'In Kleen's collections only the typical form of *Ceramium acanthonotum* is to be found, but some specimens have the spines in certain parts of the frond so arranged as in the variety distinguished by Kleen. This variety resembling the typical form in all respects...it may be considered as rather little independent, though it deserves perhaps to be specially mentioned.'

Specimens with the spines in whorls have been reported from Norway (Kleen, 1874; Foslie, 1894) and Faroes (Børgesen, 1902), but apparently not from Iceland (Jónsson, 1902). From the literature it might appear that the number of spines formed at each cortical band is related to latitude. This opinion must be rejected for a number of reasons. First, over the whole range of the species there is little constancy in the number of spines produced, so that adjacent cortical bands in the same axis may bear a single spine or a whorl of spines; secondly, all intermediate states between the two extremes occur also, and thirdly, the whorled condition may result from the formation of a number of primary spines or from the subsequent development of secondary adventitious spines.

From this discussion it is obvious that there is no justification for the taxonomic separation of those thalli in which more than one spine is formed in each cortical band.

Kützing (1862) figured *Acanthoceras shuttleworthianum β longiarticulatum*, reputedly characterized by the extreme length of the axial cells in the mature parts of the thallus.[2] That there is no justification for the separation of *β longiarticulatum* is obvious, even from the original illustrations given by Kützing (1862, pl. 96, figs. a–f). Kützing gives a figure (pl. 96, fig. c) of the basal portions of *A. shuttleworthianum* and two figures (pl. 96, figs. e, f) of the basal portions of *A. shuttleworthianum β longiarticulatum*. Calculation of the 'index of cortication' for these three illustrations gives a mean value of 3·66 for *A. shuttleworthianum* and values of 1·25 and 4·25 for the two illustrations of *β longiarticulatum*. Examination of Kützing's original material of *β longiarticulatum* shows that the range of variation of the index of cortication in these specimens is from 0·75 to 5·0, which is not significantly different from the range in the species as a whole, based upon a series of measurements of a large number of specimens from a wide range of localities. There is thus no justification for the separation of this variety.

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[1] For comments on the type material of this variety, see Appendix.

[2] For a discussion of the type material and validity of publication of this entity, see Appendix.

THE INTERRELATIONSHIPS OF *CERAMIUM CILIATUM* AND *CERAMIUM SHUTTLEWORTHIANUM*

C. shuttleworthianum has been confused only with *C. ciliatum*. Harvey (in Hooker, 1833) regarded the species originally as a variety of *C. ciliatum* and this opinion has been repeated recently by Lucas (1950), who states: 'It is doubtful whether *C. acanthonotum* is a good species, for sometimes parts with whorls of spines and parts with spines on the outer side of the node only are found on the same plant.' It is obvious that a detailed study of the interrelationships of these two species is necessary if this confusion is to be overcome.

The two species were distinguished originally on the basis of spine distribution. It was supposed that in *C. ciliatum* the spines occur in whorls, whilst in *C. shuttleworthianum* a single spine occurs in each cortical band. From the previous discussion it is clear that more than one spine may occur in the cortical band of *C. shuttleworthianum*, whilst in *C. ciliatum*, although the spines occur frequently in whorls, there may be a reduction in the number of spines, so that in extreme cases only a single spine occurs at each cortical band. From this evidence it would appear that the separation of the two species is not justified. Careful investigation shows that this conclusion is incorrect, and that, although the *distribution* of spines is of little taxonomic significance, the two species are completely distinct.

In connexion with the opinions expressed by Lucas (1950), it should be noted that the re-examination of his material, now in the Rijksherbarium, Leiden, shows that the statement of this author as to the status of *C. shuttleworthianum* must be discounted, as none of the specimens identified by him as '*C. acanthonotum*' is of this entity; the specimens are of *C. ciliatum*, with a reduced number of spines.

The *morphology* of the spine is the most obvious character by which the two species can be distinguished. In *C. shuttleworthianum*, each spine is a conical structure, composed of from three to ten cells, two to four cells broad at the base (Fig. 3). The cells of the spine are of similar size (15–25 μ in diameter) and they retain their chromatophores and cytoplasm throughout the life of the plant. In *C. ciliatum*, the spine is formed of a uniseriate filament of three, or occasionally four or five, cells which differ markedly in size (Fig. 7). In mature three-celled spines the lowermost cell occupies more than half the length of the spine ($30–50\,\mu \times 20–30\,\mu$), the second cell is smaller ($20–30\,\mu \times 10–20\,\mu$), whilst the third cell is minute and triangular in shape. In four- and five-celled spines the differences in size between the cells of the spine are not so marked as in three-celled spines, but the lowermost cell is always the largest, whilst the terminal cell is always small and triangular. When first formed, the cells of the spine of *C. ciliatum* have dense cytoplasm and chromatophores, but as a result of the enormous increase in cell-size which takes place during development, the mature cells are frequently hyaline, although occasionally the remnants of cytoplasm and chromatophores may remain, forming curious patterns on the wall of the cell (see Feldmann-Mazoyer, 1940, fig. 55).

The two species may also be distinguished by the number of pericentral cells formed by each segment of a principal apical cell. Four pericentral cells are formed in *C. shuttleworthianum*, whilst six to eight are formed in *C. ciliatum*.

The two species can be distinguished, even in the field, by their size; with a good hand lens, the construction of the spine is clearly visible.

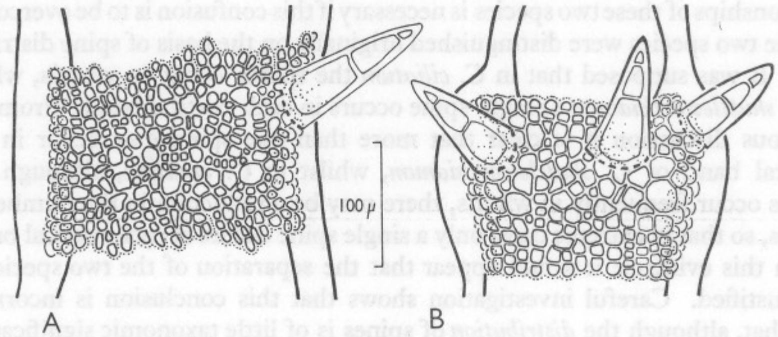

Fig. 7. A, B, Distribution of spines in *Ceramium ciliatum*.

APPENDIX

NOTES ON TYPE SPECIMENS

Acanthoceras shuttleworthianum β longiarticulatum Kützing, 1862, p. 29

Kützing's original reference to *A. shuttleworthianum β longiarticulatum* is extremely brief,

'3076. *Acanthoceras Shuttleworthianum β longiarticulatum.*—Ad oras Angliae.'

but, as this is accompanied by an illustration (Kützing, 1862, pl. 96, figs. d–f) showing the essential characters, the name must be regarded as validly published [see Article 43 of the International Code of Botanical Nomenclature (Lanjouw, 1956)]. According to manuscript notes written by Kützing on a packet, containing four clumps of material, now in the Rijksherbarium, Leiden (Herb. Lugd. Bat. 940.265.154), the entity was based upon material collected by Dickie at Aberdeen. The four clumps of material are mounted on three pieces of card, each of which is labelled, in Dickie's hand, '*Ceramium acanthonotum* Carm Aberdeen Sept. 1845 GD'. A lectotype has been selected from the material available.

Location of lectotype: Rijksherbarium, Leiden (L), as Herb. Lugd. Bat. 940.265.154. Location of syntypes: as above. Locality of the type material: Aberdeen, Scotland.

Ceramium acanthonotum var. *coronata* Kleen, 1874, p. 19

It has not been possible to locate the original material of this variety, as the present location of Kleen's herbarium is unknown. It is obvious from the various comments made by Kjellman (1883) that he had examined numerous specimens from the Kleen herbarium, but no mention is made of the location of the herbarium. Only a single Kleen specimen of the species has been located, in the Rijksherbarium, Leiden (Herb. Lugd. Bat. 940.265.25). This specimen, labelled in Kleen's hand '*Cer acanthonotum* Carm Nordlanden', is from the same geographical area as the type material, but from the label it would not appear to be part of it. In the absence of type material, the illustrations given by Kleen (1874, Taf. 10, figs. 5*a*, *b*) are adequate for the purposes of identification.

Location of type specimen: unknown. Locality of type material: Nordlanden, Norway.

Ceramium ciliatum β *acanthonotum* Carm. ex Harv. in Hooker, 1833, p. 236

Several Carmichael specimens of *C. acanthonotum* have been located in herbaria. Neither Carmichael nor Harvey designated a holotype and no information can be obtained from the specimens, all of which are labelled, in Carmichael's hand, 'Carmichael H/A' (= 'Herbarium Appinensis'). A lectotype has been selected from the material available.

Location of lectotype: Herbarium, Royal Botanic Gardens, Kew (K). Location of syntypes: as above (2 specimens). Herbarium, Royal Botanic Garden, Edinburgh (E) (1 specimen). Locality of the type material: Appin, Argyle, Scotland.

Ceramium monacanthum J. Agardh, 1894, p. 29

The species was based on a single specimen collected by Roland Gunn in Tasmania.

Location of holotype: Botaniska Museet, Lund (LD), (as Herb. Alg. Agardh. 21162); Tasmania (no further details known).

ACKNOWLEDGEMENTS

I am indebted to Dr M. T. Martin for her encouragement and critical observations; to Prof. N. A. Burges, Dr E. M. Burrows and Dr M. W. Parke for advice and helpful criticism; to Dr A. D. Boney for permission to make use of unpublished data; to Mr R. Ross for assistance with nomenclatural matters and to Mrs Y. Butler, Miss C. I. Dickenson and Dr J. Th. Koster for help with literature and specimens. I would like to thank the Joint Committee on Research of the University of Liverpool for financial help towards the cost of visiting herbaria and libraries, and the Directors and Curators of the following herbaria for permission to examine specimens: British Museum (Natural History); Royal Botanic Gardens, Kew; Royal Botanic Garden, Edinburgh; Rijksherbarium, Leiden; Naturhistoriska Rijksmuseum, Stockholm; Museum Nationale d'Histoire Naturelle, Paris; Botaniska Museet, Lund.

The British Phycological Society has made a grant to the Marine Biological Association towards the cost of publication of these *Studies*.

