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June 1956

A CONTRIBUTION TO THE BIOLOGY OF IANTHINA JANTHINA (L.)

By Douglas P. Wilson, D.Sc., and M. Alison Wilson The Plymouth Laboratory

(Plate I and Text-figs. 1 and 2)

The summer of 1954 will long be remembered for lack of sunshine, excess rain and frequent high winds over England and Wales. In the south-west of the region the winds from June onwards until the end of the year were predominantly westerly, often reaching gale force, and the total run of the winds was often above average. During the last week of July there were persistent westerly winds from well out in the Atlantic, often strong and reaching gale force at times, particularly on the 27th and 28th. During the last 4 days the winds were generally from the north-west at Scilly and in southern Ireland. They were variable in strength and direction early during the first week in August, but occasionally blew freshly from the south-west. On the 7th it was often blowing strongly from the west, a gust of 50 knots being recorded at Scilly. It was during this first week in August that the first few specimens of *Ianthina janthina* (Linnaeus) came ashore, heralding the most extensive strandings of this species on British shores for very many years.

It is the purpose of this paper to put on record more data than have been available for any previous stranding in England, and to add some observations on the living animal, whose habits are not yet fully known.

It was in mid-August that we first noted the presence of this oceanic surfaceliving mollusc in the Padstow district of north Cornwall, where we had been shore-collecting since the early part of the month. Letters published in *The Western Morning News* and *The Times* on 26 August 1954, describing the mollusc and appealing for information of possible strandings in other districts, brought a number of replies, accompanied by actual specimens or by drawings or descriptions which left no doubt of the identity of molluscs seen by untrained observers, who ranged from holiday visitors, old and young, to beach-combers of long experience. A list of the records, with relevant information, is given below, together with our own observations on strandings. For a better appraisal of the extent and timing of the latter they are plotted on the chart reproduced in Text-fig. 1.

To check whether there had been strandings in southern Ireland a letter was sent to *The Irish Times* and published on 4 September 1954. Among replies from people who had found *Ianthina* there before the only one that gave

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information for 1954 came from Miss Mildred Sheridan, Achill Island, Co. Mayo, who stated that in the previous May, after a particularly violent storm, the strand was covered with the shells. She picked up forty to fifty perfect



Text-fig. I. Map to show positions of strandings of *Ianthina janthina* (L.) listed in Table I. Records for the same locality in the same week are summed. Figures indicate the numbers reported, and where actual numbers are not available S = several, and M = many. Numbers or letters within a single circle are strandings during the first week (1-7 August); within a double circle the second week (8-14 August); within a single square the third week (15-21 August); within a double square the fourth week (22-28 August); within a diamond the fifth week (29 August-4 September). Arrows point only approximately to the positions of strandings which are often not known to within 2 or 3 miles.

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TABLE I. STRANDINGS OF IANTHINA JANTHINA (L.) DURING AUGUST AND SEPTEMBER 1954

Date	Locality	Number	Condition	Recorder
First week (1-7.	Aug.)			
Early Aug. First week	St Agnes, Isles of Scilly St Martins, Isles of Scilly	1 5	Living	Mrs M. Hicks Mrs L. M. Hughes
Early Aug.	Tresco, Isles of Scilly	4	Empty shells	Mrs Ariadne Cook
Second week (8-	14 Aug.)			
8 A110	Gwenver, near Sennen	т	Living	Rev. P. H. T. Hartley
9 Aug.	Treveal Cove, Zennor	2	Living	Miss Tamsin and Mas- ter Timothy Procter
9–10 Aug. 10–11 Aug.	Constantine Bay, near Padstow Widemouth Bay, near Bude	2 48	_	Mrs O. Woosnam-Mills Mrs L. F. J. Gunn
II Aug.	Saunton Sands, near Barnstaple	c. 24 and more on following days	Living	Mrs Doris Wilson
II Aug.	Gwenver, near Sennen	2	Living	Rev. P. H. T. Hartley
10 or 11 Aug. About	Dollar Cove, Gunwalloe Sennen Cove	Several dozen c. 50	Living Living	Mr Frank Sabin Mr T. G. W. Fowler
10-12 Aug.	Braunton Sands, near Barnstanle	c 60		Mrs Wiseman
About 12 Aug.	Saunton Sands, near Barnstaple	40-50	Empty shells	LtCol. L. T. G. Ricketts
Second week	Lundy Island	2	One dead	Miss J. L. Bloom
Second week	Woolacombe	I	· · · ·	Mr J. Crowder
second week	Perranporth	<i>c</i> . 80	Living	Mr S. Chenoweth
Second week	Coast near Polzeath	2	Living	Mr G. Pym
14 Aug.	Porthleven Bodmithan Stone, near Bodotowi	I	Living	Mr H. B. Sargent
14 Aug.	bedruthan Steps, near radstow	1	LIVINg	MIT 1. Roberts
Third week (15-	21 Aug.)			
14-21 Aug.	Porthtowan	About I a	Living	Mr N. A. Wesley
15 Aug.	Trevone Bay, near Padstow	a or A	Living	Mr C. Roberts
15 Aug.	Trevone Bay, near Padstow	I	Living	Master R. J. H. Wilson
19 Aug.	Trevone Bay, near Padstow	Several	Living	M. A. and D. P. Wilson
19-20 Aug.	Constanting Pay, near Padstow	Several	Living	Miss Bridget Hickey
20 Aug.	Harlyn Bay, near Padstow	Many	Living	Miss H. Bibby
21 Aug.	Harlyn Bay, near Padstow	c. 36	Living and re-	M. A. and D. P. Wilson
Fourth week (22-	-28 Aug.)		toning acad	
22-28 Aug.	Porthtowan	About 4 a	Living	Mr N. A. Wesley
		day		
22 Aug.	Hayle Mother Iver's Boy peer Padater	3	Living	Miss Hartnoll
22-24 Aug.	St Agnes, near Perrannorth	2	Living	Mr W F Williams
23 Aug.	Mother Ivey's Bay, near Padstow	I I	Empty shell	Mrs O. Woosnam-Mills
23 Aug.	Daymer Bay, near Padstow	I	Living	Mr S. Lees
23 Aug.	Trevone Bay, near Padstow	Several	Living	M. A. and D. P. Wilson
24 Aug.	Gwithian	2	Living	Dr W D Oliver
About	Widemouth Bay, near Bude	ĩ	Living	Dr E. N. Rudland
24 Aug.	Constanting Paul near Padatam		Empty shall	Mar O Wesser Mills
24 Aug.	Gwithian	Several	Living	Mrs S Bennett
25 Aug.	Trevone and Harlyn Bays, near	Few	Living	M. A. and D. P. Wilson
25 Aug.	Holywell Beach, Newmay	т	Living	Mr P Rayner-Smith
25 Aug.	Perranporth	Ĩ	Living	Miss D. W. Hill
25 Aug.	Porth Kidney Sands, Hayle	c. 30	Some living, some empty	Miss Tamsin and Mas- ter Timothy Procter
27 Aug.	Gwithian	6		Mrs S. Bennett
27 Aug.	Porth Mear, Porthcothan	3		Miss H. M. Spittle
Before 28 Aug.	Woolacombe	I or 2	Living	Miss Jane Asher
Fifth week (20 A	ug4 Sept.)			
29 Aug.	Lelant, near Havle	2	Empty shells	Mrs D C Bazeley
29 Aug.	Constantine Bay, near Padstow	ĩ	Living	Mrs O. Woosnam-Mills
End of Aug.	Perranporth	I		Mr S. Chenoweth
End of Aug.	Bryner, Isles of Scilly	I	Empty shell	The late Major A. A.
About I Sept.	Marloes sand, Dale Fort,	I	Empty shell	Mr J. H. Barrett
	Pembrokeshire			

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Date Locality		Number	Condition	Recorder
Sixth week (5-	II Sept.)			
5 Sept. 5 Sept.	Carbis Bay Braunton Sands, near Barnstaple	Few	Empty shell Empty shells	Mr A. Hutton Mrs Wiseman
Seventh week	(12-18 Sept.)			
12 Sept.	Sennen Cove	I	Living	Mr and Mrs H. H. Sheldon

TABLE I (continued)

specimens and many more were broken. She enclosed the remains of a shell to confirm the identification. Dr J. R. Bruce found one living *Ianthina* sp. washed up in White Park Bay, Co. Antrim, early in July, along with thousands of dead, but fresh, *Velella* skeletons.

It may be assumed therefore that the shoal which stranded in Cornwall in August came in from the Atlantic to the south of Ireland without touching its shores. It seems most unlikely that it was part of the shoal that stranded on Achill Island in May, probably early. The stormiest weather in May was during the first week, and for the rest of that month the winds were mostly below the average.

Records of strandings during the first week of August (see Table I) are scanty. Even though the appeal for information did not appear in the press until 3 weeks later it seems clear that there were indeed few strandings at this time and all were on the Isles of Scilly. One of these was definitely a living mollusc; four of the others were empty shells when found; information is incomplete for the other five. Immediately after the appearance of the press appeal the late Major A. A. Dorrien Smith of Tresco organized a search; only one shell (presumably empty) was found (on Bryher) and was kept by the finder. From these few records it can be inferred that the oncoming shoal, drifting before the wind, almost entirely missed the Isles of Scilly, and passed, in view of what happened later, north of them.

The second week of August brought many strandings on the mainland. Early in the week a living *Ianthina* was found in the Land's End district, near Sennen, and two at Zennor a little farther north; from the middle of the week onwards large numbers were stranded along an extensive length of coastline from Land's End to north Devon. There appear to have been particularly dense concentrations near Bude and in Bideford Bay, but there were also some heavy strandings farther south at Perranporth, Sennen, and on the western shore of the Lizard peninsula. None were recorded at any time farther up the English Channel. The Perranporth record is a little vague as to date, but most probably refers to this period.

During this second week winds were at first more or less westerly, light to moderate, increasing in strength on the 9th to blow strongly from the northwest and continuing fresh from the same quarter on the 10th. Early on the 11th it was a little north of west, later swinging round to the south. It was on

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the 10th–11th that most strandings seem to have taken place, and it was most probably on the 11th at Gunwalloe. The wind continued light south-westerly over the 12th, becoming almost due west on the 13th and dropping in strength.

Relatively few strandings were recorded during the third week and these were mostly in the Padstow district, and towards the end of the week. Winds were at first light to moderate, variable in direction, freshening on the 17th and 18th, until they were blowing strongly from almost due west, veering later to north and decreasing somewhat. They remained fresh and northerly until the end of the week. Northerly winds blow straight onshore in Trevone and Harlyn Bays, but they would also strand *Ianthina* on other parts of the coast if any were sufficiently close offshore.

During the fourth week there were strandings over a longer length of coastline, that from St Ives Bay to Woolacombe. The single record from the Isles of Scilly was of an empty shell which had undoubtedly stranded earlier. Most of the records are of living specimens, never in any great number. The largest number recorded was from near Hayle on 25 August, but an unknown proportion of these were empty and must have been from earlier strandings. Until the 25th the winds were north and north-westerly, mainly moderate; they died away on the 26th, and on the 27th and 28th were light westerly veering north.

For the fifth week the only living mollusc recorded was from Constantine Bay on the first day of the week. Thereafter only empty shells, or presumed empty shells, were found. These were most probably from earlier strandings; and although a living specimen was found at Sennen on 12 September, the invasion was over. That this was due to absence in the area of further living specimens and not to the wind is certain. The week had opened with light or moderate winds from the west, veering to the south-east on 31 August and I September. They were moderate and mainly from the south-west on 2 September, increasing in strength and becoming westerly and strong on the 3rd. On 4 September there was a calm. Light to fresh rather southerly winds followed, becoming westerly. On 9 September it blew strongly from the west and remained fresh and strong until the 12th, on which day the living specimen was found at Sennen. Thereafter, for the remainder of the month winds were often strong from a westerly direction, the total run of the winds being substantially above the average. No more Ianthina came in, but they were followed from mid-September onwards by large numbers of Physalia physalis, which was also abundant on the coast of southern England.

To sum up: excepting for the one notable find of an empty shell at Dale Fort in Pembrokeshire, the strandings were confined to the north coasts of Cornwall and Devon and, in the south, the west coast of the Lizard peninsula. The shoal, or shoals, blown in from the west, missed southern Ireland and barely touched the Isles of Scilly; the main strandings were in the second week of August during a time of fresh or strong north-westerly winds.

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During the third week more, but apparently smaller numbers, came ashore in the middle of the region at a time of northerly winds. Thereafter, the number of living animals found quickly declined and one only was taken at Sennen after the end of August.

Some Previous Strandings in South-West England and Wales

It is known that three species of *Ianthina*—in current nomenclature *I. exigua* Lamarck, I. pallida Thompson, I. janthina (L.)-strand from time to time in south-west England and Wales (Forbes & Hanley, 1853; Fowler, 1947, 1948, 1949; Graham, 1954) as well as in Ireland and Scotland. Mr T. G. W. Fowler, who has searched the beaches at Sennen regularly for many years, tells us, in a personal letter, that the 1954 specimens were 'the first for quite two years'. He remarks that he knows 'there were a few at Constantine Bay in September 1937 or '38'. The main interest in the 1954 strandings is the unusually long length of coastline affected, and probably the numbers stranded were, for that locality, far greater than for very many years. Some correspondents who live on or visit the north Cornish coast and regularly search the beaches there assured us that they had never seen these shells before. We ourselves on numerous visits to the Padstow district from about 1933 had never encountered them. A few older people remembered having seen some washed up about fifty years previously. Mr C. Roberts of Trevone told us he had seen similar shells at Harlyn Bay in 1903 or 1904. Mrs Doris Wilson, writing from Braunton, remarked that her friend 'Mrs Wiseman had found some, only much smaller specimens, about fifty years ago in much the same place' (at Braunton). Miss E. M. Ferguson, writing from Somerset, mentioned finding six empty Ianthina shells at Croyde in North Devon, in 1903 she thinks. There are thus three quite independent witnesses to a stranding about that time, and fairly good evidence that there has not been an extensive stranding of Ianthina along the north coasts of Cornwall and Devon since then.

Mr J. H. Barrett, writing from Dale Fort Field Centre, Pembrokeshire, notified us that about a dozen dead shells and one live specimen were found at West Dale on 6 September 1950. Another dead, but with float, was found on Marloes sands on 20 August 1953. All were identified as *I. britannica* (=I. janthina).

COINCIDENT STRANDINGS OF VELELLA

One of the main foods of *Ianthina* is *Velella*, and it was to be expected that this latter organism would strand with it. We ourselves found a considerable number of living and recently dead *Velella* stranded at Trevone and Harlyn Bay at the same time. Mr T. G. W. Fowler reported to us 'hundreds and thousands of live *Velella*' at about the same time as the *Ianthina* strandings at Sennen. The Rev. P. H. T. Hartley saw many living *Velella* on Gwenver

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beach on 8 August, and stated that they were 'at a density of about one to the yard of tide edge'. Mrs Doris Wilson also saw a few at Saunton at the same time as *Ianthina*. Mr S. R. Nutman had seen many fresh skeletons, one with remains of living tissues, on 30 July at Polzeath. During the first few days of August a small number of living ones were stranded at Wembury near Plymouth. No doubt *Velella* were seen elsewhere but not reported; in order to avoid confusion no mention of *Velella* was made in the letters to the press.

SHELL SHAPE AND GROWTH

The very extensive and confusing synonymy of the genus has recently been clarified by Laursen (1953). Of the many species of *Ianthina* described he recognizes only five, of which only *I. janthina* is viviparous. He figures variations in shell shape, showing how two series diverge from the two large specimens which, of the four shells in the Linnean collection, he regards as representing the type. At one extreme are trochoid shells (narrow in proportion to height), at the other they are flattened (wide in proportion to height). It was on the basis of these varied shapes alone that so many species were described; anatomically they are similar.

Although among the 1954 specimens there was a considerable range of shell shape it was clear that all intermediate varieties between the extremes were present and that only one species was involved. The majority of these fragile shells were damaged but there were a fair number unbroken. Their heights and widths were measured with calipers graduated in hundredths of an inch. The width recorded was the maximum distance across the last whorl and is inclined at an angle to the height (Text-fig. 2). These measurements are recorded in Table II. No broken shell was larger or smaller. In the graph (Text-fig. 2) the height is plotted against the ratio width/height, and it will be seen that in spite of much variation between individuals of similar heights the general tendency is for the ratio to get smaller as the shell grows. Mr G. M. Spooner has kindly estimated the regression of width on height and finds that this tendency is significant. The line drawn through the points in Text-fig. 2 represents the best fit, assuming a linear relation between the ratio and height. through the plots of the thirty-eight observations listed in Table II. It will be seen that the additional points also fall on either side of this line, including the projected portion beyond a height of $I \cdot I$. Wide flattened types (= I. planispirata Adams & Reeve) are commoner among the smaller shells than the larger. The only shell in which height and width were equal came from Saunton, and it is interesting that four of the eight measurable shells from that district were somewhat taller types than those from elsewhere. This may be without significance; on the other hand, the shells stranded at Saunton may have come from the borders of the shoal, for Ianthina was not reported farther east along the coast.

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The diagrams of shells given by Laursen in his fig. 15 (1953) have been carefully drawn and are reproduced natural size. Nos. 3, 7 and 12 are from the original material of Linnaeus. These diagrams have been measured with the calipers and the results plotted in Text-fig. 2, along with those for the 1954 shells. It will be seen that they lie about the same curve, though it is noteworthy that the large and relatively broad shell no. 7 (identical with the type from the Linnean collection) falls farther to one side of it than do any of the others. Also plotted are measurements of two shells of *I. planispirata*

Height (in.)	Width (in.)	Ratio: width height	Height (in.)	Width (in.)	Ratio: width height
Shells from T	revone and Ha	rlyn Bays, 1954	Shell fr	om Porthcoth	an, 1954
0.55	0.72 0.81	1.309	0.20	0.82	1.171
0.70	0.83	1.186	Shell	from Lelant,	1954
0.70	0.90	1·286 1·169	0.80	0.96	1.200
0.72	0.90	1.250	Shell	from St Agnes	5, 1954
0·78 0·78	0·95 0·89	1·218 1·141	0.88	0.92	1.105
0.79	0.94	1.190	Shells	from Sauntor	1, 1954
0.80	0.95	1.188	0.72	0.80	I.III I.I.22
0.81	0.96	1.185	0.83	0.92	1.108
0.84	0.98 1.02	1·167 1·230	0.90	0.95	1.056
0.88	1.10 1.06	1·250 1·191	0.92	1.03	1.120
0.93	1.08	1.101	0.99	1.07	1.091
0.94	1.03	1.096 1.126	Shells sent fro Fowler some	om Sennen by e years ago (<i>pl</i>	Mr T. G. W anispirata
0.97 0.98	1.13	1.165 1.051	variety)		
1.01 1.01 1.02	1·12 1·15 1·10	1·109 1·139 1·078	0.31	0·40 0·49	1·290 1·324
		10/0			

TABLE II. MEASUREMENTS OF SHELLS OF IANTHINA JANTHINA (L.)