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J. mar. biol. Ass. U.K. (1960), 39, 391–412
Printed in Great Britain

THE NEW AQUARIUM AND NEW SEA-WATER CIRCULATION SYSTEMS AT THE PLYMOUTH LABORATORY

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(Plates I and II, and Text-figs. 1–6)

Before describing the new aquarium some mention should be made of the final state of the old, which was described in detail some years ago (Wilson, 1952). Various suggestions for improvement made at that time were subsequently carried out. Thus the central table tanks were removed in 1953 and the central curtains, after shortening, were hung from the ceiling above the front top edge of the south-side tanks. This gave greatly improved viewing of the tank contents through exclusion of direct daylight to the public hall, and the viewing was still further improved when the south-side windows were blackened inside and the tanks lit solely by electric light. Modifications to the reservoirs (described below) brought about a clarity of the sea water never before attained.

The end came when the slate backs of several south-side tanks developed serious cracks, through which at one time water was pouring at over 70 gallons an hour and finding its way out of the building through ventilators in the south wall. No more than temporary repairs could be effected. The cracks resulted from the rusting of iron bolts pinning together the slate slabs of which the tanks were built. The bolt heads had been covered with slate dowels bedded in a red-lead compound which had kept the water back for nearly 70 years; it had at last penetrated to the bolts and expansion due to rusting cracked the slates.

The old aquarium was closed to the public for the last time on 27 September 1958 and demolition of the old tanks and fittings took most of October. It is of interest to record that the cast-iron window frames—which were moulded with the name of Leete, Edwards and Norman, London, a firm well known in Victorian days for its constructional work on big public aquaria—were in excellent condition and doubtless would have served for many more years. The condition of the iron tie-bars was on the whole also good, even in places where they had never been repainted and had a thick coating of rust, though here and there they had become dangerously thin. Much of the slate was in poor condition, splitting easily where rusting iron had cracked it and it would certainly not have held out much longer.

All the more valuable fish removed from the old tanks were, during the rebuilding, kept in tanks outside in the yard, or in the sea-water reservoirs, the water being kept in circulation. In the dimly lit reservoirs the fish flourished and grew, particularly *Pagellus*, *Spondyliosoma* and *Morone*. The *Polyprion*, mentioned in Wilson, 1953, p. 207, had a reservoir to itself and lengthened noticeably.

THE NEW AQUARIUM

Over many years various tentative plans for a new aquarium had been drawn and discarded. The necessity of erecting the new tanks within the existing tank room, where the central columns supporting the floors above must be retained, imposed severe limitations within which it was difficult to achieve a harmonious design pleasing to the viewer and at the same time providing greatly improved servicing facilities and a healthier environment for the animals. In the final plan these desiderata have largely been satisfied though at a cost of innumerable compromises. Thus, because of the restricted ceiling height the depth of water in the tanks is the maximum possible consistent with barely reasonable headroom over the cat-walks, and the latter have had to be kept several inches closer to the water surface than is desirable. Similarly the length and width of the tank room has influenced the shape of the tank windows, which are several inches shorter than they could otherwise have been. And so on throughout the whole structure.

In 1952 Garnaud suggested new shapes for aquarium tanks, until then almost always based on the rectangle. He proposed that the side walls should be built at 45° angles instead of at right angles. By so doing, triangular tanks alternate with others in which, owing to refraction and reflexion of light, the side walls cannot be seen through the windows when the tanks are full of water. This idea of angled-sides was adopted for the new aquarium at Plymouth, but modified from Garnaud's original scheme to accord with requirements within the available space.

In planning the aquarium the main objectives have been: (1) provision of the best possible conditions for the animals; (2) that as seen by the viewer each tank shall present as natural looking a scene as possible, well illuminated and with no 'works' showing; (3) ease of maintenance and day-to-day servicing. The first of these objectives has always taken precedence over the other two and the second almost always over the third. Only by so doing can a healthy and attractive aquarium be attained. In addition, the public hall and its approaches have been made as well proportioned and pleasing as possible.

The architect was Mr F. L. Preston, F.R.I.B.A., A.A.Dip., of Messrs Easton and Robertson, Cusdin, Preston and Smith, London, and the contractors Messrs John Garrett and Son Ltd, of Plymouth. The rockwork was designed and executed by Mr H. R. Allen, A.R.C.A., of Westerham, Kent.

Much technical help was given by members of the laboratory staff, especially Mr A. N. Bennett in the planning of the circulation system and Mr F. J. Warren in electrical fittings. Mr F. G. W. Ryder helped with many constructional details and overall supervision.

To all the above and others from whom I received assistance during the planning and construction of the new aquarium I wish to record my grateful thanks, and also to the Director, Dr F. S. Russell, F.R.S., for his continued support and encouragement.

The public hall

In the old aquarium[1] the tanks lined the north and south walls of the building and because they were wider on the north than on the south side the pillars occupied an asymmetrical position between them. By making the new north- and south-side tanks of equal width (see Text-fig. 1) these pillars are now centrally placed and one, the former easternmost pillar, has been removed to enable the largest tank to be constructed at the east end of the room. The weight of the floor above has been taken by two new concrete pillars merged with the central mullions of this tank. The public hall, as will be seen from the plan, widens at the east end. The new layout has in itself greatly enhanced the general appearance of the aquarium (Pl. I) and this has been further improved by an acoustically tiled ceiling with inset lights, hung below and concealing from public view the old vaulted ceiling and the unsightly overhead piping supplying tanks in the laboratory on the floor above. Underfoot a floor of dark red asphalt is a pleasing substitute for concrete with iron gratings. The public reach the aquarium along a partly reconstructed and newly decorated hall and passage and enter it through swing-doors and a small low-ceilinged lobby.

Wooden sides to the lobby, fluted and polished, are service doors which enable staff to cross it between north- and south-side service areas. These service areas, or short passages, are cut off from the public hall by a fluted polished screen of Afrormosia wood in which, to the north of the lobby, are three small angle-iron tanks, one below and two above, attractively framed in the screen (Text-fig. 2, section AB). In the south-east corner an emergency exit has been constructed utilizing one of the old window arches. A circular seat has recently been put around the pillar nearest the large tank.

On the sills in front of the tanks (Pl. I) frames of Afrormosia wood hold picture labels (lettered water-colour drawings sealed between Perspex). Each frame holds five labels which can be slid in from either end and screwed up against interference. A removable wooden hand-rail on iron supports inserted

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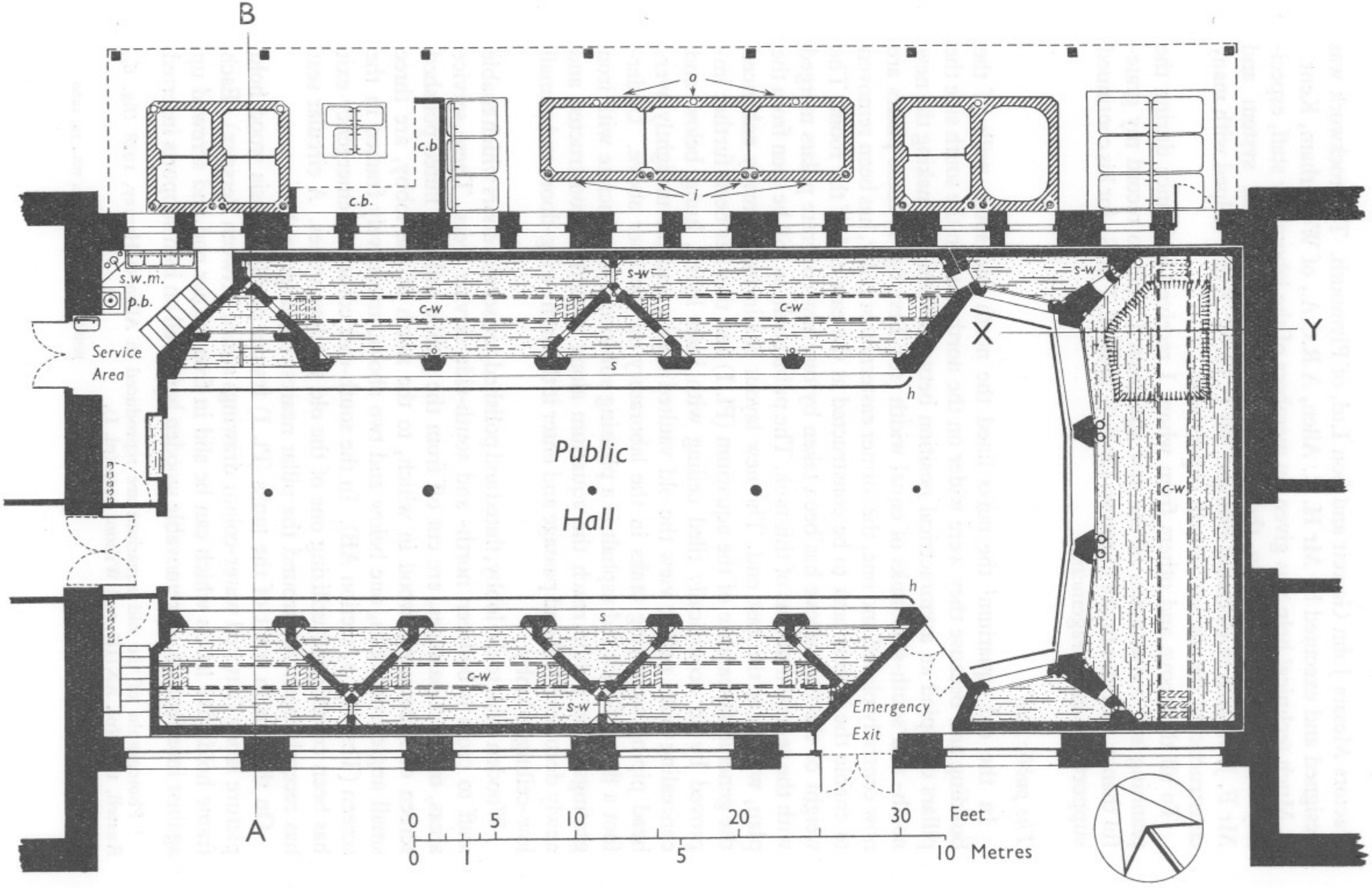
[1] Photographs of the old aquarium are reproduced in Allen & Harvey, 1928 (fig. 6), Russell, 1948 (pl. XXIII), and Wilson, 1952 (pl. I).



Text-fig. 1. For legend see facing page.

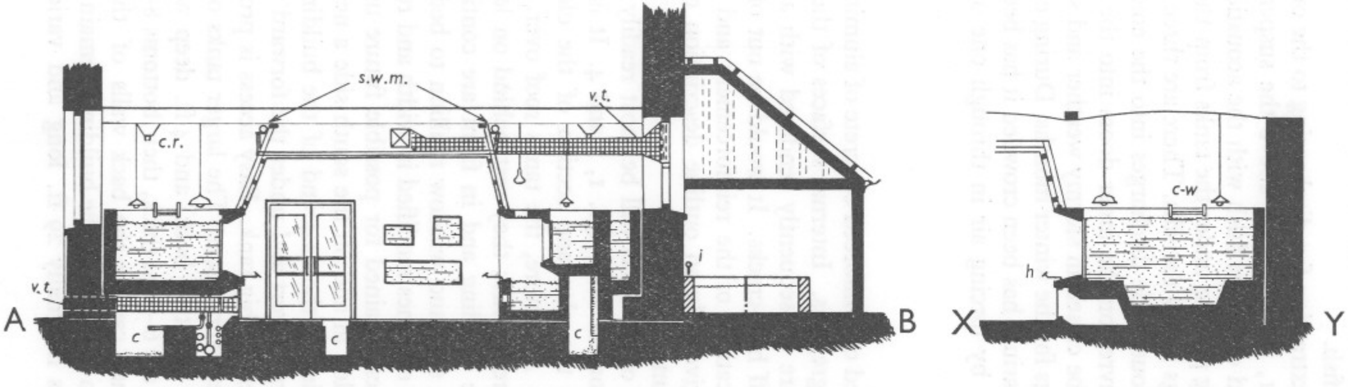


Fig. 2

Text-figs. 1 and 2. Plan and sections of the new aquarium and new outside circulation. Water in the exhibition tanks is indicated by line and dot stippling. *c*, sea-water return culvert; *c.b.*, circulation bench; *c.r.*, overhead conveyor rail (Henderson track); *c-w*, cat-walk; *h*, hand-rail; *i*, inflows; *o*, overflows; *p.b.*, plunger bucket; *s*, sill; *s-w*, swim-ways; *s.w.m.*, sea-water main.

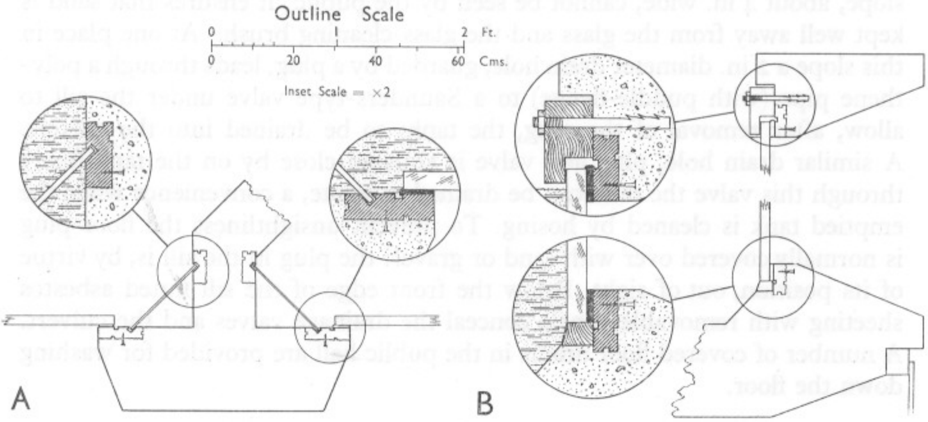
in the sill, about 3 ft. above floor level and nearly 2 ft from the glass, gives some protection to the latter and to the label frames and is a comfortable support to lean on whilst watching the fish.

The hall is ventilated by an extraction fan discharging to the outside at the north-west corner (Text-figs. 1, 2). Trunking above the suspended ceiling draws air through three louvred openings flush with the acoustic tiling. Air enters the hall through trunking passing under the tanks from the outside of the building to louvred openings below the sills. There are three such trunks on each side, but one on the south side discharges into the emergency exit passage, and then through louvres on the inner doors into the public hall. Louvres on the south side can be closed in stormy weather and storm covers are fitted on the outside openings for the winter months. During exceptionally hot calm weather when the aquarium has been crowded it has been necessary to augment normal ventilation by forcing air in through one of the intake trunks on the north side.

Basic construction of the tanks

The new tanks are constructed of reinforced concrete of aluminous cement mixed with local sands and aggregates. Internal surfaces of the back walls and parts of the side walls were subsequently rendered with a waterproof cement and sand mix to seal off hair-cracks. It would be out of place here to give full engineering specifications of the reinforcement and methods of construction; it is feasible to give only an outline description of the tanks as they can be observed in a completed state.

The arrangement and shapes of the tanks will be most readily understood by a study of the plan and sections in Text-figs. 1, 2 and 4. It is instructive to compare these figures with the plan and section of the old aquarium (Wilson, 1952, text-figs. 1, 2). As before, the tanks roof over culverts returning overflow water to the reservoirs; they rest behind on ledges at the bases of the main walls of the building and in front are continuous with concrete pillars extending each stile and window mullion to bedrock below floor level. The culverts are the old ones modified in width and re-asphalted. The old central culvert has been retained for possible future use. The old drainage trenches have been filled in and on the south side a new trench to carry services to the laboratories at the east end of the building has been excavated alongside the southern culvert and under the forward parts of the tanks. These services pass under the big tank. Easy access is provided to all culverts and to the service pipes everywhere. The larger tanks on the north and south sides are 6 ft. wide (front to back) and 4 ft. deep with a water depth of 3 ft. 6 in. Their walls are 6–7 in. thick, their bottoms 8–9 in. thick. Creosoted soft-boards used when casting the back walls of the tanks, to prevent the concrete adhering to the walls of the building, remain in position. The big tank at the east end is internally 29 ft. long and varies in width from about 8 ft. 4 in. at the centre to about 9 ft. 3 in. near each end. The bottom of this tank is about 10 in. thick, and at the north end it drops down to a lower level over an area irregular in shape, thereby increasing the water depth at this place by about 1 ft. 3 in. The small tanks with a water depth of rather less than 2 ft. 6 in. occupy the corners between the ends of the big tank and the north- and south-side series. On the north side at the west end a shallow triangular tank overlaps a floor tank which is divisible into two with a removable partition or, as at present, by built-in rockwork. The floor tank is viewed only through the water surface and is designed for the display of flatfishes on contrasted bottom shingles. Except for this floor tank the water surface in all the tanks is at a uniform height, permitting openings to be made between tanks as described below (p. 402).



Text-fig. 3. A. Plan of a stile between a triangular tank on the right and a larger tank on the left, including a portion of the dividing wall with polythene sheets slid into slate slots to form inflow ducts. Inset are details of slotted slate inserts keyed to the concrete by grooving and rustless-steel screws. In the right inset is shown the edge of a glass pane with sealing compound ('Glasticon', drawn solid black) between it and the slate.

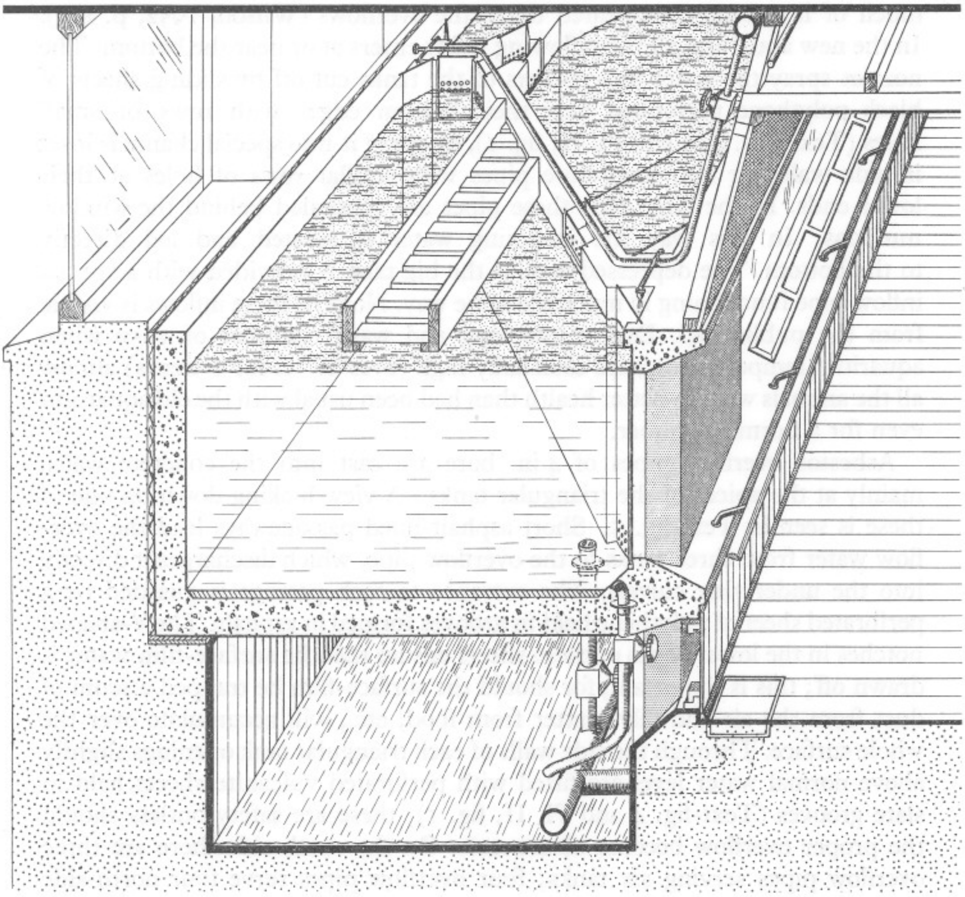
B. Section of a tank front showing lintel walk-way and sill. Inset above are details of teak turnbuckle on rustless-steel rag-bolt, top edge of glass, water level, etc. Inset below shows bottom edge of glass resting on teak block on ledge of sill with details of grooved slate inserts, sealing compound, etc.