Adams & Reeve, collected by Mr T. G. W. Fowler near Sennen and sent to us some years ago; his figures of a similar shell (1946) and one of *I. britannica* Forbes & Hanley (1948) from near Sennen Cove, were measured with calipers, and the results, adjusted according to the scale given on the plates, are also plotted.

Measurements of the 1954 shells thus confirm Laursen's conclusion, based on comparative evidence, that these varied types belong to one species. He was unable to explain their origin, suggesting that it might be related to variations in shell shape at the veliger stage brought about by differing spatial conditions during embryonic growth. Measurements of veliger larvae obtained



Text-fig. 2. Graph to illustrate the relation of shell width to shell height in *Ianthina janthina*, expressed as ratio of width to height, based on specimens and drawings. The diagram at the side indicates the shell dimensions measured: AB the height, CD the width. Shells collected in August 1954 at Trevone, Harlyn Bay, Porthcothan, Lelant and St Agnes are indicated by dots; shells collected the same month at Saunton are shown by ×'s. A dot within a circle with a number over it indicates a similarly numbered drawing in Laursen (1953, fig. 15). Two shells of the synonymous *I. planispirata* collected by Mr T. G. W. Fowler at Sennen prior to 1954 are shown by +'s. A similar cross in a circle indicates Fowler's *I. planispirata* from *J. Conch.*, Vol. 22, p. 186, plate I. A × in a circle indicates Fowler's *I. britannica* from the same volume, p. 308. For explanation of the line see text, p. 297.

in 1954 (see below) gave ratios width/height between 1.54 and 1.75. Veligers are thus considerably broader relative to height than any of the shells plotted in Text-fig. 2.

THE FLOAT

The size of the float relative to that of the animal varied greatly, sometimes being quite large with the older portion ragged and worn as in Pl. I, fig. 1, in others smaller and without a degenerating end as in Pl. I, figs. 2 and 3. Mr Peter David regards the degenerating end as atypical, and informs us that in the hundred or so specimens he has taken at sea while in *Discovery II* he has never seen such a thing, and he wonders if it is due to an unfavourable environment. Laursen (1953) figures the curved float of *I. exigua*, and shows such an end, remarking that 'when the parts of the float grow old, they go to pieces and are broken off' (*loc. cit.* p. 6). It may be noted here that while the greater part of the combined animal and float is under water quite a light puff of breath directed at the float will make the snail scud along before it.

A few of the least damaged of our specimens, which had been gathered directly from the sea, added to their floats while kept in dishes of sea water. The method of building has been described several times before, the earliest account being that of Coates (1825). Jeffreys (1867) gives a good account of early observations. Fraenkel (1927) watched a species that appeared at Naples (apparently I. pallida Thompson). We proved, as others had done, that an Ianthina sunk to the bottom of a vessel by partial destruction of its float is unable to rise to the surface, but that if the water-level be lowered until the propodium is able to break through the water surface, the snail will be afloat again in a few minutes. It is the function of this part of the foot to form mucus-coated bubbles of air and to attach them to the proximal end of the float-briefly, the propodium is stretched upwards, the upper part bends back at right angles and flattens out on the water-surface film, with its intensely black secreting surface upwards, in contact with the air. Its centre is then depressed so that the whole organ becomes spoon-shaped, then hoodshaped; the edges of the 'hood' (Pl. I, fig. 2) contract together, meeting closely enough to prevent water entering the cavity. The propodium is then drawn under the water and the bubble smartly clapped against the base of the float (Pl. I, fig. 3), held in position for a few seconds and then cemented in place by a side-to-side motion of the propodium, wiping over it and presumably spreading additional mucus. Sometimes the new bubble fails to be attached and floats away as a tiny glassy sphere. By pressure the bubbles become polyhedral. The completed float is firm between the fingers, springy and dry-it is not in any sense sticky.

One individual of *I. janthina* formed a bubble in about 65 sec, making perhaps ten in succession and then pausing for a while. Fraenkel's animals took only 30–40 sec over it, but, apart from being another species, at Naples in May they were probably at a higher temperature.

THE EPIPODIUM

When the animal is alive the shell is very slippery. Possibly this may bear some relation to the lateral extension of the foot—the epipodium. As described by Adams (1862), in lively individuals it is 'reflexed on the right side on the penultimate whorl of the shell' (Pl. I, figs. 1–3). The margin is irregularly notched, when fully expanded the right-hand lobe is thin and transparent; only the left-hand lobe is pigmented. Master Richard Wilson noticed rippling movements of the expanded right-hand lobe and suggested a possible connexion with the passage of water over the gills.

Laursen (1953) thinks the epipodium may serve to give the animal a better balance in the water: we saw no sign of its acting as a fin for balance or propulsion, and our specimens never of their own accord moved away from any position where they happened to be floating against the side of the jar or basin, even after many hours. Incidentally, Adams in his 1862 paper did not make the statement attributed to him by Laursen that it co-operated in the animal's movements. It had been made by earlier writers, and the point was discussed by Moerch (1860). Movements of the animal are mainly contractions and extensions of the body, bringing the shell close to the float or about its width lower in the water, and also twisting the body. We had an impression that although *Ianthina* has no eyes the expanded animal when in a glass jar could perceive our near approach and would contract into the shell. Our animals discharged red-violet liquid when handled, but the amount was small. The ink streamed downwards and was soon dispersed.

FEEDING

Ianthina is said to feed on a number of pelagic animals (see Laursen, 1953, p. 14 for brief summary), but appears to subsist mainly on *Velella*. As the adult has, so far as is known, no power of swimming it can only attack its prey when by chance it drifts against it. We introduced our specimens to living, though battered, *Velella* which had come ashore with them, but the *Ianthina* did not eat them even when their snouts were fully expanded, with the forked tentacles erect, and mandibles and teeth exposed as if ready for food.

We are indebted to Mr Peter David for permission to publish the following notes, which he made in 1954 aboard *Discovery II* when watching *I. janthina* collected at Station 3098, 42° 36' N., 20° 43' W. The species was identified by Dr J. E. Morton from specimens brought back by Mr David.

Several large specimens were found with *Velella* tentacles adhering to them and several *Velella* were taken with small *Ianthina* attached to the under surface. Some of these were kept alive for two days, and at the end of this time the *Ianthina* were still quite active, and apparently browsing on the *Velella*; the latter seemed to be lifeless, but from previous experience of *Velella*, it was known that, when dead, their tentacles drop off; the specimens with *Ianthina* on them did not break up in this way.

It was observed that the *Ianthina* exuded their purple dye periodically (fairly frequently) while feeding, and it seems possible the dye may be used to anaesthetize the *Velella*. Clean *Velella* floats were seen and taken, and may be all that *Ianthina* leaves of its food.... The small individuals feeding on *Velella* had no floats in most cases, though in one case a detached float was attached to the rim of the *Velella*; the float would be in the way while the animal was eating, as it seems to be attached to the foot, and the normal gastropod eating habits are used.

Mr David adds that on the November 1954 cruise of *Discovery II* he also observed an unidentified ovigerous species.

To quote from his letter. 'This animal also feeds on *Velella*, but in a different way; instead of abandoning its float and browsing on the under side of the *Velella*, this species is held by surface tension against the rim of *Velella*, and proceeds to chew semicircular pieces from it, in much the same way as a caterpillar does on the edge of a leaf. As far as I could determine no purple was released, but then the *Ianthina* is out of reach of the *Velella* tentacles.'

REPRODUCTION

On not very complete evidence the Ianthinidae are thought to be protandrous hermaphrodites. *I. janthina* is viviparous, the other species attach egg capsules to the under-surface of the float. In Graham's material (1954) of *I. janthina* the males were all markedly smaller than the females. This was in agreement with earlier observations of Ankel (1930) on another species. Laursen (1953), however, could find males and females of the same size in the one collection, and also saw very large males, sterile individuals and hermaphrodites; it would seem that *Ianthina* can pass through more than one breeding cycle.

We had two active specimens gathered from the margin of the sea, which respectively shed male and 'female' genital products. Both were of about the maximum size we saw. In the later part of the day after collection one animal shed singly at intervals at least thirty-six dark brown cylindric pellets, about $\frac{1}{10}$ in. long, and at first thought to be faecal. They fell to the bottom of the container (a white china basin) and quickly disintegrated, releasing a number of fully developed veliger larvae with brownish purple shells, swimming with a bilobed velum. Twenty or more were in each packet, varying from 100 to 230 μ across the shell at its maximum width. They gyrated actively over the bottom, neither moving upwards, nor congregating towards nor away from the light. Fraenkel's veligers (1927) (probably *I. pallida* Thompson) swam evenly in the aquarium, showing neither geotaxis nor phototaxis, although they had eye-spots.

As a prelude to the shedding of a packet the propodium was withdrawn from its normal resting position appressed to the base of the float, and was furled up and twisted from side to side.

Extrusion was so rapid that it could be missed in the momentary shifting of

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the gaze, so that only once was it seen. Master Richard Wilson was looking down on this animal when from between the bottom of the foot and the gills a 'little bullet' suddenly shot upwards and out over the (morphologically) left-hand side of the shell, that which is not covered over by the epipodium (Pl. I, figs. 2, 3). Several packets were seen shortly after emergence and there was no doubt that they came out from this side.

The organization of larvae into packets which are violently extruded seems not before to have been noted. Laursen (1953), having described the embryoduct as leading to the inside of the mantle cavity some distance from the rectum, says only that 'the embryos now leave the mother animal and swim freely into the ocean'. This only happened in our animal the next day, when it was less active, and a small number of veligers emerged singly at their own pace.

The second animal, which was in another container, several times shed over the left-hand side of the shell a quantity of mucus containing a number of elongated whitish droplets, about the same length as the larval pellets. They fell gently to the bottom. Further observation was impossible without a microscope, but preserved material showed they must have been aggregates of spermatozeugmata. These seem not to have been seen alive in *I. janthina*, but closely resemble those of a species (probably *I. pallida*) described in detail by Ankel (1930). Each is made up of an oligopyrene spermatozoan, whose head is a flat lanceolate plate with a thicker densely granular base from which emerges a tail. To this are attached by their heads so many eupyrene spermatozoa as to give it the appearance of a fox's brush. The spermatozeugma moves forward by means of undulations of the plate's margin and lashing of the eupyrene spermatozoa.

As *Ianthina* has no powers of locomotion the sexes can only meet when accidentally drifted together and as, too, there are no copulatory organs the method of transference of spermatozoa poses a problem. Graham (1954), indeed, finds nothing in the reproductive physiology of *I. janthina* incompatible with a possibility of self-fertilization, while Ankel (1930) only obtained his spermatozeugmata by dissection. Our observation of the actual discharge of aggregates of these elaborate structures supports the view that they are an adaptation enabling spermatozoa to make the relatively long journeys between individuals of a shoal.

EPIZOIC ANIMALS

On a shell $(2 \cdot I \text{ cm high})$ of a living *Ianthina* picked up at Trevone there were growing four living specimens of *Lepas pectinata* Spengler. The capitulum of the largest barnacle was $I \cdot 3$ cm long, of the smallest $I \cdot I$ cm. They were attached in a cluster close to the mouth of the shell beside the columella, and in the normal floating position of the snail the barnacles would be growing more or less upright, pressing perhaps against the base of the float, which was

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not present when they were found. Over part of the capitulum of one barnacle there was growing a colony of the hydroid *Laomedea geniculata* (L.). Another colony of the same species of hydroid was growing on the shell of the *Ianthina* whose photograph is reproduced in Pl. I, fig. I. Both colonies of the hydroid were kindly identified by Dr P. L. Kramp, who remarks that the species is particularly inclined to attach itself to floating objects.

Grateful thanks are due to the many who have made this paper possible and whose names are recorded in the text. In addition we should like to thank Professor A. Graham and Dr J. E. Morton for placing their knowledge of the Ianthinidae at our disposal. For our account of the winds we acknowledge our indebtedness to the Daily and Monthly Weather Reports of the Meteorological Office, London.

SUMMARY

1. During the exceptional westerly weather of August 1954 large numbers of *Ianthina janthina* (L.) were found on the north coasts of Cornwall and Devon, in what was almost certainly the largest stranding of this species on English shores for fifty years. The strandings are clearly correlated with periods of west to north winds.

2. With the Ianthina there were often stranded many living Velella.

3. A sufficiently large number of unbroken shells were obtained to allow of some investigation into the relationship between width and height. It was found that while there is considerable variation at any one height the width is relatively less in older shells than in young ones. In the past these varied shapes have led to many different species being described. The results in the main confirm Laursen's conclusions (1953); when his careful drawings of different shell types were measured, it was seen that their ratios were in general agreement with those of the 1954 specimens.

4. Earlier accounts of float-building were confirmed from observations of healthy specimens obtained in 1954; a few new details were added.

5. The epipodium as observed in life is described and its function discussed.

6. Some notes on the feeding habits of this species, made by Mr Peter David on board *Discovery II*, are reproduced by permission. He makes the interesting suggestion that the purple dye of *Ianthina* can anaesthetize its main prey, *Velella*.

7. Shedding of larvae and sperms was observed in living specimens. In both sexes the genital products, organized in packets, were shot out of the mouth of the shell on the morphologically left side, that which is not covered by the epipodium. Our observations support the view that the elaborate organization of the sperms into compound structures is an adaptation enabling them to travel from males to females floating well apart.

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WILSON AND WILSON. PLATE I



(Facing p. 304)

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EXPLANATION OF PLATE I

(Black and white photographs from Kodachrome originals, taken by electronic flash. Reproduced about twice natural size.)

- Fig. 1. Lateral view of a living *Ianthina janthina* L. floating against the side of a cylindrical vessel: the meniscus is arched where the float contacts the glass. The snout and tentacles are not quite fully extended. The colourless translucent epipodium of the right side and its serrated border are well shown. The propodium in its contracted state is seen at rest against the proximal (anterior) end of the float. The distal extremity of the float is disintegrating and losing air. A hydroid is growing on the shell.
- Figs. 2, 3. Views from above of another specimen adding a bubble to its float. In Fig. 2 the edges of the expanded hood-shaped propodium are contracting together to enclose a bubble of air. Within the hood is visible the dark epithelium, which secretes a coat of mucus around the bubble. In Fig. 3 the propodium is pressing the bubble against the base of the float and cementing it into position. In these photographs the snout and tentacles are fully extended. The irregular white patches are highlights where wet, and therefore shiny, rounded parts just break the surface film. In this view only the top of the bubble float, which is entirely above water, is visible. The epipodium of the right side (left side of each picture) is seen wrapping around the shell surface. Gill lamellae within the mantle cavity are glimpsed through the shell mouth, especially in Fig. 3. It is through this open portion of the shell mouth, on the left side of the snail, that the genital products were shed (see page 303).

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NOTES ON THE BIOLOGY OF SERTULARIA ARGENTEA L.

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(Text-figs. 1-5)

A fishery has developed in recent years in this country for certain hydroids collectively termed 'white weed'. The hydroids, particularly *Sertularia* and, more recently, *Hydrallmania*, are raked up from the sea-bed, processed, dyed and used, largely in the United States of America, for decorative purposes. Fishing for white weed is not new, for it was practised in Germany between the wars. German scientists, notably von Reitzenstein (1913), Pax (1928), and Thiel (1938), examined various aspects of the fishery, and of biology of the hydroids concerned.

The main centre of the industry is the Thames Estuary, where the hydroids grow in extensive beds, on a bottom of sand and shells, on which the weed can be fished commercially by boats equipped with simple iron rakes.

TAXONOMY

There has been some difference of opinion on the naming of the various species among the Sertulariidae. The two species concerned in this work were first named by Linnaeus (1758) as Sertularia cupressina and S. argentea. He subsequently renamed them (1767) S. cupressina and S. cupressina var. β argentea. Since then various authors, including Hincks (1868), have maintained their independence, while others, notably Broch (1918), followed by Kramp (1938) and Leloup (1938), have placed them together as S. cupressina. Broch (1918) considered that Hincks's (1868) distinction between the two species was based on characters which show too much variation. He later (1928) referred to them as S. cupressina forma typica (Broch) and S. cupressina forma argentea (L.). Von Reitzenstein (1913) followed Hincks (1868), and throughout his description of the hydroid used in the German whiteweed fishery used the name S. argentea (Ellis & Solander, 1786). Thiel (1938), however, figured and described the same species as S. cupressina, basing his description on that of Broch (1928). Others, including Nutting (1904) and McLean Fraser (1944), have removed them as separate species to the genus Thuiaria Fleming, the distinction between Sertularia and Thuiaria being the arrangement of the hydrothecae, which are in opposite pairs in Sertularia and alternate in Thuiaria.

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It is not proposed to discuss the case for a change of genus in this paper, but it is important to diagnose correctly the organisms concerned in the whiteweed fishery, particularly when referring to aspects of their biology and ecology.

The hydroid occurring in great quantity in the Thames Estuary, and used for preference in the whiteweed industry, is *Sertularia argentea* L = S. *argentea* Ellis & Solander sec. Hincks (1868). This is easily distinguishable from *Sertularia cupressina* L. sec. Hincks (1868), and there seems to be no good reason why they should be considered to be the same species. Since this paper is mainly concerned with only one of these two species, this seems to be a good opportunity to emphasize their outstanding differences.