Except for the shallower tanks all the window openings are of uniform size, 5 ft. 7½ in. long by 3 ft. high. One advantage of this uniformity is that a single spare pane of glass fits all tanks except the shallow ones. The glass panes, 1 in. thick, overlap the window opening 1½ in. all round. These openings are formed of slate inserts keyed to the concrete (Text-fig. 3). The slates are grooved to give facings exactly 1½ in. wide. This is necessary to achieve uniformity of pressure on the sealing compound and to aid in positioning the glass. The glass is pressed by water pressure against the sealing compound 'Glasticon' ('Glasticord' 304) laid in strip form on the facings (for method of glazing see Wilson, 1952, p. 195). A single teak turnbuckle fixed to the frame above the middle top edge of each pane prevents accidental falling inwards of the glass when the tank is emptied.

The top edges of all window openings are 5 ft. 7 in. above floor level all round the aquarium. The heads or lintels are wide and flat topped, they carry the sloping sides of the suspended ceiling and form convenient walk-ways for servicing the tanks (Pl. II, fig. 1), especially for glass-cleaning. The sills are also wide and carry externally the label frames and support the hand-rail already described. Within each tank the sill provides a ledge $1\frac{1}{2}$ in. wide on which the bottom edge of the glass pane rests, though indirectly with two teak blocks near either end between it and the concrete (Text-fig. 3). From this ledge the sill slopes downwards at 45° to the tank floor (Text-fig. 4). This slope, about 4 in. wide, cannot be seen by the public; it ensures that sand is kept well away from the glass and the glass-cleaning brush. At one place in this slope a 2 in. diameter drain hole, guarded by a plug, leads through a polythene pipe (with puddle-flange) to a Saunders-type valve under the sill to allow, after removal of the plug, the tanks to be drained into the culvert. A similar drain hole, plug and valve is situated close by on the tank floor; through this valve the tank can be drained to waste, a convenience when the emptied tank is cleaned by hosing. To prevent unsightliness the floor plug is normally covered over with sand or gravel: the plug in the sill is, by virtue of its position, out of sight. Below the front edge of the sill fluted asbestos sheeting with removable panels conceal the drainage valves and the culvert. A number of covered floor drains in the public hall are provided for washing down the floor.

Circulation

At the time of writing the same two centrifugal pumps mentioned in a previous paper (Wilson, 1952, p. 204) maintain the circulation, but new pumps of larger capacity will be installed in the near future. The old 4 in. vulcanite main rising from the engine room in the north-west corner (Text-fig. 1) feeds into a new 3 in. black polythene ('Alkathene') pipe which divides into two branches, each controlled by a Saunders valve, one to the north-side tanks and one to the south. These two mains run close to the true ceiling above the corner of the suspended ceiling (Text-figs. 2, 4); there they are readily accessible. Cleaning eyes are provided at bends where needed. From these high-level mains down-dropping $1\frac{1}{2}$ in. pipes, also of black polythene and controlled by Saunders valves, lead through smaller branches to nozzles injecting water into the tanks (Text-figs. 4, 5 and Pl. II, fig. 1). In the old aquarium the mains lay along the tops of the tanks not far above water level and numerous nozzles injected water and air bubbles into the tanks. Not only were these mains an obstruction to servicing but the inflow method was inefficient, for only a portion of the water ever reached tank bottom and



Text-fig. 4. Section through a north-side tank incorporating perspective view facing east and showing portions of three tanks and part of the public hall. Behind the tank is the main wall of the building with a window. The back of the tank rests on a footing of the wall, but indirectly on copper plates forming a sliding bearing to allow for possible movement; the plates are sealed from the sea-water circulation. Between the back wall of the tank and the wall of the building is a layer of creosoted soft-board which during construction prevented the liquid concrete from adhering to the building. Under the tank is an asphalt-lined sea-water return culvert within which is a drain pipe running to waste From this drain pipe there is a connexion, through a valve, to the tank floor and through an open pipe another branch leads to a covered sump in the public hall. A drain in the tank sill, controlled by a valve, can discharge water into the culvert and so back to the reservoirs. At the apex of the triangular tank there is an overflow serving all three tanks, a swim-way between the two larger tanks, and to the latter an inflow each. These structures are shown in greater detail, viewed from above, in Text-fig. 5. A portion of a cat-walk is shown, and in the wall on the nearside a safety overflow from the triangular tank is seen. Still farther forward are two inflows, one of them to the triangular tank. The polythene branch pipe, with Saunders valve, serving the inflows, leads down from the sea-water main at ceiling level. Nearby is the main compressed-air pipe, but no valves or branch connexions to this are shown. In the public hall are seen the hand-rail with supports inserted in the concrete sill; label frames between it and the glass; and below the sill, fluted asbestos sheeting down to floor level.

much of it quickly disappeared down the overflows (Wilson, 1952, p. 199). In the new aquarium all the inflowing water enters at or near the bottom. The nozzles spray the water into corners of the tanks cut off by sliding sheets of black polythene perforated near their bottom edges with rows of small holes (Text-figs. 4, 5 and Pl. II, fig. 1), or spray it into special channels inset in side walls, or into large-bore pipes with similar rows of holes at their lower ends. In the large tank these pipes are concealed behind the window mullions. In this way the incoming water is aerated and led directly to the bottom. The depressed area in the big tank is provided with a special inflow pipe functioning in much the same way. None of these inflows is visible from the public hall. During the long and warm summer of 1959 when aquarium temperatures were unusually high (over 18° C for 6 weeks) almost all the animals were in better health than had been usual with the old aquarium even for a normal summer.

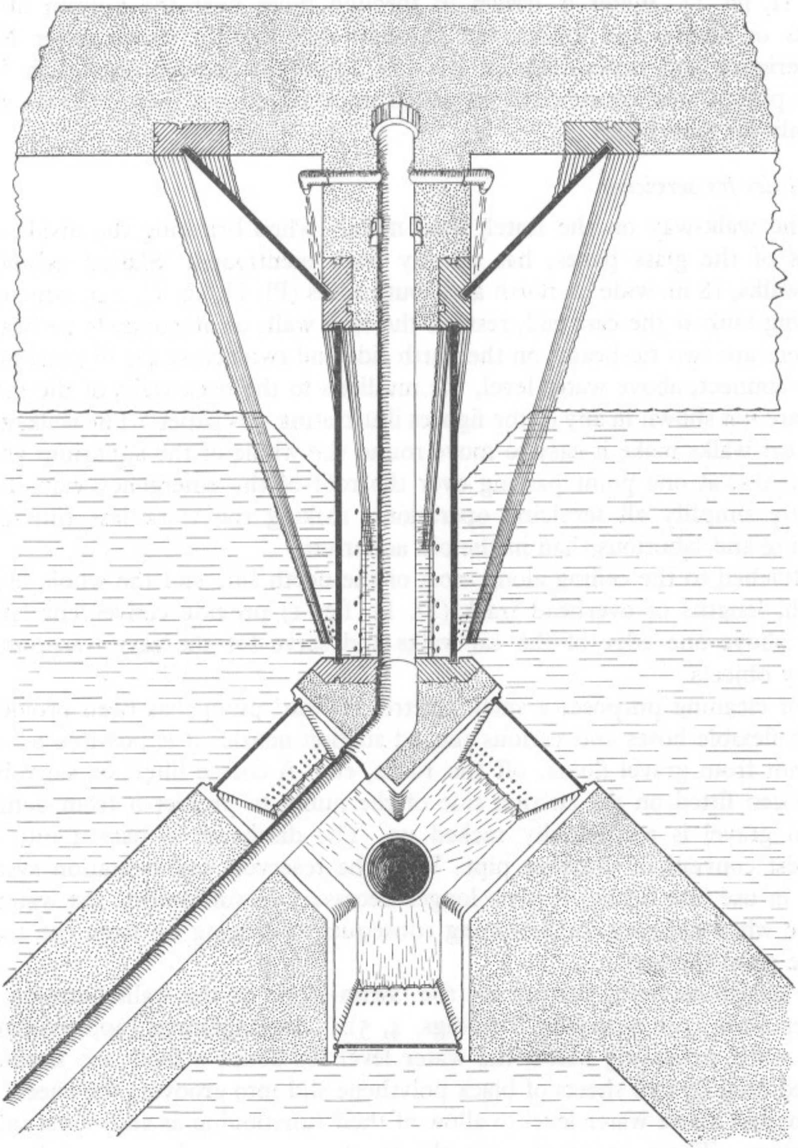
Asbestos overflow pipes of 4 in. bore are cast into the concrete walls, mainly at the apices of the triangular tanks. A view looking down on one of these is seen in Text-fig. 5. Short asphalt-lined passageways lead the overflow water from three tanks to the overflow pipe, which discharges it directly into the underlying culvert. The entrance to each passage is guarded by a perforated sheet of polythene held in grooves formed in asphalt. The V-shaped notches in the lower edges of these sheets ensure that the surface-film water is drawn off; this is important, for should the surface-film be trapped a scum of dust from the air and oily matter from food, etc., will accumulate over the whole surface. Through the side walls of each triangular tank openings slightly above normal water level are fitted with perforated vulcanite sheets held in slate grooves (Text-fig. 4 and Pl. II, fig. 1); these are safety outlets should the proper overflow become obstructed. On the south side there are three overflow pipes serving six tanks; four overflow pipes serve four north-side tanks, the big end tank and the two corner tanks, and all seven tanks can overflow into one another. It is thus impossible for tanks to overfill unless all overflow pipes of a series are simultaneously blocked, which is virtually impossible.

The divisible floor-tank in the north-west corner has two large-bore overflow pipes draining away surface-film water to keep it clear.

Compressed air

In the new aquarium compressed air is used for two purposes only: (1) for lifting water from lower levels to the surface, thereby assisting in maintaining water movement within the tanks; (2) for imparting a rippled surface to bring about a play of light and shade over rocks and gravel, as occurs naturally in shallower regions of the sea.

The air is bubbled up inside pipes of 3 in. bore (concealed behind two window mullions on the north side), or in tank corners behind polythene sheets



Text-fig. 5. Perspective drawing looking down on an overflow serving three tanks, a swim-way between two tanks, and inflows to two tanks. The top faces of the concrete are stippled; of the slate inserts hachured; while the top edges of the sliding polythene sheets are solid black. The top edges of the asphalt lining of the overflow channels are unshaded. Water is shown by dashed lines.