In the Thames Estuary, although most of the weed is normal S. argentea, there appears with it, in smaller proportion, a distinct form which has an altogether more luxuriant bushy growth. This form, which we shall call for convenience the 'bushy type', is easily distinguished by fishermen, and is less acceptable to the processers, who prefer to have many colonies per unit weight. The fresh weed is bought from the fishermen by weight and sold, when processed, as bunches of colonies. This bushy form shows no anatomical differences from the normal type, with the exception that the side branches are more subdivided and greatly elongated, as though the colony has been subjected to better growth conditions (Fig. 1F, K). The proportion of bushy type Sertularia is small in winter and spring, but larger in summer and early autumn; it may therefore be a more luxuriant growth form produced from the normal type under summer conditions. However, in early winter, when much less of this type is found, long colonies of the normal-type Sertularia are still much in evidence, with no signs of any previous extension of their side branches. At the growing point the structure of the bushy form is identical with that of the typical S. argentea. Reference to Fig. 1 will leave little doubt that these are merely growth forms of the same species.

In North Wales there is another Sertularian, so far not observed in the Thames Estuary, which agrees closely with Hincks's (1868) account of *S. cupressina*. Superficially, in growth form, it resembles the bushy type of *S. argentea*, and is probably less suitable for commercial purposes. It is characteristic of fairly exposed sand-banks off the North Wales coast, and with it occurs, in smaller quantity, some *S. argentea*, mostly of the bushy type. In the Menai Straits, towards the eastern end, *S. argentea*, normal type, occurs predominantly with only a little *S. cupressina*. All three forms have been separated easily by untrained fishermen in North Wales.

In Fig. 1 are compared the growth forms of the two species, which differ markedly. The woodcuts in Hincks are excellent representations of the two species, but in all the specimens we have seen, the apex of S. argentea has been more tapering than that of S. cupressina (Figs. 1A, E; 2). This could be attributed to variation in growth rates at different times between the two

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Fig. 1. Outline drawings showing the morphology of Sertularia. A-D, S. cupressina, North Wales; E-H, S. argentea (normal type), Thames Estuary; K-M, S. argentea (bushy type), Thames Estuary. A, E, show the arrangement of the side branches on the main axis, $\times \frac{3}{4}$; E, F, K, the subdivision of the side branches, $\times 1\frac{1}{4}$; C, G, L, the hydrothecae on the side branches, $\times 25$ and D, H, M, the hydrothecal margins, $\times 125$.

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species. A very important difference is the arrangement of the branches, which arise in a definite spiral fashion from all sides of the stem in *S. argentea*, while in *S. cupressina* they are almost strictly alternate and in one plane, with only the faintest spiralling of the main stem towards the apex of the colony. This characteristic formed the basis of McLean Fraser's (1944) separation of



Fig. 2. A, S. argentea, bushy type, Thames Estuary; B, S. argentea, normal type, Thames Estuary; C, S. cupressina, North Wales; D, E, S. argentea, two young colonies. × ½. (Photo: R. Elms.)

the two species. Broch (1928) was also aware of it when he described the two forms of S. cupressina. In S. cupressina the internodes are well defined, each bearing two opposite branches, rarely one or three, and a pair of opposite hydrothecae. Variations from two branches per internode can usually be explained by previous breakage or change in direction of growth of the colony. In S. argentea, each internode of the stem bears only one branch, rarely two, and several, usually two or three, opposite pairs of hydrothecae. It is interesting to note that in the young forms of S. argentea, on the first few centimetres of stem, the branching is in one plane, with usually two branches to each internode as in S. cupressina (Fig. 2). In Hincks's and von Reitzenstein's accounts, S. argentea is said to have two branches to each internode, but they may have been referring to the older part of the colony near the base; the branches are subdivided by regular dichotomy (Fig. 1F), and stand out rigidly from the stem. The side branches of S. cupressina are less regularly subdivided, and more elongated, giving the whole colony a more graceful appearance. The elongation of the side branches of S. argentea, bushy form, is responsible for the superficial likeness between it and S. cupressina. The slenderness of the pinnules in S. cupressina is emphasized by the position of the hydrothecae, which are alternate and each is adnate throughout most of its length (Fig. IC). The apices of the hydrothecae are less divergent than in S. argentea. The hydrothecae of S. cupressina have a more open alternate arrangement, whereas in S. argentea it would be more correct to describe the hydrothecae as subopposite (Fig. 1G). In S. cupressina the apex of each hydrotheca is produced into two almost equal teeth, but in S. argentea, the teeth are unequal (Fig. 1D. H. M).

It is agreed with Broch (1918) that slight variations in the arrangement and form of the hydrothecae are found in a single colony, particularly between parts of different age, and for this reason less importance has been attached to them in the separation of the two species. The differences described were, however, evident when examining strictly comparable parts of colonies of similar size of the two species.

These differences in the characters of the two species are sufficient for easy separation and justify their maintenance as separate species.

For completeness, the characters of the two species are here listed partly after Hincks (1868) and McLean Fraser (1944).

Sertularia argentea L.

Colonies usually up to 30–40 cm, sometimes much longer and greatly branched. Branches arise from all sides of the stem with 'bottle brush' effect, usually one branch to each internode, but in young colonies branching in one plane, two to each internode. Branches subdivided by regular dichotomy; hydrothecae usually subopposite, curved gradually outwards, margin with two teeth, one usually longer than the other; operculum of two flaps.

Sertularia cupressina L.

Colonies usually up to 30-35 cm, occasionally much longer, branches regularly alternate, on opposite sides of stem only, usually two branches to each internode, upper part of stem may be faintly spiralled. Branches subdivided alternately rather than dichotomously; hydrothecae alternate, tubular, largely immersed and not strongly turned outward, margin with two almost equal teeth; operculum of two flaps.

REPRODUCTION

Hincks (1868) and Nutting (1904) have given a general account of reproduction throughout the Sertulariidae. Von Reitzenstein (1913) has described the reproduction of *S. argentea* L. in German waters. Teissier (1923) described the development and structure of the gonangia in *Dynamena pumila* (L.).

The multiplication of polyps to form a colony might equally be considered as growth or asexual reproduction. A second method of asexual reproduction is by the ramification of the stolon over the substrate from the basal disc. When a colony is removed from the substrate it is usually found to be attached to the bases of several others. This condition could result from planulae settling among the stolon extensions of one hydroid, or from the uniting of runners from several. It can, however, be seen to result, at least in part, from the formation of small colonies at the tips of the runners. (When colonies are encrusted by other organisms treatment with acid helps to reveal details of structure.) Von Reitzenstein (1913), too, suggested that this might be a form of asexual reproduction, exhibited most often at the end of the sexual period.

The most important form of reproduction is sexual. Vase-shaped gonangia, slightly flattened in a plane at right angles to the direction of the branch, are produced from the side branches, nearly perpendicular to the plane of the hydrothecae (Fig. 3). The fully developed gonangium is about 1 mm in length. The branches bearing gonangia commence at a variable distance from the base, depending on the size and age of the colony, and extend to within a few cm of the apex. On an established breeding colony the youngest gonangia are found on the uppermost branches and towards the tips of those lower down. The most mature gonangia are usually more distant from the apex.

Thiel (1938) followed van Beneden (1866) and Goette's (1907) descriptions of the development of the female gonangium. He did not, however, describe the development of the male sex products, and disregarded von Reitzenstein's (1913) figure of the male gonotheca as being without foundation or description. Thiel's (1938) dogmatic statements, based, it seems, on the observations of other workers, concerning von Reitzenstein's work on breeding, are misleading, and it was not until after much of this work had been completed that it was found that several of von Reitzenstein's observations had been confirmed.



Fig. 3. Stages in development of the gonangium of S. argentea. A-G, female gonangia, ×33; H-J, male gonangia, ×33; K, terminal aperture of female gonangium, ×115. a, acrocyst.

The development and structure of the male and female gonangia are being studied in detail and will provide the subject of another paper. It is here intended merely to point out the gross differences between the male and female gonangia in their various stages of development, as an aid to their identification. In both sexes the gonotheca arises from the side branch as a small cup-shaped



Fig. 4. Graph showing the breeding of *S. argentea* at the Maplin Sands, Thames Estuary, in 1953. I shows the colonies bearing gonangia, expressed as a percentage of the total colonies in a sample; II–IV show the colonies bearing gonangia—II developing, III A ripe, B with female acrocysts; and IV degenerating—expressed as a percentage of the colonies with gonangia.

outgrowth (Fig. 3A), which gradually elongates and closes to give the typical form (Fig. 3C). There may be one to four, but usually two, lateral horns flanking the circular terminal aperture (Fig. 3G). Inside the aperture there is a series of, usually twelve, minute teeth (Fig. 3K). In the female gonangium, eggs are produced in a marsupium, which when ripe is extruded as an acrocyst inside which the eggs develop. An acrocyst usually contains

from two to ten eggs which develop into planulae. Rupture of the acrocyst allows the escape of the planulae (Fig. 5B).

The stages of development of a gonangium are distinguishable (Fig. 3) in fresh material under a microscope. Initially the contents are restricted to an only slightly swollen longitudinal band, enlarged terminally to fill the horns and apex of the gonotheca. Subsequently, the gonotheca becomes full when nearly ripe. In degenerating stages the gonothecae are empty, or contain a narrow strip of tissue slightly enlarged near the aperture. The ripe female gonangium is easily recognized by its content of regularly shaped pink ova, or by the presence of an acrocyst containing developing eggs. The ova can be distinguished at an early stage in the development of the female gonangium.



Fig. 5. Early development of *S. argentea*. A, a single sperm; B, planula; C, D, newly settled colony; E, F, after formation of the first few hydrothecae. A, ×4,500; B-F, ×50.

Smears of ripe gonangia from certain colonies carrying developing, mature and degenerating gonangia, but no acrocysts, showed developing and ripe sperm (Fig. 5A). These gonangia were all creamy white, in contrast to the pinkness of the full gonangia of colonies bearing acrocysts. In a study of many colonies, no male gonangium was found on a colony with female acrocysts, nor any female acrocysts on colonies with gonangia containing spermatozoa. It was concluded that there are separate male and female colonies, readily separable when ripe by the colour of the gonangia. Subsequently, the male

colonies have been found with a form of acrocyst protruding from the gonangia, but here it is smaller, densely white and full of mature spermatozoa (Fig. 3J). The male 'acrocyst' has a thin membrane enclosing the sperm, and is less regularly round than that of the female. It seems to be a more transient structure, less likely to be found.

In fresh specimens the sexes can be readily separated by the colour of the ripe gonangia. A further aid to identification of the male is the presence of a dark reddish brown band of pigment, the spadix, which is readily seen in developing male gonangia within a regularly oval translucent sac. This is less easily seen when the ripe gonangium is filled by sperm (Fig. 3H, I). The degenerating male and female gonangia are very similar. A reddish brown spadix is also present in the female gonangium, but tends to be obscured by the more opaque ova.

There is convincing evidence that each gonangium, male and female, produces more than one liberation of sperm or eggs. This aspect of reproduction will be discussed in a future paper.

The extent of the breeding season was studied by taking random samples of *Sertularia argentea* from dredged catches from the Maplin Sands, Thames Estuary. Only those colonies 70 mm in length and larger, which could be assumed to be capable of breeding, were included within a sample. Shorter colonies were not often taken in the breeding condition on the Maplin Sands.

In each colony the occurrence of developing, ripe and degenerating gonangia was noted. The number of colonies with gonangia has been expressed as a percentage of the total, and the number of colonies with each stage of gonangium is given as a percentage of the total number of colonies with gonangia. The results are shown in Fig. 4. The first sample was taken on 6 May 1953, when there was a high proportion of colonies with developing and ripe gonangia, and slightly less with degenerating gonangia. Evidently the beginning of the breeding season had been missed. By 4 June the number with developing gonangia had dropped, but there were nearly 100% with both ripe and degenerating gonangia. After this date the number with ripe gonangia became less. After a slight increase, the percentage with developmental stages also declined until towards the end of July when a second maximum of colonies with developing gonangia was found. This was followed in mid-August by a peak in the percentage with ripe gonangia and, in early September, by a peak in the number with degenerating gonangia. Although the colonies bearing gonangia formed a high percentage of the total colonies at the time of the first breeding maximum in May/June, their number decreased in July, corresponding with the falling off in the number of colonies with developing and ripe gonangia, and increased only slightly for the second breeding peak in July/August. Thus the second burst of breeding is less intense. Although, in November, the proportions of gonangia-bearing colonies with developing and ripe gonangia were high, yet only 25% of all colonies carried gonangia, so that the total amount of breeding was small.

These observations were made from preserved samples and no attempt was made to distinguish the sexes, but where colonies bearing female acrocysts were present they were noted, and their number expressed as a percentage of the total colonies with gonangia. These reached a maximum in late May. It was later found that the sexes could be quickly distinguished in preserved colonies by dehydrating a mature side branch and examining it in a clearing agent.

To estimate how much earlier than 6 May the breeding season had commenced, ten randomly selected colonies from each of the first three samples were examined more closely, and the stages of the gonangia from every fifth branch counted and recorded. To count and identify the gonangia on every branch would have taken much time; the total number of gonangia on several colonies was therefore counted, and the proportion of each stage compared with the results of counting every fifth branch. This gave a reasonably accurate comparison. The three groups distinguished were: I, early developmental (without horns); II, late developmental and ripe; and III, degenerating; their numbers have been expressed as a percentage of total gonangia in Table I. It seems that the gonangia must first appear during April, but the position of the peak of ripe gonangia at the beginning of June is confirmed (Fig. 4).

TABLE I. THE PERCENTAGES OF THREE STAGES OF GONANGIA IN SERTULARIA ARGENTEA

I developing, II ripe, III degenerating, counted on every fifth branch from the colonies in samples from the Maplin Sands in 1953.

		Stage		
Date	Í	II	III	
6 May	21	41	38	
27 May	14	58	28	
4 June	I	69	30	

The distribution of the various stages in the development and degeneration of the gonangia on a colony was also confirmed by these counts. For example, from the sample of 27 May 1953, a female colony of 420 mm length carried the gonangia shown in Table II, with the youngest gonangia towards the apex and the oldest lower down. Below the eightieth branch from the apex there were a few additional branches, then a region of 60 mm devoid of branches, a usual condition in older colonies.

Von Reitzenstein (1913) found that the breeding period of *S. argentea* in Germany in 1908–9 extended from April to early June, and that when the spawn was released, the empty gonangia fell off. At the beginning of July he could find no more colonies with gonangia; there followed in August a second less important reproductive period when a smaller proportion of colonies

carried gonangia. This second breeding period lasted until November when an occasional colony was taken with gonangia, but none in winter.

There is some evidence that the breeding period may vary in length on whiteweed grounds separated by only a few miles. For example, in a sample taken from near West Buxey, about 4 miles from the Maplin Sands, on 25 November 1953, 78% of the colonies bore gonangia, and 28% of the colonies with gonangia carried acrocysts. This was quite a different picture from that obtained on the Maplin Sands (Fig. 4). Occasional colonies with female acrocysts or male gonangia with developing and ripe spermatozoa have been taken throughout the winter months, but the great majority have none.

TABLE II. THE NUMBERS OF GONANGIA ON EACH FIFTH SIDE BRANCH OF A 420 MM COLONY OF SERTULARIA ARGENTEA

Branch,		Stage	
from apex	Ĩ	II	III
0	as a <u>m</u> rcenta	15285 <u>70</u> 73	
5	ust f os t appe	n sise n es sel	
IO			
15	16	n n de la serie	
20	16	78	
25	9	55	6
30		67	I
35	DAT2 TRATS	61	28
40		38	16
45	h. 3. 1. 1 () (<u>1. 1</u> . 4 () () ()	8	IO
50		13	4
55		Ī	3
60		3	5
65		I	2
70			
75			
80			

The stages are I early developmental, II ripe, III degenerating gonangia.

The developing eggs within the acrocysts are about $40-50 \mu$ in diameter. Typically the head of each spermatozoan is an elongated triangle (Fig. 5A), 2-3 μ long and 1-1.5 μ wide, with a tail 30-40 μ long.

DEVELOPMENT

Rupture of the acrocyst allows escape of the ciliated planulae, each of which assumes an elongated form, about 0.5 mm in length, with a somewhat blunt anterior end (Fig. 5B). The planula revolves with a forward swimming, creeping motion. In the laboratory the planulae were not seen to swim near the surface, but remained near the bottom. It seems likely that they are confined to the bottom and are not pelagic. This would increase the tendency for the hydroids to form a dense covering of the substrate, and would lead to

the formation of fairly discrete beds, as observed. Hydrographic conditions would clearly exert a considerable influence.

The settlement of the planulae and early development of the colony have been followed in the laboratory. The planula attaches to the substrate, usually a piece of shell or stone, and produces a semi-spherical holdfast—irregularly lobed when viewed from above (Fig. 5 c, D). The planulae under observation hatched from acrocysts placed in an aquarium on 8 May 1954. By 11 May they had assumed the form shown in Fig. 5 c. This agrees with von Reitzenstein's (1913) estimate of a free swimming period of 2–3 days. By 17 May elongation of the main stem had occurred with a node near the base, and the first two polyps, each fully furnished with a hydrotheca, had been formed. On 20 May, young colonies with three polyps were observed, but after this date development ceased, due to some unfavourable condition, and the young colonies died (Fig. 5E, F). Under laboratory conditions, the initial growth to a length of less than 2 mm took almost 2 weeks. The settlement and early growth of *Dynamena pumila* (L.) have been described by Teissier (1923).

GROWTH

Several attempts have been made to observe the growth rate of S. argentea throughout the year in the Thames Estuary. Shells bearing Sertularia were dredged, some colonies measured, and the shells attached to concrete blocks which were buoyed, or attached to beacons, and returned to the sea bottom. These experiments were of short duration because the concrete blocks and shells were frequently lost or buried by shifting sand in bad weather. It was found difficult to keep colonies of Sertularia alive in the laboratory conditions for long enough to observe growth rates. It is believed that excessive silt in the water supply, due to bad weather, was responsible. The most successful method was to suspend the colonies from a piece of cord stretched across a large tank filled with sea water, shaking the cord periodically to dislodge the silt. The results available from the laboratory, the River Crouch and the Maplin Sands, are given in Table III. In the field quite young colonies were used and the growth rate varied from 0.3 to 1.3 mm per day. This agreed closely with the measurements of growth in the laboratory in which the average increment varied between 0.1 and 1.7 mm per day. An attempt is being made to study the growth rate in the Thames Estuary throughout the year in 1955. The majority of colonies attached to blocks showed negligible growth during February, the maximum recorded being 6 mm in 28 days—that is 0.2 mm per day. During March all but a few colonies showed growth, and a maximum of 0.4 mm per day was recorded.