(Pl. II, fig. 1). Water is drawn in through holes near the bottom of the pipes or sheets and gushes out through slits slightly above water level. Experience and experiment in the old aquarium showed that such 'air-pipe pumps' use compressed air much more effectively than diffusers sited openly on tank floors.

Facilities for servicing

The walk-way on the lintel, used mainly when brushing the inside surfaces of the glass panes, has already been mentioned. Slatted ash-wood cat-walks, 18 in. wide on north and south sides (Pl. II, fig. 1), 2 ft. wide over the big tank at the east end, rest on the tank walls or on concrete tie beams. (There are two tie-beams on the north side and two across the big east tank; they connect, above water level, the mullions to the back walls of the tanks, but are not shown in any of the figures illustrating this paper.) The walk-ways and cat-walks make it easy to move round the whole of the aquarium above the tanks, at one point passing over the roof of the emergency exit. They greatly simplify all servicing operations, making the work less time-consuming and laborious than in the old aquarium.

Attached to the ceiling along most of the north side and the whole of the south, lengths of overhead track (Pl. II, fig. 1) provide convenient hand-rails above one edge of the cat-walks and serve for the easy transport of heavy objects.

For cleaning purposes a small electric 'Mono' pump has been provided. With flexible hoses and various shaped suction nozzles it is possible to suck out silt from gravel floors, off the rocks, etc. A coarse filter, or sieve-box, has been fitted on the suction side of the pump to protect it from damage when gravel is accidentally sucked up. The discharge is passed into the nearest convenient overflow pipe. With the reservoir sedimentation system now in use (see below) it is no longer necessary to run muddy sea water to waste when cleaning, necessitating subsequent pumping up from the sea to make good the loss.

A special servicing feature are the 'swim-ways' in the walls between the larger tanks (see especially Text-figs. 4, 5). These openings (approximately 1 ft. wide, extending below the water level for about a foot) are normally closed each by two sheets of black polythene slid into grooves; the sheets are perforated above water level to allow of their functioning as additional safety overflows. These openings, once the sheets are removed, permit fish to be swum from one tank to another as desired. Thus during a major tank-cleaning operation the fish of one tank will be netted and removed to storage tanks in the yard, choosing for netting easily caught and not readily damaged species such as dogfishes and conger eels. The swim-way adjacent having been made watertight (with a bolted-on cover and sealing compound) this tank will be emptied, cleaned and reflooded. The swim-way will then be opened and the fish in the next tank (species such as whiting which are easily damaged by netting) will be driven through into the cleaned tank and shut off there. Their tank in its turn will be emptied and cleaned and made ready for the reception of fish from a tank farther on. Finally, when the whole series has been emptied and cleaned one at a time, the fish will be driven back into their own tanks and the dogfishes and conger eels brought back from the yard. In this way handling of fish will be reduced to a minimum.

In the north-west service area (Text-fig. 1) a number of small asbestos tanks are used to store live food (shrimps, crabs, mysids, worms, etc.) and to accommodate recently caught small animals until such time as they are placed in the exhibition tanks. This corner also houses the 'plunger-bucket' (to work 'plunger-jars' in a laboratory above) which is supplied with water from the north-side series of tanks.

Lighting

It is hardly possible to light an aquarium satisfactorily by daylight. Daylight is too variable in intensity and whatever the orientation of the tanks some will always be more brightly lit than others. When the sun shines strong reflexions of the sunny side will be seen in the darker side unless a curtain, as in the old aquarium, be hung down the middle of the public hall. Too much daylight induces rapid growth of small algae which on dying break up and produce silt; the result is dirty tanks. Back-lighting from windows behind the tanks, a standard feature of many Victorian public aquaria some of which still survive, illuminates the sides of the fish away from the viewer and leaves the backs of the tanks in semi-darkness. A few translucent objects—some sea anemones, ascidians, dogfish eggs, etc.—look well when back-lit but the majority of opaque animals do not. The tanks should be more strongly lit than the public hall, to avoid as far as possible reflexions of people in the glass and to make the tanks appear as a series of bright living pictures within their darker frames.

To exclude daylight the south-side windows have been fitted inside with asbestos sheeting. On the side facing the glass the sheeting is enamelled dark blue, purely as an architectural feature when seen from outside the building. Three windows have been left to open to obtain ventilation while admitting a minimum of daylight (Pl. II, fig. 1). On the north side the windows are sufficiently screened from the sky by the roof over the new outside tanks (see below).

The public hall (Pl. I) is lit mainly by light passing through the tanks aided by a series of recessed lights in the suspended ceiling. It is dim but not completely dark, there being sufficient illumination to see any object on the floor and to allow the Guide Book to be read.

Over the tanks two lines of electric conduit tubing are fixed at main ceiling level, one between the cat-walk and the glass and the other between the cat-walk and the backs of the tanks (Pl. II, fig. 1). At selected points screwed waterproof three-pin sockets are provided from which hang the lights, the heavier ones on chains. Over most tanks there is one main light (usually a 200 W., occasionally 100 W. bulb inside a watertight reflector fitting) 12 in. above water level and 12 in. from the top edge of each glass pane. The back lights are more numerous and more variable; they are mostly 100 W. bulbs in watertight fittings, but fluorescent tubes, protected from damp, are used in places. The back lighting has been arranged to give the most effective illumination of the rock scenery and therefore varies from tank to tank; the front lighting is more constant as it is intended mainly to illuminate the animals. The triangular tanks have only one light, the front one, but special effects can be arranged if needed. Front and back lights are independently fused and switched.

In addition to the main lights, low-wattage bulbs in waterproof plastic bulkhead fittings fixed at a small number of places on the ceiling directly above the tanks (Pl. II, figs. 1) are switched on whenever the main lights are off. These night-lights give sufficient illumination for a number of active fishes to avoid obstructions at night. They probably help the mackerel and some other pelagic fish and they definitely do help Smooth Hounds (*Mustelus mustelus*) and Spur Dogs (*Squalus acanthias*) to avoid bumping their snouts on rocks in the dark. The provision of night-lights was recommended long ago by Saville Kent as a result of his experiences in the former Manchester Aquarium (opened 1874) and their benefit to these same species was noticed independently at Plymouth some years ago.

The floor-tank is lit partly from above by flood-lamps shining down through holes in the canopy over the tank, and partly from lamps behind plate-glass windows in the front wall below water level. The lights are so masked and positioned that they illuminate only the floor of the tank, and none of the surrounds above water level. No lamps or their reflections are visible from normal viewing positions.

At suitable points on the walls behind the tanks three-point 5-amp switch sockets are provided. These are intended for the electric cleaning pump but are available for special or temporary lighting if required.

Rockwork

Few fish are completely at ease in a bare-walled tank. Many invertebrates and some fishes need to be provided with rocky nooks and crannies and with a floor of natural sands or gravels. When an aquarium is intended to attract a paying public the appearance of this rockwork and the treatment of the tank walls is of paramount importance in providing an aesthetically pleasing background against which the animals are viewed. The success or otherwise of the scenic presentation cannot fail to influence receipts at the cash desk.

As the Plymouth aquarium is intended almost entirely for local marine life it was decided to base the scenic presentation on local rocks and of these the beautiful Devonian limestone forming the northern boundary of the Sound was considered most suitable. The rock is very hard and is often bluish white in colour, pink or streaked with pink. Water-worn rocks of various sizes could be picked up from higher tidal levels, and by careful attention to bedding planes could be built into natural-looking cliffs in the tanks. In addition to the use of real rocks rubber-latex moulds were made of small portions of water-worn cliff faces and used to produce artificial rock 'tiles'. One face of each tile exactly reproduces the shape and texture of the natural rock on which the mould was made. The other face, being flat and scored, forms a 'key' for cementing to the back walls, especially of the triangular tanks where it is necessary to keep the thickness of the added rockwork to a minimum. Joints between adjacent rock tiles are filled with cement and sand and modelled to merge the natural mouldings of the various tiles into one apparent solid rock face. A little of the rockwork in one triangular tank is seen in Pl. II, fig. 1. A strong mix (1:3) of sulphate-resisting cement and crushed limestone which had passed a $\frac{1}{4}$ in. sieve was used in making the tiles. Before filling the moulds with the mix the rubber was wetted with a strong solution of 'Teepol' to prevent the adhesion of air bubbles and, after filling, the moulds were vibrated to eliminate all air trapped in the mix. For fixing the tiles to the tank walls a stronger mix (1:2) of sulphate-resisting cement, fine sands and waterproofer was used. Finally, the artificial rock faces were painted to resemble natural rocks. The epoxy resin paints used are non-toxic, are very hard and should withstand repeated cleaning. The final effect is excellent, it being difficult to distinguish artificial rocks from natural and impossible once they are covered with natural growths.

Where the back wall of a tank is left bare it is painted with epoxy resin paint of a moderately dark-green shade to simulate the effect of the greenness seen on looking through many feet of sea water. Near the backs of certain tanks frosted (sand-papered) sheets of Perspex pleasantly diffuse the background to give an appearance of distance; they eliminate shadows which would otherwise show on the walls. Scenic paintings of apparently distant rocks on the walls behind such sheets increases this illusion of remote vistas. The sheets are mostly 6 in. in front of the back wall of the tank, but sometimes are farther away and fish allowed to pass behind. They are held by slotted slates hidden in the rockwork. In arranging such sheets it is essential that side and bottom edges be concealed from view, for if seen the illusion is destroyed.

The angled-out side walls of the larger tanks are painted white (Pl. II, fig. 1), again with epoxy resins. This white surface is, of course, invisible to the public and it helps to reflect back into the tank some light which would otherwise be lost. To conceal the far corners of these tanks, with their inflows and swim-ways, rock cliffs are built against the side walls a little in front of them.

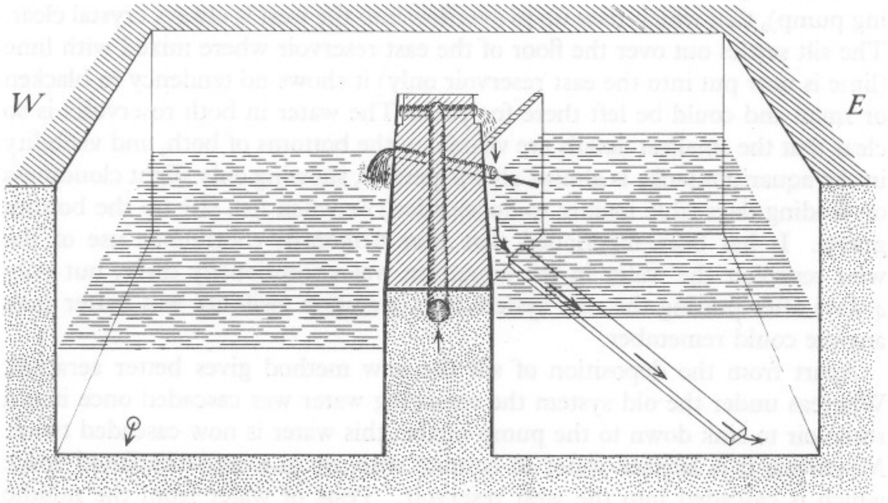
Fish can pass out of sight behind these cliffs but most fishes remain in view. Only lobsters, dogfishes, conger eels and wrasses have been troublesome, often hiding in the concealed corners, and special measures are taken to deal with them. Thus if there are more lobsters in a tank than there are hidden corners some will be forced to occupy holes in full view. Fish swimming into view from behind these cliffs and disappearing again behind them seem to come and go as they would naturally do among rocks in the sea.

After the rockwork was built the bottom of every tank was covered with a layer of sulphate-resisting cement and sand, to which a suitable yellow colouring agent had been added, and rendered to a thickness of an inch. While still wet the rendering was strewn with sand or gravel, gently patted in by hand and given a rippled surface as on a sandy sea shore. Now when fish disturb the loose sand or gravel the rippling helps to retain it in position and where patches of floors are uncovered they match well the sand or gravel and do not look like bare concrete. It is important that the bottom screeding be carried out after the rockwork is in position so that rocks emerge from it as from a natural deposit.

Aquarium reservoirs and water treatments

The provision of clean well-aerated sea water of as near normal chemical and physical constitution as possible is essential to the well-being of an aquarium. Until very recently the water supplied to the tanks of the Plymouth aquarium (from reservoirs for a description of which see Wilson, 1952, p. 204) has always been loaded with varying quantities of silt, although generally satisfactory in other respects. Quite early in the history of the place much effort was expended to free the water from silt, as well as to improve it in other ways. There is frequent reference to these efforts in early Reports of Council and Director's Reports published in early volumes of the *Journal*. Various filters were devised which seem to have functioned for a time but which cannot have proved satisfactory for long. Conditions at one time were evidently so bad that doubts were expressed concerning the efficiency of closed sea-water circulation systems and a single use of water, at least for the laboratory, advocated (*J. mar. biol. Ass. U.K.*, Vol. 4, pp. 77 and 417; Vol. 5, pp. 98–99).

The first major improvement to the condition of the circulating sea water was made when regular treatment with slaked lime (to remove carbon dioxide and restore the pH) was instituted sometime after 1922 (Atkins, 1931). The silt trouble remained and occasions when it was possible to view with some clarity the backs of the largest tanks through 9 ft. of water were regarded as almost noteworthy. Most of the silt was formed in the tanks by the decay of plant growths, the breaking up of faeces, etc., and it was kept in suspension by the stirring activities of the animals, especially bottom fishes. All but the heavier components were carried away in the overflow water and discharged at the surface into one of the two underground reservoirs. From this reservoir water was being drawn off to the pumps at a point about 3 ft. from the bottom, and with it any silt still in suspension. There was thus a steady build-up of suspended particles and the longer the water had been circulating the cloudier it was. The cloudiness of the water in the reservoirs was such that the bottom at a depth of 11 ft. was rarely visible; often it was not possible to see anything at even half that depth. Allowing each reservoir to rest and sediment alternate weeks was only partially successful in clearing the water (see below). The system has been described and criticized in Wilson, 1952, pp. 204 and 209. A method of sedimenting off the silt there suggested has now in modified form been adopted with excellent results.



Text-fig. 6. Diagram of the sea-water reservoirs (not to scale and with roof omitted) to show method of circulation now in use. The direction of water flow is indicated by the arrows.

The method now in use involved no more than minor modifications to the existing reservoirs. These are shown diagrammatically in Text-fig. 6. Water returns from the aquarium along a 1 ft. diameter pipe in the wall dividing east and west reservoirs. At its northern end there is a T-junction where sluices divert the water to one or other of the reservoirs as required; in the old days it would be the reservoir from which water was being pumped, there being then no communication between reservoirs.

During the construction of new underground reservoirs for the new laboratory circulation (see below) the east reservoir had to remain empty for 6 months and only the west reservoir was in use. During this period the water became so dirty that in the aquarium anything farther from the glass than about 2 ft. disappeared from view in a fog of suspended silt. This gives some measure of the partial success of the old method of alternating reservoirs. While the east reservoir was empty a wall was built across its north-west corner and from the bottom of this wall a culvert of brick sides with removable slate top was constructed across the reservoir floor to near its south-east corner. A 6 in. drain pipe was inserted through the dividing wall at the north end, passing under the larger return pipe from the aquarium. With both reservoirs flooded the return water now discharges into the corner cut off by the wall and passes along the culvert to emerge near the south-east corner at the bottom as shown by the arrows in Text-fig. 6. This brings about a continuous overflow of surface water from the east to the west reservoir from whence it is drawn off to the pump through the old suction pipe in the south wall. However dirty the incoming water (as with silt-laden water from the discharge of the cleaning pump), that which rises up to overflow into the west is always crystal clear. The silt settles out over the floor of the east reservoir where mixed with lime (lime is now put into the east reservoir only) it shows no tendency to blacken or smell and could be left there for years. The water in both reservoirs is so clear that the smallest details are visible on the bottoms of both, and visibility in the aquarium tanks is almost always perfect, showing only slight cloudiness on feeding days (due mainly to defaecation) or when fish stir up the bottom gravel. It has been mentioned that after 6 months continuous use of the west reservoir the water in the aquarium was exceptionally dirty, but only 4 days after putting the new system into operation visibility was better than anyone could remember.

Apart from the deposition of silt the new method gives better aeration. Whereas under the old system the returning water was cascaded once into a reservoir to sink down to the pump intake, this water is now cascaded twice. Moreover, it is surface water in contact with air in a well-ventilated space which is cascaded into the west reservoir. Tests of water from the middle depths of the latter have shown close approximations to 100% oxygen saturation.

Means are provided whereby it is easy to revert to the old system of using one reservoir only. This is occasionally necessary for a day or two while one or other of the reservoirs is emptied and cleaned. The method of refilling from the sea was described in Wilson, 1952, p. 205. Sometimes the west reservoir is only partially emptied and the system freshened with new water from the sea pumped into the east reservoir.

The total quantity of sea water held by the reservoirs is about 110,000 gallons when both are completely full, while the total quantity of water in aquarium and service tanks is roughly 17,000 gallons. At the present time the water is circulated at a rate of about 3000 gallons an hour (for description of the pumps see Wilson, 1952, p. 204). This rate is barely adequate, especially in hot weather, and it is desirable to increase the rate to 4500 gallons per hour or even more.

NEW CIRCULATION

An ever-increasing need for more live-specimen storage accommodation, and for research purposes cleaner water less heavily stocked with animal life, led to a decision to build an entirely new circulation system independent of the main aquarium and its ancillaries. Thus, commencing in October 1955 new reservoirs were excavated in the yard between south and north buildings and a new series of outside tanks were built to replace the smaller series illustrated and described in Wilson, 1952, pp. 202–3. The new system was brought into operation for the first time early in September 1957. The contractors for these new reservoirs and new outside tanks were Messrs A. N. Coles (Contractors) Ltd., Plymouth.

New reservoirs

A large hole was excavated in hard limestone to the east of the aquarium reservoirs. In this hole new reservoirs were constructed in concrete (using sulphate-resisting cement) and lined with a rendering of waterproof concrete coated with bituminous paint. They were roofed over at road level with concrete and tarmacadam. The roofing is designed to take a load of 12 tons. At convenient places manholes give access to the reservoirs below. Each reservoir holds about 16,000 gallons of sea water when full and there is a well-ventilated air-space of about 2 ft. between the underside of the roof and the water surface. The dividing wall between the reservoirs has three wide openings 8 ft. 9 in. above reservoir floor level. Water returning from the tanks cascades into a partitioned-off space in the south-east corner of the east reservoir and is there forced to descend to the bottom where silt is deposited. As this east reservoir fills up it overflows the dividing wall through the openings mentioned and cascades into the west reservoir. The depth of the water as it passes over the flat top of the 12 in.-wide wall is very shallow; thus the whole volume of the water as it circulates is at these places brought into close contact with air. From a position 4 ft. above floor level at the west end of the west reservoir the water is sucked away through a black polythene pipe of 3 in. bore to the pumps. The east reservoir is limed weekly through an inspection cover. Provision is made for working from either reservoir only while the other is emptied and cleaned. Each reservoir is provided with a drain hole and plug at its south-west corner and the floor slopes downwards slightly to the drain hole. The 4 in. drain pipe passes under the floor of the new west reservoir and passes through the south end of the old east reservoir of the aquarium circulation to join the main drain. The depth of water in the new reservoirs varies between 8 and 9 ft. when full. The reservoirs are filled through a 4-in. bore iron pipe and through valves connecting with the pumping system used for filling the aquarium reservoirs (Wilson, 1952, p. 205). Compressed air can be supplied to the west reservoir should it ever be needed.

Electric lights in watertight bulkhead fittings are fixed to the roof of each reservoir and are switched from the pump-room in the basement of the south building.

New outside tanks

Under a new roof a new series of outside tanks was used for the first time in September 1957. They comprise (Text-fig. 1 and Pl. II, fig. 2) three blocks of concrete tanks (painted internally with bituminous paint) and nine large (100 gallon) and four small (20 gallon) asbestos tanks on raised plinths (Text-fig. 1). A double tier of slate shelving, built partly against the main building and partly against a wall at right angles to it, forms a circulation unit for bowls and jars. Four of the concrete tanks are divisible by asbestos sheets sliding in grooves; a fifth is bowl-shaped to accommodate squid and cuttlefishes. The water depth of the smaller concrete tanks is roughly 19 in., while the water depth of the large central tank can be varied at will at 23, 31 and 36 in. by placing rubber bungs in the lower overflow holes. All overflow pipes pass down inside the thickness of the tank walls and are fitted with plastic bowl-shaped sieves ('salad-shakers' from a local store) to prevent the ingress of large objects. These overflows discharge into a culvert below ground level which returns overflow water to the reservoirs. The culvert and the lower ends of all overflow pipes are readily accessible through a series of manholes. Inflow pipes are also within the thickness of the walls and discharge into the tanks close to the bottom.