Von Reitzenstein (1913) found that growth was not continuous throughout the year. The peak of growth (four-fifths of the total) occurred in the months of May to September. His results for *Sertularia* grown in culture boxes in the

				Average			Average
Date	Length	Remeasured	Growth	per day	Remeasured	Growth	per day
RIVER CROUCH							
15 July 1953	28	24 July	6	0.7	14 Aug.	27	1.3
15 July 1953	33	24 July	3	0.3	-	_	_
15 July 1953	58	24 July	5	0.6	-		
15 July 1953	58	24 July	IO	I.I		_	
15 July 1953	74	24 July	IO	I.I			
15 July 1953	78	24 July	4	0.4	6 [6h	—	—
MAPLIN SANDS, TH	IAMES ESTUAR	Y					
3 Sept. 1954	68	I Oct.	0	0	5 Nov.	22	0.6
LABORATORY							
20 Aug. 1053	149	26 Aug.	7	I.2	3 Sept.	I	0.1
20 Aug. 1953	172	26 Aug.	A	0.7	3 Sept.	I	0.1
20 Aug. 1953	206	3 Sept.	10	0.7			
20 Aug. 1953	207	26 Aug.	8	1.3	3 Sept.	8	I.0
20 Aug. 1953	236	3 Sept.	2	0.1			
20 Aug. 1953	278	3 Sept.	4	0.3			
20 Aug. 1953	303	26 Aug.	2	0.3		_	
20 Aug. 1953	352	3 Sept.	24	1.7			_
4 Aug. 1954	28	IO Aug.	0	0	16 Aug.	2	0.2
4 Aug. 1954	42	IO Aug.	6	1.0			
4 Aug. 1954	145	IO Aug.	9	1.2	16 Aug.	4	0.7
4 Aug. 1954	175	IO Aug.	4	0.7	16 Aug.	I	0.2

TABLE III. GROWTH OF SERTULARIA ARGENTEA All measurements in millimetres.

sea at Hörnum in 1908 may be summarized as follows, all measurements being in mm:

	Average	growth	Maximur	n growth
Growth period	Over the period	Average per day	Over the period	Average per day
10 Apr.–20 May 1908	3.1	0.05	10.0	0.24
21 May-9 July 1908	12.5	0.25	30.0	0.60
10 July-12 Sept. 1908	50.0	0.77	80.0	1.25
12 Sept4 Nov. 1908	26.2	0.20	40.0	0.75
5 Nov26 Mar. 1909	10.0	0.07	15.0	0.12

He also cultured *Sertularia* in the sea on a board and on a basket lid, from May to November of the same year. By both these methods the growth rate in the summer months was greater than by the box method. Combining all his results, he arrived at the figure of 228.4 mm average growth and 285.0 mm maximum growth between 10 April 1908 and 26 March 1909.

Von Reitzenstein's growth rates are of the same order as those obtained for the Thames Estuary. The difficulties of obtaining growth measurements have been described; von Reitzenstein's results are open to the criticism that he included many colonies of different sizes which may well have had quite different growth rates, and further, the results were not based on the same colonies over the whole period. Von Reitzenstein himself, however, was aware of the weaknesses in his methods. Thiel (1938), commenting on von Reitzenstein's results, stated that the growth recorded must have been much lower than that occurring under natural conditions, but gave no reasons for this opinion. The maximum growth recorded by von Reitzenstein between 10 July and 12 September 1908 averaged 1.7–1.8 mm per day, which agrees closely with our maximum growth increment which averaged 1.7 mm per day during August to September 1953 under as near as possible natural conditions.

It is felt that von Reitzenstein's estimate of about 26 cm annual growth in the sea is not unreasonable. He also gave an indication of the slowing of growth rate with increase in size of a colony. His conclusion that the largest colonies of 60–70 cm length were 2–3 years old was based on the assumption that large and small colonies have the same rate of growth.

Von Reitzenstein also found that colonies cast off branches and side branches in winter when growth virtually ceased. This process is responsible for the lack of side branches in the lower regions of older colonies. Eichelbaum (1912) found that whole colonies, usually those over 30 cm, became detached in autumn, and concluded that some dispersal of the species was effected when the colonies, covered by gonangia, were carried away by currents.

REGENERATION

From the fishery aspect the question of regeneration is of great importance. In a sample of white weed taken from a commercial rake it was found that only 16% of the colonies had been taken with their basal discs intact. The stems of the remainder had been broken just above the base, some across obviously living white stem, others across the dark thickened lower stem close to the point of attachment, a region which has little appearance of being alive.

Using methods similar to those described on growth studies it was found that colonies cut at all levels and returned to the sea were capable of regeneration, even those cut through the blackened region close to the basal disc. Regeneration of the latter was usually by small white sprouts appearing near the cut ends, while in the remainder a continuation of the terminal growth took place. In July 1953 the rate of regeneration by this method was found to vary between 0.1 and 1.4 mm per day (Table IV).

Since cut blackened bases of *Sertularia* colonies are capable of regenerating in this way, it seems likely that the holdfast of a cut colony can also continue to bud vegetatively from the stolon as described earlier (p. 312).

In order to discover whether side branches lost at the approach of winter are capable of becoming attached to form new colonies, several side branches were detached from a mature colony and attached vertically to a glass plate, held in a laboratory tank with running sea water. The experiment was continued from I to 21 September 1954, and although none of the side branches produced a holdfast, most of them had begun growing from the cut end. One had produced two small branches, each with four opposite pairs of hydrothecae, and most of the others were growing in a similar way, but nothing

resembling a basal disc or stolon was produced. The experiment ended with the death of the branches, probably caused by excess of silt. Many young colonies have been inspected to see if any had an unusual growth form which might have resulted from the attachment of a side branch, but none was found. It is probable that when the side branches are lost the polyps and tissues have been retracted and that they consist merely of skeletal matter, and would therefore be incapable of settlement. The retraction of tissue into the stolon of *Dynamena* (= *Sertularia*) *pumila* (L.) in autumn and winter, followed by the reforming of the polyps in the old thecae in January and February, has been described by Haddow (1936). It does not seem likely that the shedding of branches of *Sertularia argentea* constitutes a form of asexual reproduction. The experiment, however, demonstrated the remarkable powers of regeneration possessed by these hydroids.

TABLE IV. REGENERATION OF SERTULARIA ARGENTEA

All measurements in mm.

Date	Length	Cut to	Remeasured	Growth	Average growth per day	Remeasured	Growth	Average growth per day
RIVER CROUCH								
15 July 1953	43	33	24 July	4	0.4	-		
15 July 1953	45	18	24 July	3	0.3			
15 July 1953	48	38	24 July	2	0.2	14 Aug.	22	I.0
15 July 1953	49	38	24 July	I	0.1			
15 July 1953	60	38	24 July	2	0.2			
15 July 1953	65	38	24 July	I	0.1	14 Aug.	12	0.6
15 July 1953	65	48	24 July	4	0.4	14 Aug.	3	0.1
15 July 1953	75	43	24 July	3	0.3		_	
15 July 1953	80	48	24 July	3	0.3	14 Aug.	23	I.I
15 July 1953	IIO	63	24 July	4	0.4			
15 July 1953	158	70	24 July	3	0.3			
15 July 1953	158	108	24 July	I	0.1			
15 July 1953	180	158	24 July	13	1.4			_
15 July 1953	190	178	24 July	II	1.0		—	-
MAPLIN SANDS								
3 Sept. 1954	21	13	I Oct.	13	0.2	5 Nov.	16	0.2
3 Sept. 1954	32	22	I Oct.	9	0.3	5 Nov.	14	0.4
3 Sept. 1954	63	37	I Oct.	8	0.3			
3 Sept. 1954	69	39	I Oct.	4	0.1	5 Nov.	8	0.5
3 Sept. 1954	98	48	I Oct.	29	1.0			
3 Sept. 1954	118	33	I Oct.	8	0.3	5 Nov.	7	0.5

A number of colonies, both male and female, have been found bearing gonangia each with a small vegetative branchlet emerging from the mouth. Sometimes this new growth was branched several times, but more usually there was a simple stem with three or four hydrothecae. Dissection showed that in some the theca of each branchlet was continuous with the gonotheca, which contained an extension of the coenosarc. In others the new branch emerged from inside the gonotheca. The arrangement of hydrothecae on the new branches was found to be more like those of the remainder of the colony, than of a newly settled form. Each gonotheca was of adult dimensions, with horns, and contained an extension of the coenosarc continuous with that of the new growth. It seemed likely either that in the course of degeneration of the

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gonangium the coenosarc had grown through the gonotheca, or that the gonangium had aborted during its development and reverted to vegetative growth. The result was a number of small branchlets in the same plane as the gonangia, that is perpendicular to the normal direction of growth.

Commensals and Predators

Sertularia and other hydroids provide a satisfactory habitat for a number of free and fixed epizoic forms. Most often associated with Sertularia are encrusting bryozoans, particularly Membranipora pilosa (L.), which may cover stems, branches and even gonothecae, obviously in some cases with harmful effects. One colony of length 510 mm was found to be covered from 70 to 410 mm from its base by the bryozoan, and another of 280 mm was covered from 40 to 240 mm. Up to 85% of the colonies in a sample of white weed taken from the Maplin Sands in August 1953 carried encrusting Bryozoa. A thickly encrusted main stem is often devoid of side branches, and shows the effects of severe competition and suffocation. The settlement of Bryozoa reduces the commercial value of white weed.

To a lesser extent encrustation by other hydroids such as *Clytia johnstoni* Alder, *Tubularia* sp. and *Obelia* spp. also occurs. Where present they often form a dense covering as do some peritrichous ciliates.

The larvae of several bivalves find a suitable settling place in the fronds of white weed, which may be found with many thousands of mytilid spat on their branches. *Sertularia* taken from Fleetwood in August 1954 was in such a condition, and these accumulations of developing bivalves must be of great interest to demersal fish. From the Maplin Sands samples the largest numbers of bivalve spat were taken in July.

Sertularia also provides a home for a number of free-living forms, in particular, caprellids and pycnogonids. Caprella linearis (L.) may occur in abundance, up to an average of five per colony being taken on the Maplin Sands in July 1953. Nymphon brevirostris Hodge occurs frequently, and it and the caprellids are hard to distinguish from the Sertularia because of their similar colouring. The nudibranch Idulia coronata (Gmel.) is frequently taken with its spawn.

It is questionable whether any of these animals feed directly on *Sertularia*. At certain times of the year the lower parts of the older colonies are devoid of branches. This might be due to the feeding of some predator. However, denuding of side branches is almost always confined to the lower part of the stem, and is more likely to be due to the annual decline of the colony towards the end of the year when the lower branches are shed. This has been described by von Reitzenstein (1913).

Colonies have also been taken regularly in which only the bases of certain side branches remained, covered by Bryozoa, while other branches were intact.

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Where a bryozoan was present at the base the rest of the branch was dead. This would also contribute towards the loss of side branches.

Of twenty flatfish taken from a whiteweed bed at Fleetwood in August 1954, only two dabs contained isolated fragments of *Sertularia*, which were amongst vast quantities of mussel spat in the stomach. The heavy settlement of mussel spat on *Sertularia* has been mentioned previously and the presence of the *Sertularia* was believed to be incidental.

Hunt (1925) took fragments of hydroids from the stomach of *Leander*, and Mistakidis (in press) has recorded occasional fragments of *Sertularia* from *Pandalus*.

Harrison (1944) mentions that several observers have maintained that caprellids feed on hydroids and algae, but that such an occurrence is probably exceptional. He found that caprellids fed on copepods and nauplii from the plankton. During frequent observations made by the writers caprellids were observed feeding in the manner suggested by Harrison and did not take *Sertularia*.

Idulia has not been observed feeding, but Browne (1907) has described the intensive feeding of *Tergipes* on *Syncoryne*.

It is considered unlikely that the exploitation of white weed can be substantially detrimental to commercial fisheries, while many fishermen believe that the constant harrowing of the sea-bed by the rakes is beneficial to the development of benthos generally, and of assistance to many fish during feeding.

SUMMARY

There has been considerable divergence of opinion on the naming of species of *Sertularia*. It is suggested that Linnaeus's (1758) original names *S. cupressina* and *S. argentea* relate to distinct species, which may be separated on certain anatomical characters, notably the manner of branching. The 'white weed' fished commercially in the Thames Estuary is *S. argentea*.

A study of the reproduction of *S. argentea* in the Thames Estuary showed that separate male and female colonies exist, and a general description of the development of the gonangia in both sexes is given. The main sexual breeding occurs in May and June, with a second, but less intense, period in July/August. The early growth, following settlement of planulae, was observed in the laboratory.

Measurements of growth were made in the field and laboratory. Growth is seasonal, occurring mostly in the summer months. A maximum growth of 1.7 mm per day was recorded.

Examination of natural and experimental material showed that regeneration of cut stems is possible at all levels, and that even detached side branches can continue to grow to form new branches.

The main commensals and predators of *S. argentea* are mentioned with their possible effects on the host and the whiteweed industry.
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STUDIES ON THE BIOLOGY OF LIMPETS

III. HERMAPHRODITISM IN THE THREE BRITISH SPECIES OF *PATELLA*

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(Plate I)

Sex phenomena in molluscs have been widely investigated, and the relevant literature on the subject has been reviewed by Coe (1943, 1944). Coe recognizes ambisexuality (monoecism, hermaphroditism) and unisexuality (dioecism, gonochorism) and further subdivides ambisexuality into functional ambisexuality (functional hermaphroditism), consecutive sexuality, rhythmical consecutive sexuality and alternative sexuality. Of these, functional hermaphroditism is of widespread occurrence: it is encountered in all the main groups, with the exception of scaphopods and cephalopods. Of the more than 20,000 species of living gastropods approximately half are functional hermaphrodites when fully adult (Coe, 1944). Limpets of the genus Patella are unisexual, though there is evidence that sex change may occur in some of the species (Orton, 1920, 1928, in Patella vulgata; Bacci, 1947, in P. coerulea). Little is known with certainty of the mechanism of sex-determination in these animals, but sexuality appears to be labile since it seems that more than 90 % of individuals of P. vulgata change sex at some stage in their life history. Aberrant sexual forms might therefore reasonably be expected to occur. In the present paper thirty hermaphrodite gonads encountered in an examination of 64,576 limpets are described and their significance in the wider context of sexual phenomena in molluscs is discussed.

The late Prof. J. H. Orton suggested this study and collected most of the hermaphrodite gonads with which it deals. I am most grateful to Dr A. J. Southward for checking Orton's records of hermaphroditism and sex-change in *Patella*, to Dr Margaret Lang and my wife for invaluable assistance with the histological work, and to Mr D. R. R. Burt who identified the cysts of *Ophryocotyle*.

MATERIAL AND METHODS

The series of hermaphrodite gonads described here contains examples from each of the three British species of *Patella*. The specimens were obtained between December 1945, and December 1948, either by the late Prof. J. H. Orton during his routine examination of populations of limpets for breeding

data, or by myself. They were collected from widely separated stations round the British coast. All specimens were fixed in Bouin's fluid in sea water and stored in 70% alcohol. Prior to dehydration and embedding, each gonad was drawn and described in ventral surface view. The gonad was then removed from the visceral mass, divided along its longer and shorter axes into four equal parts, and the dorsal and cut surfaces of each part also drawn and described. Serial sections were cut at either 5 or 15 μ thickness, and the sections stained with Mallory's triple stain or Heidenhain's haematoxylin with eosin or erythrosin orange G as a counterstain.

PREVIOUS RECORDS OF HERMAPHRODITISM

Previous records of hermaphroditism in limpets are limited to Patella vulgata. Gemmill (1896) examined approximately 250 specimens of P. vulgata and obtained three hermaphrodite gonads. They were normal in size, shape and anatomical position, but their colour was mottled 'showing all shades between olive-green of ovary and the light yellow of testis'. All regions appeared fully ripe, and Gemmill stated that microscopic examination showed 'not only ripe ova and spermatozoa but also segmented ova and even ciliated freely moving embryos'. One specimen showed a patchy distribution of male and female tissue with an excess of ovarian over testicular tissue; in the second specimen, one side of the gonad was purely male, whereas the other side was female, and in the third specimen only a small patch of ovarian tissue was found. Gemmill's remarkable record of developing ova and trochophores in these gonads is quite unique: in spite of a careful search during the present work no developing eggs have been found in the gonads examined. Pelseneer (1926) found one hermaphrodite gonad in 2750 specimens examined: it came from an individual 53 mm in length and in describing it he says 'c'était un testicule dans lequel, entre les acini mâles il y avait des rangées rectilignes d'ovules'. Orton (1928) records that in his investigations at Plymouth he never encountered hermaphroditism of the type described by Pelseneer. M. D. Jones (1933, unpublished record) examined 3000 specimens of P. vulgata and found only one hermaphrodite. This specimen was 46 mm in length and the gonad contained mainly testicular tissue: there was a small ovarian region at the anterior end. The two areas were fairly distinct apart from a few ova deeply embedded in testicular tissue. Smith (1935) examined more than 1000 specimens of P. vulgata and found only one hermaphrodite. Relevant data concerning these previous records are summarized in Table I.

STRUCTURE OF THE GONADS

The structure and development of the normal limpet gonad have been described and illustrated in a previous paper (Orton, Southward & Dodd, 1956). In connexion with this work many gonads of both sexes at all stages of

Author	Date	Locality	No. of specimens examined	No. of herm- aphrodites	% herm- aphroditism
Gemmill	1896	Millport	c. 250	3	c. I·2
Pelseneer	1926	Wimereux	2750	I	0.036
Orton	1928	Plymouth	1000+	0	Nil
Jones*	1933	Aberystwyth	3000	I	0.033
Smith	1935	Plymouth	1000+	I	<0.1

TABLE I. PATELLA VULGATA: PREVIOUS RECORDS OF HERMAPHRODITISM

* Unpublished record.

development and depletion were sectioned and examined, and all were entirely of one sex. In both sexes the gonad lies on the ventral surface of the visceral mass and, initially, the germinal epithelium lines a flattened sac-like structure. This epithelium later becomes greatly folded and the folds, supported on trabeculae of connective tissue, penetrate the cavity and obliterate it. Gametogenesis appears to be further advanced in the dorsal regions of the gonad, i.e. those in contact with the visceral mass.