The asbestos tanks are fitted with black polythene piping for inflows and overflows. They can easily be removed and other tanks of different sizes put in their place.

At the time of writing, all tanks east of the circulation benches are supplied from the new reservoirs, while the benches themselves and the tanks west of them are on the aquarium circulation. It is possible for the largest concrete tank and the three asbestos tanks near its western end to be supplied with water from the aquarium circulation should this ever be necessary.

Electric lights for viewing the outside tanks at night are provided under the roofing. It is intended at some future date to fit shutters which in summer will slide up out of the way under the roof, but which in winter can be pulled down to enclose the tank space and protect the system from frost.

New pumps

The new circulation is maintained by paired 'Mono' pumps with stainless-steel impellers inside rubber stators. Driven by 3 h.p. three-phase motors each unit delivers about 3600 gallons an hour. One pump is run for several weeks while the other is serviced and rests as a stand-by. Adjustments to the gearing of the V-belting will enable these pumps to give a greater output should this in future be needed. At present the output is more than ample as it is serving only the outside tanks and those on the first floor of the main laboratory (as described in Wilson, 1952, p. 203,[1] and illustrated in Russell, 1948, pl. XIX).

Circulation efficiency

The total capacity of the outside tanks and those on the first floor is about 2600 gallons; this being less than a twelfth of the reservoir capacity, a much smaller proportion of tank volume to reservoir volume than in the aquarium circulation. The relative rate of flow of the water is also much greater. Even when eventually more experimental tanks in the new block of buildings now being planned are added the new circulation will contain less animal life per unit volume than the aquarium circulation, and be relatively more efficient in every way except temperature stability. There is no regular means of heating or cooling either circulation, and while temperature changes are slow the new circulation is more affected by the weather than is the old. This is because the total volume of water is less than in the aquarium circulation and a greater proportion of it is exposed to air temperature and wind in the yard. When shutters are fitted to close in the outside tanks in winter it will be possible to reduce the rate of loss of heat, though it is doubtful if shutters will help to check rise of water temperature during hot days in summer.

My thanks are due to Mr G. A. W. Battin for making the drawings for this paper and Mr A. C. G. Best for help with the photography.

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[1] Except that the overflow water from these main laboratory tanks no longer runs into exhibition tanks in the aquarium below but is conducted by new piping to the return culvert to the new reservoirs.

EXPLANATION OF PLATES

PLATE I

General view of the new aquarium from the public entrance lobby. Note the handrail, label frames, ceiling with inset lights, etc. (A photograph of the old aquarium from almost the same viewpoint is reproduced in Russell, 1948, pl. XXIII, fig. 1.)

PLATE II

Fig. 1. View along the tops of the tanks of the south side from the west end. Note especially the shapes of the tanks, the lintel walk-way and cat-walks, the overhead conveyor track, details of inflows and overflows so far as visible, sea-water and compressed-air pipes (one of the latter on tank-back near right foreground), light fittings, etc. Compare especially with Text-figs. 4 and 5.

Fig. 2. View of new outside circulation tanks and circulation bench from the western end. Note in right foreground a pair of concrete tanks painted internally with black bitumen. Further on is the double-tiered circulation bench for bowls, and, in front, four small asbestos tanks on a low circulation table. Behind the circulation bench the outer of three large asbestos tanks, on a raised plinth, is seen. Farther on still is the large and deep concrete tank, then a pair of shallower concrete tanks similar to those in the foreground. Beyond these part of a row of three large asbestos tanks is just visible. (For photographs of the old outside circulation which these tanks replace see Russell, 1948, pl. XXII, fig. 2, and Wilson, 1952, text-fig. 4).

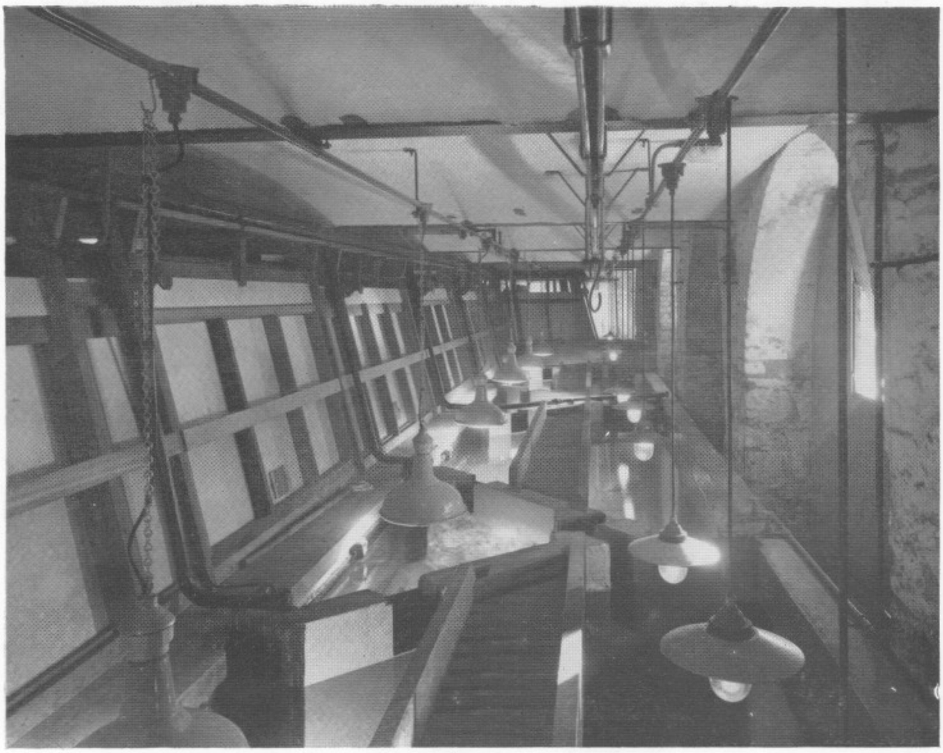

Fig. 1.

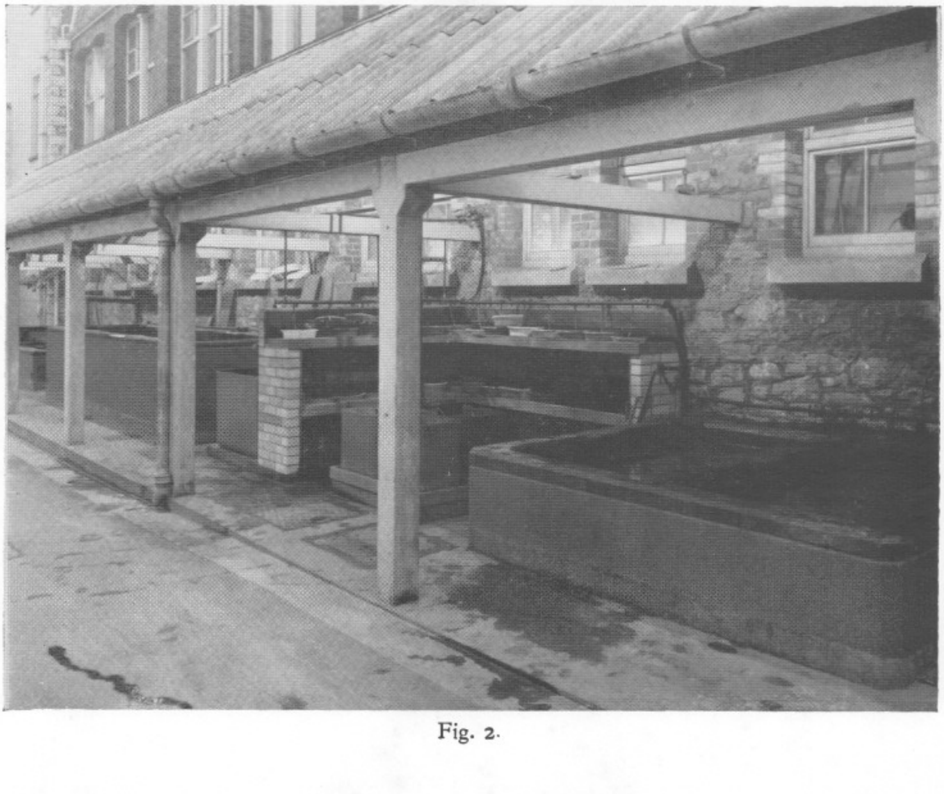

Fig. 2.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Boney, A. D., Corner, E. D. S. & Sparrow, B. W. P., 1959. The effects of various poisons on the growth and viability of sporelings of the red alga *Plumaria elegans* (Bonnem.) Schm. *Biochem. Pharmacol.*, Vol. 2, pp. 37–49.

Mercury, silver, copper and arsenic are more toxic than the non-metallic inhibitors hydrocyanic, hydrazoic, iodoacetic, fluoroacetic and malonic acids and 2:4-dinitrophenol to sporelings of *Plumaria elegans* in sea water at pH 8·1. Mercury and silver are more toxic than copper and arsenic, and the toxicities of mercury and arsenic are greatly increased when these poisons are used as lipophilic organic compounds (e.g. phenylmercuric chloride and phenarsazine chloride). All heavy metals are less toxic when used in the presence of reduced glutathione.

The toxicities of an homologous series of primary *n*-alkyl-mercuric chlorides increase to a maximum with that of $n\text{-}C_5H_{11}HgCl$. Lipoid solubilities based on methyl-oleate: sea-water partition coefficients correlate with appropriate toxicity data for the first three members of the series, but those of $n\text{-}C_4H_9HgCl$ and $n\text{-}C_5H_{11}HgCl$ increase without any corresponding rise in toxicity. The 'cut-off' in relative toxicities within the homologous series is not found in complementary experiments with crustaceans.

Mercuric iodide is much more toxic than $HgCl_2$ to *Plumaria* and crustaceans, but whereas various organic compounds of mercury become markedly more toxic to crustaceans when used in the presence of excess KI, their toxicities to *Plumaria* are not increased. E.D.S.C.