The *hermaphrodite* gonads are individually described in Table III (see pp. 335–8), together with the dates of collection, length of foot or shell and maximum thickness of gonad: these data are of significance when considering the relationship between the types of hermaphroditism here described and the transient hermaphroditism which may be associated with sex change.

Reference to Pl. I shows that, with the exception of two specimens containing trematode parasites, the hermaphrodite gonads showed well-defined areas of testicular and ovarian tissue, with some slight intermingling in the contiguous zones. Pl. I, fig. 6, illustrates a feature which was relatively frequent, viz. the presence of well developed oocytes lying in the lumen of a seminiferous tubule. In most cases these oocytes were continuous with more extensive ovarian tissue, but in a few cases they were isolated and completely surrounded by testis.

Pl. I, fig. 7, shows details of a typical region lying between predominantly male and predominantly female areas. Fully developed eggs and sperms are present in close proximity, together with young oocytes and a considerable amount of undifferentiated tissue.

Most of the gonads studied showed well developed oocytes and spermatozoa. In a few cases there were undoubted signs of spawning from both ovarian and testicular regions. From one hermaphrodite gonad a successful artificial fertilization was made between eggs and sperms, and apparently normal trochophores were obtained (cf. Dodd, 1956).

The relative volumes of ovarian and testicular tissue in each individual hermaphrodite gonad were estimated approximately. Of the twenty-six gonads

available for histological study, fifteen were predominantly male, nine predominantly female, and in two of them the two types of tissue were of approximately equal volume.

INCIDENCE OF HERMAPHRODITISM

When considering the incidence of hermaphroditism encountered in the present study it is important to note that Orton's examination of the gonad was limited to size and general appearance of the ventral surface. Orton was

TABLE II.	HERMAPHRODITISM IN BRITISH SPECIES OF PATELLA
	INCIDENCE AT DIFFERENT LOCALITIES

Locality	No. examined	No. of herm- aphrodites found	Percentage hermaphroditism
	Patella vulg	ata	
Aberdeen	4,204	Nil	Nil
St Andrews	7,744	2	0·026
Isle of May	1,507	I	0·066
Millport	4,451	I	0·022
Cullercoats	4,583	Nil	Nil
Port St Mary	8,777	I	0.011
Plymouth	6,450	Nil	Nil
Trevone	5,541	Nil	Nil
All above	43,257	5	0.015
localities	Patella asp	era	
Aberdeen Isle of May Port Erin Port St Mary Plymouth Trevone	1,436 5,844 688 3,633 2,125 2,761	2 7 2 56 2	0.139 0.120 0.291 0.138 0.282 0.072
All above	16,487	24	0.146
localities	Patella depr	vessa	
Gwbert	338	Nil	0.022
Plymouth	40	Nil	
Trevone	43454	I	
All above localities	4,832	I	0.051

mainly interested in establishing details of the breeding cycle. As he recognized, such an examination might well result in failure to identify hermaphrodite gonads in which the ventral surface was largely or entirely of one sex, e.g. specimen B 13, Table III. However, the 5844 specimens of *P. aspera* from the Isle of May, studied by the present author, were specifically examined for signs of hermaphroditism, and it is unlikely that any cases were overlooked. It is significant that the percentage frequency of hermaphroditism in this population is closely similar to the average percentage frequency for all localities. The overall percentage frequencies of hermaphroditism in the three species show interesting differences. Of 43,257 specimens of *P. vulgata* examined five were hermaphrodite: a percentage of 0.012; of 16,487 specimens of *P. aspera*, twenty-four were hermaphrodite: a percentage of 0.146; while in *P. depressa* only one hermaphrodite was found in 4832 specimens. It therefore appears that hermaphroditism is some ten times more common in *P. aspera* than in *P. vulgata* or *P. depressa*.

By reference to Table III it will be observed that the majority of the hermaphrodite specimens were taken during the spawning season of the particular species. This simply reflects the fact that by far the majority of the individuals examined were collected during the breeding season. It will be realized that hermaphrodite gonads can be recognized by superficial examination only when they are active.

The records suggest that hermaphroditism in *P. vulgata* may be more common in more northern localities: this, however, does not appear to be so in *P. aspera*.

HERMAPHRODITISM IN RELATION TO SEX CHANGE

As has already been mentioned, a change of sex appears to take place in *P. vulgata* and *P. coerulea*. Since incomplete sex-change would necessarily result in hermaphroditism it is important to consider to what extent this phenomenon might account for the hermaphrodite gonads encountered in the present study.

Bacci (1947) has made a detailed investigation of sex-change in *P. coerulea*. In this species it appears that sex inversion is not limited to a narrow size range; very immature oocytes appear in male gonads, though this is true only of gonads which are almost completely spent: and gonads are never found in which there are well-defined male and female zones. Clearly then, in *P. coerulea*, although more than 15,000 specimens were examined by Bacci no hermaphrodites of the kind described in this paper were ever encountered.

Regarding *P. vulgata*, Orton (1928) has shown that most, if not all, of the individuals are male at their first sexual maturity, the suspected change of sex from male to female occurring at an age of I year or more, though more frequently within the smaller size-groups. The percentage frequencies of the two sexes approach equality in the second year-group. In the present study of some 43,000 specimens of *P. vulgata*, only 5 (0.012%) hermaphrodites were found, and most of these belonged to the larger size-groups.

As regards the remaining British species, Dr A. J. Southward is at present preparing for publication some of Orton's later data on sex-change, and he informs me that these indicate a different state of affairs. In *P. aspera*, if indeed sex-change occurs at all, it is a much rarer phenomenon since 30-40%females are already present in the smallest size-groups in which all individuals show developing gonads. In *P. depressa*, there is strong circumstantial evidence that no sex-change ever occurs, 70% males being found in the size-groups in which all specimens have differentiated gonads. Evidently, therefore, sex-change is not an essential prerequisite for hermaphroditism, though in *P. vulgata* and *P. aspera* a possible connexion between the two phenomena must be borne in mind.

HERMAPHRODITISM IN RELATION TO PARASITIC INFESTATION

Although the hermaphrodite condition is itself abnormal, both male and female parts of hermaphrodite gonads were of normal histological appearance in most individuals. Moreover, evidence that functional spermatozoa and ova may both be produced within a single gonad has already been adduced. In six of the specimens examined, however, the gonads were recognizably abnormal not only through being hermaphrodite, but also in gross morphology (Pl. I, fig. 2). In three of these there was no evidence as to the cause of the abnormality, whereas in the remaining three, the possibility must be considered that parasitic infestation was responsible. In two of the three parasitized specimens rediae of Cercaria patellae Lebour were found (Pl. I, fig. 8), whilst in the other several cysts of the cestode Ophryocotyle sp. were present (Pl. I, fig. 9). Rees (1934) has described the effects produced by Cercaria patellae, and her main observations concerning partial castration are in full agreement with my own. Rees, however, did not encounter hermaphroditism. The parasitized hermaphrodite gonads which I have studied were subnormal in size and contained both ova and spermatozoa indiscriminately mixed. Many of the ova showed gross degeneration, and large areas of the gonad were entirely devoid of germ cells. It should be noted that a high proportion of most populations of limpets may be parasitized by C. patellae and since only two parasitized hermaphrodite specimens were found in the present study the possibility must be borne in mind that these specimens were already hermaphrodite when infested by the parasite, i.e. that they were not rendered hermaphrodite by the parasite.

The parasitized specimen (Pl. I, fig. 9) containing cestode cysts closely resembled the unparasitized hermaphrodites. The gonad was predominantly female and the ova were mostly large. A well-developed male area and some neuter tissue were associated with the largest cyst. There were restricted areas of neuter gonad tissue surrounding most of the other cysts: in one case the adjacent tissue, though predominantly neuter, contained early stages in spermatogenesis. However, since there were male regions not associated with the presence of cysts, this gonad also may possibly have already been hermaphrodite before infestation by the parasite.

DISCUSSION

In order to assess the relationship between the type of hermaphroditism here described and the unisexual condition normal in limpets, two hypotheses may be considered. According to one hypothesis, since in Patella vulgata sex reversal apparently occurs in the great majority of individuals, hermaphrodite gonads may represent an arrest of developmental change during sex-reversal. Consideration has already been given to this possibility and it would appear that sex-change does not predispose the gonad towards hermaphroditism since the incidence of hermaphroditism in all three British species is low, whereas sex-change in P. vulgata must occur in at least 90% of individuals. It has also been noted that the gonads here described may contain fully developed eggs and sperms at one and the same time: Bacci (1947) found that this was never so in P. coerulea, in which he found the sexual phases to be relatively stable, sex-change apparently occurring during the resting period. Moreover, in nearly all of the cases here described, the hermaphrodite gonads were found in large individuals, i.e. those past the time at which sex-change is most commonly thought to occur.

According to a second hypothesis, since sexuality is probably labile in limpets the small percentage of hermaphroditism may well merely represent aberrant sexuality with either a genetical or an environmental basis. In this connexion, Coe (1945) states that although less than 400 of the more than 10,000 species of lamellibranchs are normally hermaphrodite, in most of the unisexual species which have been studied a small percentage of hermaphrodite individuals has been found. He states: 'Certain dominantly unisexual species may have local races or environmental modifications which are hermaphroditic. Furthermore, accidental or developmental hermaphroditism is of occasional occurrence in most of the unisexual species and unisexual individuals are sometimes found in dominantly hermaphroditic species.' A consideration of all the evidence in the present study leads irresistibly to the conclusion that we are here dealing with a similar form of accidental hermaphroditism for which no definite cause can be assigned at present. The low incidence appears to rule out the possibility that it is a factor associated with the external environment, though it has been shown that an abnormal internal environment due to the presence of cestode cysts can result in a fairly clear local action on the gonad structure. So far as concerns a possible genetical explanation of this phenomenon, Montalenti (1950) and Montalenti & Bacci (1951) have put forward a hypothesis that sex in Patella is determined by multiple genes. They postulate three pairs of alleles which segregate independently and can therefore produce sixty-four possible genotypes, one of which is a genetic male and one a genetic female, these two genotypes being represented by the small percentage of individuals which do not change sex. The remaining genotypes contain both male and female potentialities and any individual possessing one of these genotypes could, presumably, develop into a hermaphrodite. It should be noted that this genetical scheme was suggested to cover the entire genus, when it was thought that all species of *Patella* showed sex-change. This scheme may be considered to have less validity now that it appears that several of the species are truly gonochoristic. No doubt a formal genetical scheme could be arrived at which would cover all the known facts regarding sexuality in the genus *Patella* and allow for occasional hermaphroditism, though it would seem unlikely that any such scheme could account for the peculiar hermaphroditism here described. Conceivably these *Patella* hermaphrodites are developmental mosaics in which islands of germinal tissue originate from cells which by rare mitotic accident happen to be heteroploid. There is no case for elaborating this statement in view of the present lack of knowledge of molluscan chromosomes.

SUMMARY

In an examination of 64,576 specimens of the three British species of *Patella*, thirty hermaphrodites were encountered. The present paper describes the gonads of these animals, and discusses and compares the incidence of hermaphroditism in limpets from widely separated British localities. Three parasitized hermaphrodite gonads are described, and it is suggested that these were probably already hermaphrodite at the time of infestation by the parasite.

Consideration is given to the possibility that there is a causal connexion between sex-change and hermaphroditism, but such a connexion appears not to be supported by the available evidence.

The nature of this hermaphroditism is considered, and it is concluded that we are here dealing with accidental or developmental hermaphroditism for which no cause can be assigned, though it is tentatively suggested that the gonads may be developmental mosaics containing islands of heteroploid tissue.

Specimen	Date collected	Locality	Length of shell or foot (mm)	Maximum thickness of gonad (mm)	Description of gonad based on macroscopic appearance and examination of sections
			(1)	Patella vulg	zata
Αı	6. xi. 48	St Andrews	41.0 (shell)	7.0	Predominantly female. Great intermixing of the two elements though essentially a skin of testis over eggs which come to surface in centre region. Eggs and sperms appear mature, though there are a fair number of young eggs
A 2	5. iii. 49	St Andrews	27·0 (foot)	3.0	Male and female areas approximately equal in volume and greatly intermixed. Connective tissue septa with young oocytes have penetrated deeply into testis tissue
A ₃	16. x. 48	Isle of May	15·0 (foot)	2.0	Predominantly female, only one small male area. Abnormal distri- bution of gonad—intermixed with gut. Eggs and sperms well developed, very few small eggs
Α4	29. x. 48	Millport	70·0 (shell)	8.0	Predominantly female. Very abnormal with irregular lobed appear- ance. Ovarian region forms a large excrescence. Two regions quite distinct except at edges where there is some over-growing of female elements by male elements
A 5 (Pl. I, fig. 6)	23. iii. 46	Port St Mary	30.0 (foot)	2.0	Predominantly male. Small discrete patches of eggs in centre region which extend to visceral mass. Large oocytes found in testicular tissue

TABLE III. HERMAPHRODITE LIMPET GONADS: TABULATED DATA

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HERMAPHRODITISM IN PATELLA

Specimen	Date collected	Locality	Length of shell or foot (mm)	Maximum thickness of gonad (mm)	Description of gonad based on macroscopic appearance and examination of sections	336
			(2)) Patella asp	era	
Вг	31. x. 46	Aberdeen	_	2.0	Predominantly female. Both medium-sized and small eggs well represented. Male and female regions greatly intermixed. Testis tissue appears spent and contains many young oocytes; ovarian tissue seems to be developing	
B 2 (Pl. I, figs. 5, 7)	21. x. 47	Aberdeen	25.0 (foot)	3.0	Predominantly male. Testis region consists of a large bilobed mass. A lobe of ovarian tissue lies at the anterior end, a wedge-like exten- sion of which overlies the adjacent testis region. Most eggs seem fully developed though there are some early developmental stages at the ventral surface. Testis region contains fully developed sper- matozoa and all other stages in spermatogenesis are well represented	
B ₃	23. viii, 48	Isle of May	50∙0 (shell)	6.0	Male and female areas approximately equal in extent. Two well- demarcated areas: testis overlies ovary. Eggs and sperms well developed though developmental stages are present, especially in testicular region. A few isolated large eggs are seen deep in testis tissue. Signs of spawning from ovarian tissue only	J. M. D
B4	6. ix. 48	Isle of May	31.0 (foot)	5.0	Predominantly male. Fairly discrete crescent-shaped area of ovarian tissue which extends throughout thickness of gonad—little intermixing of the two areas. Both contain apparently fully de- veloped genital products as well as developmental stages. Signs of spawning	ODD
B5	6. ix. 48	Isle of May	31.0 (foot)	9.0	Predominantly male. Two large patches of testis separated by ovarian tissue containing several small islands of testicular tissue. Great intermixing in these regions. All areas contain fully de- veloped genital products as well as developmental stages	
B6 (Pl. I, fig. 1)	7. ix. 48	Isle of May	29·0 (foot)	8.0	Predominantly male. Consists of two large areas of testis separated by a wedge of ovarian tissue running across the shorter axis of the gonad. Some intermixing. Genital products mostly apparently fully developed. Some signs of spawning in both areas	
B ₇	19. ix. 48	Isle of May	50·0 (shell)	2.2	Predominantly female. Consists of a layer of ovarian tissue covering the visceral mass, with fairly discrete areas of testicular tissue em- bedded in the more ventral regions. Female area consists mainly of large eggs: some eggs may have been spawned. Much mature spermatozoa and all stages in spermatogenesis. Patches of sperms on connective tissue septa deep in ovarian regions	

B 8	21. ix. 48	Isle of May	55.0 (shell)	4.0	Predominantly male with patches of ovarian tissue which are fairly discrete. Female areas appear more mature than male areas. No sign of spawning
B9	23. ix. 48	Isle of May	51.0 (shell)	7.0	Predominantly $(c. 90 \%)$ male. Dorsal region consists of a loose mass of tissue with a few scattered large eggs and a small amount of relict sperm. Ventral male area very well developed. Much fully developed sperm and many earlier stages in spermatogenesis. Dorsal regions of gonad appear spent (both male and female areas)
Вю	5. vi. 47	Port Erin	35.0 (foot)	1.2	Predominantly male with a few areas of fairly discrete ovarian tissue. Little intermixing. Testis appears almost spent. Ovary consists of a few medium-sized eggs and many small oocytes—may be an early developmental stage
Вп	25. vi. 48	Port Erin	_	3.0	Predominantly male. Great intermixing of ovary and testis, though there is fairly distinct demarcation between them in the regions where they adjoin. Ovary and testis extend from surface to base of gonad and both appear fully developed; some spawning seems to have taken place from both ovary and testis
B 12 (Pl. I, fig. 2)	9. xii. 46	Port St Mary	60∙0 (shell)		Not available for histological examination. Gonad obviously very abnormal and predominantly male
B 13	12. ix. 47	Port St Mary		3.0	Predominantly male. A continuous skin of male tissue overlying basal eggs. Testis appears to be developing; eggs seem mostly mature. Very little intermixing. Eggs visible on macroscopic examination of gonad only at the edges
B 14 (Pl. I, fig. 4)	4. x. 47	Port St Mary	27·0 (foot)	4:0	Predominantly male. Consists of many scattered islands of ovarian tissue lying on ventral surface of a mass of testis tissue. These islands are fairly discrete and some penetrate entire thickness of gonad and reach visceral mass. Both eggs and sperms seem fully developed and there appears to have been some spawning
B 15	15. ix. 48	Port St Mary	48.0 (shell)	2.5	Predominantly male. Fairly discrete small islands of ovarian tissue consisting of large eggs are scattered throughout the gonad. A few rediae of <i>Cercaria patellae</i> are present: testis tissue in which they lie looks quite normal. Male areas less well developed than female areas
B 16	28. i. 49	Port St Mary	30∙0 (foot)	0.02	Predominantly male with female area at anterior end. Both regions contain fully developed genital products, though both are almost spent. A few large eggs can be seen along dorsal margin of gonad. Young oocytes are found in fair numbers in the testis tissue

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TABLE III (continued)

Specimen	Date collected	Locality	Length of shell or foot (mm)	Maximum thickness of gonad (mm)	Description of gonad based on macroscopic appearance and examination of sections
B 17 (Pl. 1, fig. 9)	17. vi. 47	Plymouth	39.0 (foot)	1.6	Predominantly female. Very abnormal in microscopic appearance. Heavily parasitized with rediae of <i>Cercaria patellae</i> . Some large eggs and apparently fully developed sperms are present in isolated patches and are completely intermixed. Some eggs appear to be degenerating
B 18 (Pl. I, fig. 8)	30. x. 47	Plymouth	30-0 (foot)	6.0	Predominantly female with a skin of testis tissue over most of ventral surface. Eggs and sperms seem fully developed and there has been some spawning. A large cyst of <i>Ophryocotyle</i> sp. is present near centre of ventral region of gonad and in this area the greatest inter- mixing occurs. Although it lies mainly in the ovarian tissue, there is a large cap of testis tissue covering its ventral surface
B 19	3. xi. 47	Plymouth			Not available for histological examination
B 20	8. v. 49	Plymouth	50·0 (shell)	2.2	Predominantly male. Patches of large eggs present, many of which inter-communicate along dorsal surface of gonad. Both testicular and ovarian regions appear mature. Dorsal region of testicular
B21 (Pl. I, fig. 3)	3. iii. 49	Plymouth	35·0 (foot)	4:0	Predominantly female. Large island of testicular tissue in central region of gonad. This lies in a hollow in the ovarian tissue and does not penetrate as far as dorsal surface of gonad. Great intermixing of male and female tissues at edges. Testicular tissue penetrates deeply into surrounding ovarian region. Few small oocytes
B 22	28. vi. 49	Plymouth			Not available for histological examination
B23	19. viii. 47	Trevone			Not available for histological examination
B 24	2. ix. 47	Trevone	-	4.0	Predominantly female. Eggs and sperms appear mature and show some intermixing
			(3)	Patella depr	ressa
Ст	2. ix. 48	Trevone	24·0 (foot)	6.0	Predominantly male. Ovarian tissue forms a thin skin on the ventral surface—does not penetrate very deeply into thickness of gonad. Eggs large in size, look somewhat abnormal and are separated by a network of tissue in which spermatogenesis is proceeding—a few
					fully formed sperms. Male areas less mature than female areas

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EXPLANATION OF PLATE I

P. aspera and P. vulgata: morphology and histology of hermaphrodite gonads.

- Fig. 1. P. aspera; specimen B6. Approx. natural size. Gonad and visceral mass freed from foot and suspended from it to show ventral surface of gonad. Testicular areas white, ovarian areas black.
- Fig. 2. P. aspera; specimen B12. Approx. natural size. Gonad and visceral mass freed from foot and the latter deflected forward to show ventral surface of gonad. Testicular areas white, ovarian areas black. Note abnormal appearance of gonad.
- Fig. 3. P. aspera; specimen B21. Approx. natural size. Arrangement of parts similar to fig. 1. Note discrete island of testicular tissue.

Figs. 4–9 inclusive. T.S. hermaphrodite gonads. Plane of section parallel to dorso-ventral axis.

Fig. 4. P. aspera; specimen B14. \times 10.

- Fig. 5. P. aspera; specimen B2. \times 10.
- Fig. 6. P. vulgata; specimen A5. × 16. Note large oocytes in seminiferous tubule.
- Fig. 7. *P. aspera*; specimen B2. × 125. High-power view of region between male and female areas; see fig. 5. Note part of large oocyte at lower edge, isolated groups of spermatozoa, young oocytes and neuter tissue.
- Fig. 8. *P. aspera*; specimen B18. \times 25. Hermaphroditism associated with parasitization. Note that tissue in immediate neighbourhood of cyst of *Ophryocotyle* is either testicular or neuter.
- Fig. 9. P. aspera; specimen B17. ×32. Hermaphroditism associated with parasitization. Note grossly abnormal appearance of gonad and presence of isolated oocytes, patches of testicular tissue and rediae of *Cercaria patellae*.

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Dodd. Plate I



(*Facing p.* 340)



ON ASSESSING THE AGE OF DEEP OCEANIC WATER BY CARBON-14

By L. H. N. Cooper, D.Sc.

The Plymouth Laboratory

(Text-fig. 1)

The rate of circulation and age of the deep water of the oceans is of much interest. Worthington (1955) has suggested an age of 100–160 years for northern North Atlantic water which has reached the Carribean and Cayman Seas. I (in part, Cooper, 1955, 1956) have suspected that the rate of circulation of much of the North Atlantic deep water may be even faster than Worthington's results suggest. Provisional direct observations by G. Wüst & G. Dietrich (private communication) also suggest that the deep circulation is quite rapid.

In strong contrast, Kulp (1952, 1953*a*, *b*) and Carr & Kulp (1954) have attributed ages of 1600 to 1950 years to seawater samples drawn from various depths in the North Atlantic (Table I, nos. 6-9a).

The discrepancy is not real, but arises from tacit assumptions as to the nature and age of a water mass which are incompatible and from peculiarities of the cycle of ${}^{12}\text{CO}_2$ and ${}^{14}\text{CO}_2$ in nature.

Kulp (1952) wrote: 'Although atmospheric carbon dioxide is in equilibrium with the carbonate in surface ocean water, the submergence of such water cuts it off from its supply of carbon 14 as effectively as does death in the case of a plant or animal.' The first clause requires proof by observation. It would be better to replace 'is in equilibrium' by 'approaches equilibrium'.

He went on: 'Since ocean water sinks in the polar regions and moves along the bottom towards the equator, the rate and direction of movement can be measured by determining the time since a unit of water left the polar surface.'...'The carbon 14 measurements of several water samples taken from the ocean floor at about the latitude of Newfoundland on either side of the Mid-Atlantic Ridge are shown in Table 4' (included here as Table I, nos. 5-9a). 'The data suggest that it takes about 1500 years for the water to reach this latitude from the Arctic. Thus the time of the turnover of the oceans must be thought of in terms of several thousand years.'

In a way the whole of this statement is true; but it is a way of no value to an oceanographer seeking a better understanding of oceanic circulation. This approach may be compared with that of a man who would measure the strength of currents in the North Sea with drift bottles, not knowing that between putting out the bottles and their stranding on a shore they had many times circled the northern North Sea Great Eddy (Tait, 1937). His results

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Ref	erence			Dept	h*	Apparent age
Kulp		Location	Sea area	ft.	m.	(years)
I.	1953 a	13° 35' N., 66° 35' W.	Caribbean	Surface		Recent
2.	1953 a	19° 24' N., 78° 33' W.	South of Cuba	Surface		Recent
3.	1953 a	41° 00' N., 54° 35' W.	West North Atlantic, south of Newfoundland	Surface	—	Recent
3 a.	1953 b	54° 35' N., 41° W.	West North Atlantic	Surface		Recent
4.	1953 a	63° 46' N., 00° 26' W.	Norwegian Sea	10,440	3182	500 ± 200
5.	1953 a	38° 42' N., 67° 54' W.	North-west North Atlantic	13,500	4115	450 ± 150
6.	1953 a	35° 46' N., 69° 05' W.	North-west North Atlantic	15,300	4663	1950 ± 200
7.	1953 a	34° 56' N., 68° 14' W.	North-west North Atlantic	16,560	5047	1550 ± 300
8.	1953 <i>a</i> , 1953 <i>b</i>	58° 19' N., 32° 57' W.	Reykjanes Ridge, Western Slope	6,000	1829	1600 ± 130
9.	1953 b	53° 53' N., 21° 06' W.	Southern tip of Rockall Bank	9,000	2743	1750 ± 150
9a.	1953 a	53° 53' N., 21° 06' W.	Southern tip of Rockall Bank	9,100	2774	1900 ± 150

TABLE I. AGE OF OCEANIC WATER ACCORDING TO J. L. KULP

* Roman figures give depths reported by Kulp: italic figures conversions by the writer.

would suggest a much more sluggish circulation than would measurements made with current meters.

To appreciate what is involved, a number of separate points in the physical chemistry and oceanography of carbon dioxide have to be examined and then synthesized into a complete whole. The material for such a study has been provided by Buch (1942, *inter alia*).

A COMPARISON BETWEEN THE RATES OF EXCHANGE OF O_2 , ${}^{12}CO_2$ and ${}^{14}CO_2$ between Air and Sea

Let P_0 , V_0 = the partial pressure and volume of a gas in the surface water of the sea when in equilibrium with the atmosphere under specified conditions.

P, V = the partial pressure and volume of a gas when not in equilibrium.

 $\gamma =$ an exchange coefficient, assumed to be the same for all three gases.

t = time.

On integration

Then

$$\frac{P}{P_0} = \frac{V}{V_0}.$$

Also, the rate of invasion or evasion of a gas from the atmosphere into the sea, or vice versa, may be written

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \gamma (P_0 - P) = \frac{\gamma P_0}{V_0} (V_0 - V),$$
$$\mathrm{d}t = \frac{V_0}{\gamma P_0} \frac{\mathrm{d}V}{V_0 - V}.$$

or

$$t = \int_{V=V_2}^{V=V_2} dt = \frac{V_0}{\gamma P_0} \log_e \frac{V_0 - V_1}{V_0 - V_2}.$$

AGE OF DEEP WATER

Let us now consider a litre of water from which 2x ml. of O₂ and 2x ml. of $^{12}CO_2$ have been removed, and then compute the ratio of the times required to reabsorb x ml. of each gas. For both gases:

$$\log_e \frac{V_0 - V_1}{V_0 - V_2} = \log_e \frac{2x}{x} = \log_e 2.$$

Consequently

 $\frac{t_{\text{carbon-12 dioxide}}}{t_{\text{oxygen}}} = \frac{V_0, \text{ carbon-12 dioxide}}{V_0, \text{ oxygen}} \cdot \frac{P_0, \text{ oxygen}}{P_0, \text{ carbon-12 dioxide}}.$

Let us now compute this ratio (Table II) for moist air conditions in the Norwegian Sea and in the tropical Atlantic, using the tables of Truesdale, Downing & Lowden (1955) for oxygen, and of Buch (1933) for carbon dioxide.

TABLE II. RELATIVE TIMES REQUIRED BY CARBON-12 DIOXIDE AND BY OXYGEN TO APPROACH EQUILIBRIUM WITH THE ATMOSPHERE WHEN UNDER-SATURATED OR SUPERSATURATED TO THE SAME EXTENT

	Norwegian Sea	Tropical Atlantic
Temperature (° C)	0	25
$V_0, \Sigma^{12}CO_2 (ml./l.)$	49.5	47.5
$P_0 O_2 (\text{atm.})$ $P_0 O_2 (\text{atm.})$ $P_0 P_0 P_0 (\text{atm.})$	0.209	0.203
Ratio of times, $t_{12}CO_2/t_{O_2}$	3880	6244

Thus, when ${}^{12}\text{CO}_2$ and O_2 are displaced from their equilibrium values by the same amount, then ${}^{12}\text{CO}_2$ requires between 4000 and 6000 days (between 10 and 17 years) to achieve an approach towards an equilibrium which oxygen may attain in 1 day.

This is a general conclusion, independent of the storminess of the sea and the actual rates of transfer. It is equally true whichever side of equilibrium the departure may be made. Whenever oxygen is not in equilibrium, it is highly unlikely that carbon-12 dioxide will be so.

When ${}^{14}\text{CO}_2$ is at an overall equilibrium state in air and water, its partial pressure and its volume will both bear the same ratio to the partial pressure and volume of ${}^{12}\text{CO}_2$. The ratio V_0/P_0 will be essentially the same for both isotopes so that the above calculation applies.

In general, however, due to radio-active decay, the volume and partial pressure of ${}^{14}\text{CO}_2$ in the water will tend to diminish. Consequently, ${}^{14}\text{CO}_2$ may require even longer to approach towards equilibrium than does ${}^{12}\text{CO}_2$.

On the Concentration Gradient of Carbon Dioxide between the Equator and the Poles

Kulp (1953a) has said that 'the C¹⁴ concentration in air at widely different geographic positions is essentially constant and is independent of time of day, rainfall, altitude and temperature'.

This apparently straightforward statement may mean either (a) the concentration of ¹⁴C per litre of air at N.T.P. is constant; or (b) that the ¹⁴C concentration per unit volume of carbon dioxide (${}^{12}CO_2 + {}^{13}CO_2 + {}^{14}CO_2$) is constant.

The alternatives are not closely related. Interpretation (a) is probably the one intended. However, in the same paragraph he stated that 'about two dozen living trees from all over the world gave the same carbon-14 concentration within about 10%'. This implies that the carbon-14 content is proportional to the amount of carbon dioxide assimilated and supports interpretation (b).

The atmospheric circulation over the North Atlantic according to Bjerknes and the distribution of carbon dioxide (${}^{12}CO_2$) according to Buch are shown schematically in Fig. 1 (Buch, 1942).

In temperate latitudes the partial pressure of carbon dioxide in the air and in surface water in equilibrium with the air is usually about $3 \cdot 1 \times 10^{-4}$ atm. In summer, in extensive areas of the Arctic, this partial pressure may sink as low as 1.5×10^{-4} atm. Polar regions in summer are the site of much solution in the sea of atmospheric carbon dioxide both as ${}^{12}CO_2$ and ${}^{14}CO_2$. There are no winter observations in the Arctic.

In the Antarctic south of 57° S. lat. in winter (Deacon, 1940) the partial pressure in surface water is about $3 \cdot 3 \times 10^{-4}$ atm. If this figure applies in the central Norwegian Sea where deep water is formed, we may reasonably assume that in winter the water sinks with the properties shown in Table III.

If a parcel of this water, sealed against gain or loss of everything except heat, were transported to the tropics and warmed to 25° C, the equilibria of the carbonate system would be strongly displaced. The partial pressure and pH would acquire the values also shown in Table III, calculated from Buch (1933). The increase in partial pressure of CO₂ is a purely physico-chemical effect. Living organisms and solution or deposition of calcium carbonate have nothing to do with it. Failure to appreciate this effect of temperature change has led to much loose thinking about decay processes in the sea. Since partial pressure of CO₂ and pH may be so misleading, only from the total concentration of CO₂ may sound conclusions be drawn about regeneration processes.

This is essentially a thermodynamic argument, so that the history of the parcel of water between sinking near the poles and upwelling by some means in the tropics is immaterial. The conclusion is that, in an azoic world, upwelling water in the tropics must have a partial pressure of ¹²CO₂, greatly in excess of the 'equilibrium value' in the tropical atmosphere. In upwelling areas the over-

lying air must be locally enriched. To balance this circulation of ${}^{12}\text{CO}_2$ in the oceans between poles and tropics a considerable concentration gradient of carbon dioxide is imposed upon the atmosphere between tropics and poles. This is what Buch found.





TABLE III

Temperature (° C)	- I to - I.8	25
Salinity (‰)	34.92	34.92
Chlorinity (‰)	19.33	19.33
Partial pressure of CO_2 (atm.)	3.3×10^{-4}	8.6×10^{-4}
ΣCO_2 (m-mole/l.)	2.20	2.20
pH	8.10	7.84

From every point of view this upwelled water is 'old' so that the ratio ${}^{14}\text{CO}_2/{}^{12}\text{CO}_2$ must be low; so must the ratio in the gas which has there escaped to the atmosphere.

The equilibrium state between air and water is not static but dynamic, and means only that in unit time as many molecules of ${}^{12}\text{CO}_2$ or ${}^{14}\text{CO}_2$ enter the

water as leave it. For the two isotopic molecular species, the balance may everywhere be struck differently. Often a tropical surface water may gain ${}^{14}CO_2$ from the air whilst losing ${}^{12}CO_2$.

If the air has arrived over an area of upwelling with an 'equilibrium' concentration of ${}^{14}CO_2$, referred either to the volume of air or to the volume of ${}^{12}CO_2$ in it, then addition of CO_2 , poor in ${}^{14}CO_2$, must displace this equilibrium. It is clear that the total concentration of CO_2 in the air and the ratio of ${}^{14}CO_2$ to ${}^{12}CO_2$ should be subject to many changes in the course of a single cycle between tropics and poles and back. Either of the interpretations (*a*) and (*b*) on p. 344 may be true, but not both.

ISOTOPIC PARTITION FUNCTIONS

Partition functions of the reactions:

$${}^{12}\text{CO}_2 + \text{H}^{14}\text{CO}'_3 \rightleftharpoons {}^{14}\text{CO}_2 + \text{H}^{12}\text{CO}'_3, \\ \text{H}^{12}\text{CO}'_3 + {}^{14}\text{CO}''_3 \rightleftharpoons \text{H}^{14}\text{CO}'_3 + {}^{12}\text{CO}''_3,$$

depend on temperature (Stranks & Harris, 1953). Between 0 and 28° the partition function of the first reaction changes from 0.957 to 0.965. At the higher temperature relatively more ¹⁴C is free as ¹⁴CO₂ and can escape. The difference lies within present limits of error of the counting technique on carbon-14.

ON CIRCULATION AND RECIRCULATION OF CARBON DIOXIDE IN THE ATLANTIC

Kulp's definition (quoted above) of the age of a water mass implies that there are bodies of water which make long journeys in the ocean whilst retaining all or nearly all their properties unchanged. No oceanographer who has studied the deep sea holds this view, but all are responsible in some measure for propagating it. The trouble starts when names such as 'North Atlantic deep water' or 'Antarctic bottom water' have to be devised to make complex concepts comprehensible. Because some dominant property may be traced for thousands of miles it is only too easy to assume that most of the water that accompanies the property has made the same journey in the same way at the same time. This is rarely so. There is no such thing as a pure-bred water mass. Attribution of a zero oceanographic age, therefore, implies some arbitrary selection of a time and place of birth and an understanding of subsequent mixing processes.

None the less 'water mass' is a useful and fruitful concept. Sometimes changes are so abrupt that it is possible to say that a new water mass has been born from well-defined parent water masses. More often exchanging and mixing processes are formless.