Bursa, A. S., 1959. The genus *Prorocentrum* Ehrenberg. Morphodynamics, Protoplasmatic Structures and Taxonomy. *Canad. J. Bot.*, Vol. 37, pp. 1–31.

The morphodynamics of *Prorocentrum* have been studied comparatively in cultures and in plankton. Plankton populations show little morphological variation. In cultures a variety of forms, often similar to other species of *Prorocentrum* which have been described from distant seas, are found. Morphological variation in *Prorocentrum* species depends upon various life phases, individual features of the clones, and various types of cysts. Formation of the morphological aberrants is also affected by ageing of cultures. All protoplasmatic structures, including the cell membrane, possess their own particular features, changing in course of life cycle. Since both physiological and morphodynamic metabolisms are inseparable in their activities, it is useful to complete taxonomic diagnoses with physiological observations. Five new species are described: *Prorocentrum cordiformis*, *P. pomoideum*, *P. pyrenoideum*, *P. redfieldi* and *P. levantinoides*. Morphodynamics in *P. micans* and *P. scutellum* was also studied. Most observations were made *in vivo*. Specific morphological differences in form and structure of protoplasmatic organelles were demonstrated in each species concerned. An attempt was made also to base taxonomic diagnoses upon the apical tooth, trichocysts, and membrane structure. A.S.B.

CARLISLE, DAVID B., 1959. On the neurosecretory system of the brain and associated structures in *Sipunculus nudus*, with a note on the cuticle. *Gunma J. med. Sci., Maebashi*, Vol. 8, pp. 183–94.

In *Sipunculus nudus* a pair of dorsally situated postero-lateral groups of neurosecretory cells in the brain contain each about thirty large cells. The axons run forward to the unpaired sensory organ, a cavity in the brain connected to the mouth region by a ciliated canal. Here the axons make abrupt loops among the sensory cells of this organ and then run into the finger organs, where they terminate in typical neurohaemal endings, vertical to the blood space surrounding the organs. These club-shaped endings are filled with a secretion which has staining properties different from those of the material found more proximally in the axons and cells. The likeness of this system to the hypothalamo-hypophysial system of vertebrates and to the major endocrine systems of crustaceans and insects is emphasized.

The cuticle consists of protein with no trace of chitin or mucopolysaccharides.

D.B.C.

CARLISLE, D. B. & ELLIS, PEGGY E. 1959. La persistance des glandes ventrales céphaliques chez les Criquets solitaires. *C.R. Acad. Sci., Paris*, T. 249, pp. 1059–60.

The ventral glands of locusts, which are homologous to the prothoracic glands of Lepidoptera and probably to the Y-organs of crustacea, normally disappear in the adult insect. In locusts in the solitary phase, however, they may persist in a functional condition.

D.B.C.

COOPER, L. H. N., 1957. Some chemical and physical factors controlling the biological productivity of temperate and tropical oceanic waters. *Proc. 8th Pac. Sci. Cong.* 1953, Vol. III A (received by the author 1959).

Differences in conditions of productivity in tropical and temperate latitudes were discussed. A pattern for observation and experiment in tropical seas was proposed. Much of the material in the paper has now only historic interest.

L.H.N.C.

CORNER, E. D. S., 1959. The poisoning of *Maia squinado* (Herbst) by certain compounds of mercury. *Biochem. Pharmacol.*, Vol. 2, pp. 121–32

When *Maia* is immersed in sea water containing added $HgCl_2$ the concentration of the poison in the blood eventually rises above that in the external medium; the concentration in the antennary glands above that in the blood; and the animals excrete small but increasing amounts of mercury in the urine. Most of the poison present in the blood is attached to protein and the concentration of mercury in the blood remains constant for several weeks after poisoned animals are returned to the sea. Mercury also concentrates in various other body tissues, and very large amounts are found on the gills. Similar results are obtained when the poison is administered to the animals by injection. When, however, the poison used is n-$C_5H_{11}HgCl$, although mercury again concentrates at the gills and in various internal organs, the amount detected in the blood is very small and none is found in the urine.

When the animals are immersed for progressively longer times in sea water containing added $HgCl_2$, or are injected with increasing amounts of the poison, the total quantity of amino-N in the urine increases, although that in the blood remains constant. The urine : blood ratio of amino-N also rises when the animals are poisoned with n-$C_5H_{11}HgCl$

although, in this case, the level of amino N in the blood rises as well as that in the urine. Animals poisoned with $HgCl_2$ and then returned to the sea show an abnormally high urine: blood ratio of amino-N several weeks later. By contrast, poisoning with $HgCl_2$ has no effect on the urine: blood ratio of total sulphate. E.D.S.C.

LOWENSTEIN, O. & WERSÄLL, J., 1959. A functional interpretation of the electron-microscopic structure of the sensory hairs in the cristae of the elasmobranch *Raja clavata* in terms of directional sensitivity. *Nature, Lond.*, Vol. 184, pp. 1807–8.

An electronmicroscopic study of the sensory epithelia in the ampullae of the semicircular canals of the labyrinth of *Raja clavata* showed that the hair processes of the sensory cells are compound structures consisting of a number of protoplasmatic filaments, one of which has the typical electron-microscopic structure of the kinocilium, namely nine peripheral plus two central longitudinal fibrillae. This kinocilium is always found on one and the same side of the hair process in a given sensory epithelium and is placed on that side of the sensory hair process which faces in the direction in which the hair process is deflected on excitatory cupula displacement. It appears that this arrangement may be of fundamental functional significance. O.L.

POTTS, W. T. W., 1959. The sodium fluxes in the muscle fibres of a marine and a freshwater lamellibranch. *J. exp. Biol.*, Vol. 26, pp. 676–89.

The efflux of ^{24}Na from the isolated ventricles of *Mytilus* and *Anodonta* has been measured at 15° C and at 5° C. The efflux of sodium in each case is divisible into an extracellular and an intracellular portion except at 15° C in *Anodonta* where the two portions are not clearly distinguishable. The mean rate constant for the efflux of sodium from *Mytilus* ventricle is $2{\cdot}44\ h^{-1}$ at 5° C and $5{\cdot}6\ h^{-1}$ at 15° C. The mean rate constant for *Anodonta* ventricle at 5° C is $4{\cdot}6\ h^{-1}$. The efflux of sodium from the muscle fibres of *Mytilus* ventricle averages 12×10^{-6} mM/cm^2/sec at 5° C and 27×10^{-6} mM/cm^2/sec at 15° C. For *Anodonta* at 5° C it averages $3{\cdot}1 \times 10^{-6}$ mM/cm^2/sec. If the efflux is maintained entirely by an active process then the energy required for the extrusion is 0·26 cal/g/h at 5° C and 0·63 cal/g/h at 15° C for *Mytilus* muscle and 0·046 cal/g/h at 5° C by *Anodonta*. W.T.W.P.

WICKSTEAD, J., 1960. A new record of *Mytilicola intestinalis* Steuer, a parasitic copepod of mussels. *Nature, Lond.*, Vol. 185, p. 258.

Two mature female *Mytilicola intestinalis* Steuer, 7·0 and 8·5 mm long, were recorded from a locality much removed from the limits of their accepted distribution. They were taken free in the plankton in the northern Malacca Strait area, 7° 12′ N., 97° 12′ E. After various considerations, no satisfactory explanation could be given for their capture at such a place in such a manner. J.W.

WICKSTEAD, J. H. & BONE, Q., 1959. Ecology of acraniate larvae. *Nature, Lond.*, Vol. 184, pp. 1849–51.

Several species of acraniate larvae were obtained during a survey of the Indo-Malayan plankton made by the Singapore Regional Fisheries Research Station. Larvae of *Branchiostoma belcheri* Gray were found at a permanent station in the Singapore Strait from mid-October to January. They showed diurnal vertical migratory movements, remaining on the sea-bottom during the day, and rising to the surface at dusk.

Examination of the gut-contents showed that feeding probably only takes place at the bottom. It is suggested that light intensity is the actuating stimulus for the migration (salinity and temperature variations being insignificant), and that it serves both to distribute the species and to enable the larvae to avoid the attacks of nocturnal bottom-feeding predators.

Larvae of *Branchiostoma malayana* Webb, and larvae of the 'amphioxides' type (but belonging to the Branchiostomidae) were obtained at another station, on the surface, at night. This station was over deep water, and examination of the gut contents showed that the larvae fed in mid-water, hence these species are probably truly pelagic, and never live near the bottom. At a third station, 'amphioxides' larvae of *Asymmetron lucayanum* Andrews were collected, which confirms the identification of *Amphioxides pelagicus* Gunther as the larva of *Asymmetron lucayanum*. Q.B.

BOOK REVIEW

DIE WESTKÜSTE SÜDAMERIKAS IM BEREICH DES PERU-STROMS

BY E. SCHWEIGGER

Heidelberg-München: Keysersche Verlagsbuchhandlung GmbH, 1959.

This comprehensive work has been written by a German who has spent thirty years studying the Peru current and its manifold influence on the neighbouring land, sea and air. Its greatest value may be as a critical digest of an enormous literature about the west coast, published in periodicals with limited circulation and mostly in Spanish. The task the author set himself was great and many chapters, naturally, do not cut deep. The author's personal interest has been in oceanography, entirely from a descriptive angle. The methods of dynamic oceanography have not been used. 'El Nino', the perturbation of the Peru current which brings death to myriads of fish and sea birds, is examined at length. It seems that much confusion surrounds the term and anyone wishing to use it would be wise to consult this book to find out what it means. The style is friendly and discursive. Anyone in search of a worth-while problem for study may find one on every page. L.H.N.C.

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, and, since that date, a new library, and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; 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. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. 27 (p. 761) and Vol. 31 (p. 193) of this *Journal*.

The laboratory is open throughout the year and its work is carried out by a fully qualified research staff under the supervision of the Director. 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, physiology and other branches of science. 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.*
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Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the library at Plymouth.

The Commissioners of Inland Revenue have approved the Association for the purposes of Section 16, Finance Act, 1958, and that the whole of the annual subscription paid by a member who qualifies for relief under the section will be allowable as a deduction from his emoluments assessable to income tax under Schedule E.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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CAMBRIDGE UNIVERSITY PRESS
BENTLEY HOUSE, 200 EUSTON ROAD, LONDON, N.W. 1
AMERICAN BRANCH: 32 EAST 57TH STREET, NEW YORK 22, N.Y.

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)