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AGE OF DEEP WATER

Thought is clarified by conceiving dominant characters of water masses. By a dominant character is meant one by which a water mass may be recognized after it has been mixed with a large proportion of other waters with poorer diagnostic characters. In this sense in the eastern North Atlantic, around 1000 m. depth, Mediterranean water is dominant after it has become mixed with many times its volume of North Atlantic Central water. The dominant characters are salinity, temperature-salinity relationship and the nitratephosphate ratio. In this case the characters of the North Atlantic Central water are all masked except for one—phosphate.

SINKING SOUTH-EAST AND SOUTH-WEST OF GREENLAND

This is the area where Helland-Hansen & Nansen (1909), Defant, Böhnecke & Wattenberg (1936), Smith, Soule & Mosby (1937), Wattenberg (1938) and Wust (1943) have considered that much deep water is formed. It is unquestionably an area where an enormous mass of water with markedly homogeneous properties is created. The mixing pot is at least 2000 m deep. Most oceanographers would consider this a good place to ascribe zero age to a water mass. If it is to have zero-age on the ¹⁴C scale, the whole of this enormous volume of water would need to be completely equilibrated with the atmosphere for O_2 , ¹²CO₂ and ¹⁴CO₂. An intensely vigorous process of exchange through the sea surface and of vertical circulation would be needed to achieve this. In fact it is not achieved, not even for oxygen.

Two of the most representative stations were Meteor stations nos. 121 and 122 (56° 37' N., 44° 55' W. and 55° 03' N., 44° 46' W.) worked on 9 March 1935 (Defant *et al.* 1936). Here, between 300 and 2000 m, oxygen lay between 90.8 and 96.2% saturated and averaged 93.0%.¹ Equilibrium with the atmosphere was not attained. It is certain that equilibrium could have been attained neither by ¹²CO₂ nor by ¹⁴CO₂. Consequently, if ¹⁴C is to be a useful tool, its concentration in a newborn water mass such as this needs to be established empirically.

ON THE ¹⁴CO₂ CONTENT OF NORTH ATLANTIC DEEP WATER

Wattenberg (1938) and Wust (1943) have critically discussed the origin of the North Atlantic deep water and the Subarctic bottom current. They suggest that, from time to time, a pulse ('Einschübe') of Norwegian Sea water through the Denmark Strait may contribute to the deep water, but is not very important. The writer believes not only that such pulses are frequent, but that they dominate much of the oceanography of the North Atlantic. The evidence is being prepared for publication. Meanwhile, for the carbon-14 problem the following summary must suffice.

 1 Recomputed from the oxygen saturation tables of Truesdale *et al.* (1955); the range is 92·1–98 % and average 94·6 %.

The North Atlantic deep water would seem to arise, not at any one place, but by a continuing process all the way from Jan Mayen to Labrador (Cooper, 1956). Many waters with varying contents of ${}^{14}CO_2$ will contribute to it.

Let us first consider the North Atlantic Drift and the Norwegian Sea.

The superficial waters of the North Atlantic Drift, subjected to intensive vertical mixing in winter but the site of intense photosynthesis in spring and summer, offer opportunity for equilibration of O_2 , ${}^{12}CO_2$ and ${}^{14}CO_2$ between sea and atmosphere. Much of this water enters the Norwegian Sea and, with the drainage from North-western and Northern Europe, contributes to the surface water of the Norwegian Sea. This alone may be said to have zero age on both an oceanographic and a carbon-14 time scale. In old polar ice, which also contributes by melting, the ratio ${}^{14}CO_2/{}^{12}CO_2$ may be slightly low.

In the area of sinking of Norwegian sea water to form deep water the physical equilibrium becomes neutral so that equilibrium of O_2 and ${}^{12}CO_2$ between air and water might well be maintained to great depths; ${}^{14}CO_2$ is, however, constantly decaying. If the vertical mixing is so vigorous that all the water is equilibrated with ${}^{14}CO_2$ within a score or so of years then all of it may be said to have zero ${}^{14}C$ age. Since such vigour is unlikely, Norwegian Sea deep water at the time and place of sinking should have a positive ${}^{14}C$ age compared with North Atlantic drift surface water.

Over much of the polar basin there is an ice seal, complete in winter and broken by leads of brackish water in summer. Over the whole of the ice-covered seas exchange of gases between air and deeper Norwegian Sea water is prohibited. The ¹⁴C age of this deeper water must be steadily increasing. Similarly, the cover of ice and brackish waters in the East Greenland Current provides a complete seal. Consequently, the water between 200 and 500 m depth in the Norwegian or Greenland Sea which is being sucked towards the passes into the Atlantic must have acquired a ¹⁴C age measured in scores or, maybe, centuries of years.

This water undergoes mixing with other waters, few of which have been near the surface for a very long time. In the confined area of the Denmark Strait, the relatively warm and saline north-bound Irminger current is adjacent to the outgoing cold bottom current. It may contain some water which has equilibrated with the atmosphere fairly recently and also deeper more mature water which has recently been upwardly displaced. By turbulent, lateral mixing some of this deeper water of the Irminger current should become incorporated in the outwardly flowing cold, heavy bottom current. On a smaller scale similar events should have occurred over the Iceland-Faeroe Rise (Cooper, 1955).

The dominant characters of the waters which result are their high density, low temperature and low content of silicate.

After passage through the Denmark Strait the temperature of the Norwegian Sea water, though remaining relatively low, increased by more than 1° C. This has come about by admixture with other deep waters. Some of this is Iceland-Faeroe water which has navigated the eastern slope of the Reykjanes Ridge and turned into the western basin in 50–52° N. latitude. This is comparatively young, though itself subjected to mixing with older water during its journey. However, much of the admixing water will already have circumnavigated the deep North-western and North-eastern Atlantic Basins in an anticlockwise sense at least once. All of these contribute to the water which comes to underlie the enormous homogeneous mass of water around Southern Greenland already discussed. It should have acquired an apparent carbon-14 age likely to be measured in centuries; this although its dominant component had been calved only a few years earlier in the Denmark Strait or Iceland-Faeroe Channel.

On this view there is constant and considerable recycling of water around the deep basins of the North Atlantic. On each cycle the waters are rejuvenated by a proportion of relatively young Norwegian Sea water but the process is never complete. This eddying or recycling involves water which is getting ever older. The currents which may be measured either directly or by dynamical calculations are the sum of movements of water which has newly sunk and of water which is being recycled. Moreover, all three dimensions of space have to be considered.

In the course of this circulation of the deep North Atlantic, deep water from south of the Equator will become incorporated. In its turn the South Atlantic deep water will have acquired parcels of water from Antarctic, Pacific and Indian Oceans. The simplest interpretation of the world distribution of nutrients suggests that these other oceans have a much more lethargic deep circulation than the Atlantic, and that their carbon-14 age will prove to be much higher.

Analyses of carbon-14, therefore, present the oceanographer with a very powerful weapon for attacking this complex problem.

THE PUBLISHED DATA FOR ¹⁴CO₂ IN THE NORTH ATLANTIC

Let us now examine the data (Table I) published by Kulp (1953 *a*, *b*). That the four surface waters are recent is to be expected. The first three are far from regions of sinking. The fourth is about 300 miles south-east of Cape Farewell, Greenland. However, the nearby 'General Greene' station 1994 worked by Soule & Graves (1937) on 3 August 1935 at 54° 47' N., 41° 52' W. does not suggest that the region is one of sinking deeper than 1000 m at most. None, therefore, gives a clue as to what composes the North Atlantic deep water at its places of origin.

The deep sample from the Norwegian Sea is of much interest. Helland-Hansen & Nansen (1909) suspected that this deep water might be of great age, a view not supported by the high oxygen content. Kulp's result indicates that water at 3182 m north-east of the Faeroes cannot have an 'age' exceeding $500+200 \ (=700)$ years. It may well be very much less. Necessarily there must be an escape of water with density exceeding σ_{t} 28.0.

The sample at 58° 19' N., 32° 57' W. on the western slopes of the Reykjanes Ridge at 1800 m depth was well placed. The water thereabouts is composite in origin. The 'dominant' water which gives the water its salinity inversion is young and has come from the Iceland–Faeroe Ridge contouring around the slopes of the Reykjanes Ridge. From the results of the research vessels *Dana, Atlantis* and *Meteor*, especially from oxygen determinations, it is possible to conclude that there is also a slow deep drift of old, oxygen-poor water from the South Atlantic along the western slopes of the Mid-Atlantic Ridge. This takes place mostly at a depth considerably greater than 1800 m. Nevertheless, in the western basin north of 52° N., upward displacement and homogenization should be a very vigorous process at all depths, accounting for the large apparent age found for the 1800 m sample.

Water from this position continues to move northerly and then westerly until it is forced by the configuration of the sea bed to move south-west over and alongside the cold heavy water sinking from the Denmark Strait. Lateral and vertical mixing between the two very different parallel water masses must then occur. One result should be a rapid 'maturing' of the heavy water from the Denmark Strait on its way to form North Atlantic Deep Water.

The sample or samples from the southern tip of the Rockall Bank are not well placed. The water thereabouts has a highly characteristic temperatureoxygen relationship which suggests either a rapid increase in 'age' from a depth of about 2300 m towards the bottom or that the consumption of oxygen in the deep ocean is largely confined to the bottom and the water immediately above it. The organic carbon being oxidized by this process may have lain on the bottom for very many years. When transferred to the water by oxidation and upward mixing, it would be expected to impart a fictitiously high age to the water.

These several arguments suggest that whilst we are building up our knowledge of its distribution it may be wiser to report ${}^{14}CO_2$ in concentration units (per unit weight of carbon dioxide or per unit volume of water) which make no tacit assumptions about history.

Again, the significance of a determination of carbon-14 on a sample of sea water cannot be assessed unless the content of carbon-12 dioxide and everything else that has been discovered about the water is published. Date, depth, records of current, temperature, salinity, oxygen, nutrient salts and pH need to be reported or, alternatively, a reference to where these have been published and discussed should be given. No sound conclusions on age of water masses may yet be drawn.

AGE OF DEEP WATER

DEVELOPMENT

There is a strong case for directing effort to atmosphere and ocean in places and on occasions where conditions are likely to be extreme. Knowledge of extreme conditions should help evaluation of cases which are more average. Unfortunately, many of the places where extreme conditions may be expected are difficult of access.

The Atmosphere

Apart from places where coal and oil are burnt in large quantities, the highest concentrations of ${}^{12}CO_2$ are likely to occur over tropical areas of strong upwelling during quiet weather. Upwelling in the Pacific is likely to bring up more ${}^{12}CO_2$ than upwelling in the Atlantic. The upwelling waters off the desert coast of Peru are likely to produce the highest natural concentration of ${}^{12}CO_2$ in the air above to be found in the world. However, there is no reason to believe that ${}^{14}CO_2$ should there be exceptionally high. The ${}^{14}CO_2/{}^{12}CO_2$ ratio of air over upwelling water might be best determined during moderate south-easterly winds at a place on the coast of Peru in about 9° S. lat. The fetch of the air over upwelled water would then be several hundred miles.

Vegetation will assimilate all isotopes of carbon. The partition ratios for the several isotopes will be slightly different from the concentration ratios but within the limits of error of our present study, these differences may be ignored.

Areas of strong coastal upwelling are usually bordered by desert continental land. Even so the ratio of ¹⁴C to ¹²C in such vegetation as exists at places like Walvis Bay and the Peruvian guano zone is worthy of examination. To obtain samples it would be worth while to grow plants in pots. The ratio may be markedly lower than average. Moreover, in such places a strong seasonal variation in the isotopic ratio of the carbon assimilated may exist (cf. Currie, 1953), low at seasons of strong upwelling, average when upwelling is in abeyance.

To contrast with such samples, others for analyses of ${}^{12}\text{CO}_2$ and ${}^{14}\text{CO}_2$ are needed from (*a*) the bitterly cold air which stagnates in winter over Siberia at places like Verkhoyansk, Oymyakon or Yakutsk. (Here is an area likely to be particularly favourable for transfer of ${}^{14}\text{CO}_2$ from stratosphere to troposphere), (*b*) air which has sojourned for some time over Antarctica or over the Arctic sea ice, (*c*) air from these sources and from temperate latitudes which has blown for hundreds of miles over areas of oceanic sinking.

The Ocean

The following are needed:

Samples of water from outstanding regions of upwelling such as the Peruvian coast, and from the thick fast currents which set away from these coasts under the influence of the trade winds. Samples from outstanding areas of sinking, such as the Norwegian Sea south of Jan Mayen, the oceanic area around Southern Greenland and the areas of formation of Antarctic bottom water.

Samples from precisely defined places where key processes in the circulation of the oceans are suspected of occurring. The Denmark Strait may be one such place and key positions are: (a) North of the Sill where the current at 200-500 m is flowing towards the south-west (say 68° 30' N., 24° 40' W.). (b) South-west of the sill crossing the meridian 27° 45' W. between 66° 10' and 66° 35' N. latitude where on occasion the bottom current is believed to run fast on the continental terrace and parallel to the coast for the next 70 miles (130 km). In some years this position is overlain by ice. A more accessible position some miles to the south-east is unlikely to sample the water in question. Since the outflow is likely to be intermittent, it would be essential to establish that the desired water was being sampled. The season from March to June would be most appropriate. (c) At 66° 10' N., 30° 30' W. in what appears to be a submarine canyon extending south-east from the fjord Kangerdlugssuak.

Living organisms

The ratio of $Ca^{14}CO_3$ to $Ca^{12}CO_3$ in shells and of ${}^{14}C/{}^{12}C$ in shore plants and animals from the special areas listed above should be of interest. There should be a considerable difference between shells and organisms from, say, Spitzbergen or Jan Mayen on the one hand, and Peru or South-west Africa on the other.

SUMMARY

The carbon-14 method for determining the age of deep oceanic water gives ages much higher than are suggested by physical and chemical oceanographic observations. The discrepancy arises from tacit assumptions as to the age and nature of water masses and from peculiarities of the cycles of ${}^{12}\text{CO}_2$ and ${}^{14}\text{CO}_2$ in nature. These are:

(1) When surface water is under or over saturated to the same extent with oxygen or ${}^{12}CO_2$ equilibrium between atmosphere and ocean is much more rapidly restored with oxygen. An approach towards equilibrium which oxygen may achieve in 1 day requires 10–17 years for carbon-12 dioxide. Carbon-14 dioxide should behave similarly to carbon-12 dioxide.

(2) When polar water is transported via the deep ocean to upwell in the tropics, heating causes the partial pressure of ${}^{12}\text{CO}_2$ to increase about three times. Upwelling water must, for physico-chemical reasons, be super-saturated with ${}^{12}\text{CO}_2$ with respect to the atmosphere. A compensating concentration gradient for ${}^{12}\text{CO}_2$ must therefore build up in the atmosphere between tropics and poles. The corresponding gradient for ${}^{14}\text{CO}_2$ should be different.

(3) Due to the vast masses of water in areas of oceanic sinking which have to be equilibrated for ${}^{14}CO_2$ with the atmosphere and the complexity of the processes, it is unlikely that a water mass which an oceanographer would consider newly born, will sink with a zero age on the present carbon-14 scale. The content of ${}^{14}CO_2$ in sinking waters needs to be determined empirically and used as the starting point of a carbon-14 time scale.

(4) In the deep North Atlantic basin there is much recycling of ever-ageing water. This is rejuvenated by descent of Norwegian Sea water from the sills of the Denmark Strait and the Iceland-Faeroe Rise.

The significance of existing measurements of carbon-14 on deep oceanic waters is discussed. No sound conclusions on age of water masses may yet be drawn from them. It may be wiser, for the present, to report ${}^{14}\text{CO}_2$ in concentration units which make no tacit assumptions about history. On any sample, submitted for carbon-14 analysis, all the standard oceanographic measurements need to be reported.

Attention is directed to places where the concentration of ${\rm ^{12}CO_2}$ and ${\rm ^{14}CO_2}$ in atmosphere and ocean are likely to be extreme. Determinations in such places should hasten the assessment of determinations where conditions are more average.

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THE GROWTH RATE OF CHTHAMALUS STELLATUS (POLI)

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(Text-figs. 1 and 2)

Detailed data have recently been given on the growth rate, under varying conditions, of the common barnacles, *Balanus balanoides* (L.), *B. crenatus* Brug. and *B. balanus* (L.) da Costa (Barnes & Powell, 1953; Barnes, 1955; Barnes & Barnes, 1954). This work has now been extended to *Chthamalus stellatus* (Poli). Some observations have been made on populations growing in their natural habitat, but most relate to animals growing under conditions of continuous immersion such as are obtained by exposure from a raft.

THE MATERIAL AND METHODS

Pieces of rock on which adult barnacles were growing or on which young spat had recently settled were detached from the shore and fastened to panels that could be mounted on frames for raft exposure. With few exceptions (see later, p. 357) all the material was taken from within the well-marked Chthamalus zone, which at Millport forms a narrow band lying above Balanus balanoides. On each piece about ten individuals were selected for measurement and their unrestricted growth ensured by the removal of the remainder, together with any other sedentary forms. At about monthly intervals the pieces of rock were brought into the laboratory and, in accordance with previous practice, the length of the base of each individual barnacle along its rostro-carinal axis measured. For the smaller individuals a binocular microscope with scaled ocular was used; the larger animals were measured with a vernier measuring microscope. At each inspection the stones were thoroughly cleaned to remove newly settled animals and, as far as possible, all algal growth. The observations have extended over a period of 2 years; during this time several sets of exposures have been made, of which seven are shown in Fig. 1. It should be pointed out that the irregular outline of Chthamalus, and the fact that the measurements have been made on individuals growing on rough natural sandstone, has led to rather less accurate results than with the species previously studied; the latter were usually grown from spat settled directly on glass or plastic panels.

For every set, the mean length of the selected individuals was calculated

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at each inspection; these values, together with the mean specific growth rates (the increase in length per unit length per day) are shown in Figs. I and 2.



Fig. I. The growth of *Chthamalus stellatus* over several seasons under conditions of total immersion. The mean lengths of each set at each date of inspection are shown. The growth of *Balanus balanoides* is shown for comparison.





THE RESULTS

At Millport *Chthamalus stellatus* produces a number of broods during the summer months, but only that of the late summer and early autumn leads to a successful spat-fall. As is evident from the figures some growth takes place, under raft conditions, during the autumn and early winter following settlement, but becomes virtually negligible in the late winter months. After

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7 months' growth, spat settled in September has reached a mean size of some 2.0 mm by the following April. During the late spring and summer of the first year, growth is renewed and at a greater rate, to fall off again in the autumn months. Twelve months from settlement a size of 3-4.5 mm has been reached. In the second year growth is slower, but the same pattern is repeated, although the contrast between summer and early winter growth is less striking. The same pattern is evident in all the series, but the uniformity from one series to another is less than with some other species. A length of 6-7 mm is reached by the end of the second year. The experiments were not continued beyond 2 years, but it would seem that those individuals, of maximum size some 10–15 mm, found on the shore, are at least 4 years old.

There is some evidence that for any size-group there is an enhanced growth rate directly after the change to conditions of total immersion; the initial parts of the growth curves are somewhat steeper than the central parts when animals of the same size and when growth at the same part of the year is considered. (Compare, for example, the appropriate parts of Series II*b* and VII, II*b* and II*c*, Fig. 1.) Further evidence that a sudden change to conditions of continuous immersion leads to an enhanced growth rate was obtained by following the growth, when transferred to raft conditions, of individuals which had been maintained at known levels on the shore for many months. These experiments were made possible through the kindness of Mr J. Connell, who allowed some of his experimental blocks to be used.

TABLE I. COMPARISON OF THE GROWTH OF CHTHAMALUS STELLATUS UNDER COMPLETE AND CONTINUOUS IMMERSION AFTER TRANSFER FROM DIFFERENT HABITATS

	Mean in m	Increase in mean length		
Conditions prior to total immersion	20. vi.	26. viii	(mm)	
High-tide level Mid-tide level	3·I	4.9	I·8 0:4	
Between mid- and low-tide level	2.3	2.9	0.6	
Continuous immersion from settlement	2.8	3.0	0.5	
Series VII, high-tide level	5.2	6.0	0.8	
Series II <i>b</i> , continuous immersion from settlement	5.4	5.2	0.1	

It is evident from Table I that when animals are transferred from the upper part of the shore to conditions of constant immersion, the initial growth rate is greater than that of similar individuals—of the same size and at the same time of the season—which have been completely immersed since settlement. Further, this enhancement of the initial growth rate is most marked with animals taken from the upper levels of the shore. This has not been demonstrated for *Balanus balanoides*; there is no evidence from the results so far

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available that it occurs in the sublittoral *B. balanus* on transference from the natural habitat to raft conditions (Barnes & Barnes, 1954). The capacity to react rapidly to immersion is clearly of importance to an intertidal animal since it will ensure maximal feeding when it is covered by tide. However, continued immersion, at least with *Chthamalus stellatus*, results in the establishment of a steady normal growth rate and, presumably, metabolic activity. This would appear to be another example of acclimatization (see Bullock, 1955, for a recent discussion), a return being made, under the new conditions of the environment, to the general metabolic level of the animals under 'equivalent' intertidal conditions.

The mean specific growth rate (Fig. 2) during the growing season decreases with increasing size. Due no doubt in part to the difficulties of making accurate measurements (see p. 355) the spread of the results is greater than was found for other species; there is, however, some evidence (Hatton, 1938) that growth in *Chthamalus* does vary considerably from year to year. The rate of change of growth rate with length is greater than for *Balanus balanoides* when both sets of measurements are expressed in terms of maximum size attained during the first growing season.

COMPARISON WITH OTHER RESULTS

The literature contains very few references to the growth rates of *Chthamalus* stellatus. Hatton (1938), working in the St Malo area, found that growth in an exposed situation was most rapid at the lower tidal levels during the first 9 months after settlement; at mid-tide level a length of 4.1 mm, and at a position slightly above high-water neaps 2.6 mm was attained in the same period. There was considerable variation from year to year; for example, only 2.7 and 2.0 mm were reached at these same levels in another year. During the second season the mid-tide population grew very little, but that at the higher level increased in size from 2.6 mm to between 4 and 5 mm. He could detect no significant seasonal difference in growth rates, but this may have been a consequence of the methods he used for these very slow-growing barnacles. (The growth of individual barnacles was not followed and he sometimes obtained a decrease in mean size in his samples.) In less exposed localities Hatton found that the more rapid growth at his lower levels was continued into the second season. Moore & Kitching (1939) have suggested that there was some unfavourable influence at work at the lower levels examined by Hatton which became progressively more effective with increasing age of the barnacles. These workers found that at Plymouth growth over a period of 4 years was always greater at the lower levels, even though the two levels examined were only about I m apart. (These authors give sizes in terms of (length+width)/2; for the purposes of comparison this will give somewhat smaller values than length alone.) At their upper level (+1.36 m) the mean

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size at 12 months from settlement was 2.0 mm, and after 24 months 3.7 mm; at their lowest level (+0.41 m) the sizes reached, during the same period, were 3.9 and 5.0 mm. Similar growth rates have been obtained for shore populations at Millport. The growth rates under conditions of continuous submersion are clearly very similar to those encountered on the shore. It would seem, therefore, that the harmful effect of continuous immersion postulated by a number of workers to explain the restriction of *Chthamalus stellatus* in some places to the highest levels of the intertidal zone is not warranted: it is not the necessity of alternate wetting and drying which ever limits *Chthamalus* to the upper levels of the shore in any region.

DISCUSSION

It is evident from these results that Chthamalus stellatus, kept under the stated conditions on a raft, grows at a much slower rate than Balanus balanoides under the same conditions (Fig. 1); the latter species virtually reaches its maximum size in the first season's growth, i.e. some 6 months after settlement. Equally striking is the small effect that continuous immersion has on Chthamalus in comparison with its growth rate on the shore. At similar sizes the growth rate under the experimental conditions is greater than on the shore either at high or low levels, but in contrast with Balanus balanoides the difference between the growth rates is much less striking. It has been shown that, in the latter species, whilst increased opportunity for feeding contributes to enhanced growth rates under raft conditions, the fact that the experimental panels are kept free from algal and other growths is of paramount importance (Barnes & Powell, 1953; Barnes, 1955). The smaller effect in Chthamalus may be due in part to the fact that the comparison of growth rates has been made with individuals which in their natural habitat are subject to a much smaller depressing effect of algae. However, it is well known that Chthamalus is found most abundantly in wave-swept positions; the advantages to be gained in feeding opportunity and freedom from algal growth under the experimental conditions may, therefore, be offset in this species by the lack of violent water movement under conditions of complete submergence.

C. stellatus and Balanus balanoides are two competing barnacles in the intertidal region; the former is a tropical-Lusitanian form and the latter Boreo-Arctic in its distribution and both are at the limit of their distribution in the British Isles. In general, towards the north, where conditions are more favourable for the breeding of Balanus balanoides when the two species co-exist, Chthamalus stellatus as a major community is restricted to a level above that of the former species. Towards the south, as conditions become more favourable for the breeding of Chthamalus, it is found lower down the shore, extending into the Balanus zone, which it may ultimately replace. Southward & Crisp (1954) have stressed that since both species are at the

limits of their distribution in Britain, they are, therefore, very sensitive to changes in the environment. This is reflected in the comparatively rapid changes which take place in the total and relative numbers of the two species at different levels of the shore. Changes favourable to Chthamalus result not only in an increase in its numbers at the upper levels but also in its spread down the shore. Many factors play a part in any competition between these two species, but ultimately many of these become effective through the difference in growth rate in the struggle for intertidal space. Balanus balanoides spat, settled on experimental rocks on which Chthamalus was growing and exposed on the raft, rapidly overgrew the latter; a 6-months-old Chthamalus settlement (2 mm long) was obliterated in a *few weeks* by a moderate spat-fall of *Balanus*, and full-grown Chthamalus (9-15 mm) were completely overgrown in 2 months. Where conditions are favourable to the breeding of Balanus, i.e. towards the north and where there is, therefore, a good spat-fall each spring, Chthamalus settled in the previous autumn has little chance of survival on the lower parts of the shore (although occasional individuals may be found). The growth rate of any which do survive is perhaps even more affected by algal cover than is that of Balanus balanoides. Chthamalus becomes, therefore, as a major community, restricted to the upper level of the shore, usually above that of Balanus, where it survives presumably by its greater capacity to withstand desiccation. As one proceeds southwards conditions become more marginal for the breeding of *B. balanoides* and more favourable for *Chthamalus*; the annual spat-fall of the former becomes progressively reduced and the latter can maintain itself even in the lower parts of the shore. Any change in the environment, from whatever cause, which affects the breeding, annual spat-fall and survival after settlement of the two species will be reflected in this competition for space which in turn is intimately related to the growth rates.

SUMMARY

1. Data are presented on the growth rate of *Chthamalus stellatus*; growth is slow in the first few months after settlement, virtually ceases in the winter and is renewed during the following spring.

2. Directly after transferring from the shore to raft conditions of constant submersion there is an acceleration, at all sizes, of the growth rate. However, acclimatization with a return to the slower rate soon takes place.

3. Growth rate under raft conditions is not greatly different from that on the shore. This is in marked contrast to *Balanus balanoides* and is ascribed in part to the relative lack of smothering algae in the upper parts of the shore so that there is less contrast in the conditions after transfer.

4. The effect of growth rate on competition between *Chthamalus stellatus* and *Balanus balanoides* for space in the intertidal zone is stressed.
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ON THE SCYPHOMEDUSAE NAUSITHOË ATLANTICA BROCH AND NAUSITHOË GLOBIFERA BROCH

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(Plate I and Text-figs. 1-6)

Broch (1913) described two new species of the coronate scyphomedusa *Nausithoë* from the North Atlantic, *N. atlantica* and *N. globifera*. Bigelow (1928, p. 498) was inclined to think that these two species might finally prove to represent extreme variants of the one species *N. rubra* Vanhöffen, though a much larger series of specimens in a better state of preservation would be needed to give a definite decision. Kramp (1947, p. 46) considered that *N. globifera* at any rate was a good species.

I have recently seen four specimens, two of which agreed with Broch's description of *N*. *atlantica* and two with that of *N*. *globifera*. Examination of these medusae leaves no doubt about the correctness of Broch's identification. These specimens were collected in a 2 m stramin ring trawl by R.V. *Sarsia*, the two *N*. *atlantica* (35 and 25 mm in diameter) at 47° 12' N., 7° 40' W. on 21 July 1955 with 450 fathoms of wire out, and the two *N*. *globifera* (22 and 11 mm in diameter) at 46° 49' N., 5° 44' W. on 6 September 1955 with 500 fathoms of wire out (vertical haul).

The two species were at once distinguishable both by their shape and coloration, and a closer examination showed other differences.

Nausithoë atlantica

The largest specimen of N. *atlantica* recorded by Broch was 28 mm in diameter; my largest specimen is about 35 mm in diameter, the diameter at the coronal groove being 19 mm (Text-fig. 1; Pl. I). In this specimen three of the gonads are the same shape as drawn by Broch (1913, pl. I, fig. 2), but five of them have reached a further degree of development not yet recorded. The central part of each gonad is extended towards the umbrella margin so as to be between the septa and ending only a short distance from the base of the marginal tentacle (Text-fig. 2). The only other respect in which my specimens differ from Broch's description is that the pedalia are all about the same length. Broch stated (and his pl. I, fig. 1, shows) that the rhopalar pedalia were shorter than the tentacular pedalia. In my specimens all pedalia are

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approximately equal in length; if anything the rhopalar pedalia are slightly the longer, and this is rather to be expected because the distance between the coronal groove and the rhopalium is longer than that between the coronal groove and the base of the marginal tentacle.



Text-fig. 1. N. atlantica. Adult medusa, 35 mm in diameter.



Text-fig. 2. N. atlantica. Semi-diagrammatic view of subumbrella with buccal walls of stomach cut away. The stippled areas indicate regions of fusion of upper and lower endoderm surfaces. c.g., coronal groove; c.m., coronal muscle; g., gonad; g.f., gastric filaments; s., septum.



Text-fig. 3. N. globifera. Adult medusa, 22 mm in diameter.



Text-fig. 4. N. globifera. Semi-diagrammatic view of subumbrella with buccal walls of stomach cut away. Details as in Text-fig. 2.

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In my specimens the exumbrella surface is considerably pitted; these pits appear to be due to the pressure of radiolaria into the jelly, presumably during the process of collecting. I have not shown them in Text-fig. 1, but they can be seen in Pl. I. The marginal lappets also were mostly frayed, though there was sufficient intact margin to supply evidence of their true outlines which I have shown in Text-fig. 1. There are twenty or more gastric filaments on each phacellus, making over 160 in all, and each filament arises singly.

Sections of the gonad show that the mature ova are each completely enveloped by a layer of densely packed oval bodies lying immediately beneath the egg membrane. These bodies, the largest of which are about 12–14 μ in length, appear first in the smallest ova as minute granules. As the ova increase in size so the granules grow and move towards the periphery. The bodies have a central core, but no other structure is visible.

The colour of the whole medusa, when freshly preserved in formalin, is chocolate red identical with that of *Paraphyllina ransoni* (Russell, 1956). As in that species, sections show that the coloration is limited to the mesogloea and forms a dark membranous layer immediately beneath the endoderm. The brownish yellow colour also occurs faintly throughout the whole mesogloea so that the umbrella jelly has not the striking transparency of that of *Paraphyllina ransoni*. As in the latter species the stomach walls are especially densely coloured, both under the endoderm and the ectoderm, and the mesogloea of the marginal lappets is coloured throughout. The whole rhopalium is coloured, and the underside of the hood is especially dark (Text-fig. 5). After storage in formalin and sea water for several months the whole medusa becomes much more transparent and dark amber in colour.

Nausithoë globifera

The largest specimen of N. globifera recorded by Broch was 17 mm in diameter; my largest specimen, which was perfectly preserved, is 22 mm in diameter, the diameter at the coronal groove being 10 mm (Text-fig. 3 and Pl. I).

My specimens agree in every respect with Broch's description.

The gonads in the smaller specimen, a male, are shield-shaped, and their interradial edges are folded inwards towards the subumbrella. This fold continues round the lower margin of the gonad to within about one-third of the upper end of the perradial side. At the latter point the fold ends and joins the main body of the gonad at its inner edge (Text-fig. 6d). In the larger specimen, in which the gonads are further developed, this sudden reduction in the width of the upper part of the gonad makes it look as though there is a protruding thumb when viewed from the exumbrellar side (Text-fig. 3).

The gonads in the smaller specimen were white except for fine flecks of pigment, and they showed in striking contrast against the dark colour of the



Text-fig. 5. *N. atlantica. a, b,* exumbrellar and subumbrellar views respectively of rhopalium.





Text-fig. 6. N. globifera. a-c, exumbrellar, subumbrellar, and lateral oblique views respectively of rhopalium; d, male gonad of specimen, 11 mm in diameter seen from subumbrellar side. stomach. In the larger specimen the gonads were coloured reddish brown, but they were still very obvious against the dark stomach wall.

The gastric filaments, of which there are about ten in each phacellus, making eighty or more in all, are mostly simple, but on any one phacellus there may be two or three roots which each give rise to two to four filaments.

The rhopalia are bent at right angles so that they are hidden from sight when viewed from above but can be seen in a lateral view.

The whole medusa is perfectly transparent except for the stomach, the marginal tentacles, and part of each rhopalium. The colour of the stomach was deep purple-red when freshly preserved in formalin and sea water, being darkest over the summit. The colour of the marginal tentacles was a more orange red; a short portion at the base of each tentacle was uncoloured. Only the ventral bulb of the rhopalium was coloured and this only faintly (Text-fig. 6).

Sections show that the coloration is limited to a membranous layer lying in the mesogloea immediately beneath the endoderm of the stomach. In the buccal walls of the stomach the whole mesogloea is coloured. There are in addition pigment granules present in the endoderm cells lining the whole stomach, and in the walls of the gonads. The mesogloea of the marginal tentacles and gastric cirri is also coloured.

The essential differences between the two species may be summarized as follows:

	N. atlantica	N. globifera
Shape Colour	Somewhat flattened Whole medusa chocolate red; coloration in mesogloea only	High domed Umbrella transparent; stomach deep purple red and marginal tentacles orange red; coloration in both meso- gloea and endoderm cells
Gastric cirri	About 160 in number, generally single	About 80 in number, several compound
Gonads	Situated mainly in marginal disc region	Situated above coronal groove
Rhopalia	With large wedge-shaped flat basal cushion and exumbrella carina. Under side of hood and ventral bulb deeply coloured	With small high wedge-shaped basal cushion and exumbrella carina bent at right angles. Ventral bulb only faintly coloured

There is now sufficient evidence to prove that N. globifera Broch cannot be identified with N. rubra Vanhöffen. I think also that N. atlantica Broch must be regarded as a good species for which we now have an adequate description, and that it is not possible to decide whether it is the same as N. rubra.

My thanks are due to Captain C. A. Hoodless and the crew of R.V. Sarsia who collected the specimens; to Dr D. P. Wilson for the upper photographs in Pl. I; to Dr J. S. Alexandrowicz for the preparations and photographs in the lower half of Pl. I; and to Miss M. L. Weir for the preparation of sections.

ON NAUSITHOË

SUMMARY

Specimens of the coronate scyphomedusae *Nausithoë atlantica* Broch and *N. globifera* Broch were caught in deep water off the mouth of the English Channel in July and September 1955 respectively.

These were well preserved and there is now no doubt that these are two distinct species.

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POSTCRIPT

Since the above account was written I have seen three more specimens of N. *atlantica* and seventeen of N. *globifera*. These were from samples collected in the 2 m. ring trawl, the details being as follows:

Date	Position	Diameter at coronal groove (mm.)						
	N. atlantica							
20. vii. 55 7–8. ii. 56	47° 12′ N., 7° 40′ W. 46° 46′ N., 5° 47′ W.	Female, 9 Females, 12, 14						
	N. globifera							
17. vi. 55	46° 49′ N., 5° 44′ W.	Female, 8						
20-22. vi. 55	47° 12′ N., 7° 40′ W.	Males, 8, 8, 9, 9.5, 10						
7. ii. 56	46° 46′ N., 5° 47′ W.	Females, 6.5, 7, 7 Males, 6, 7.5, 10.5, 11						

The only additional information obtained by examination of these specimens was:

N. atlantica: all the gonads may extend nearly to the bases of the marginal tentacles.

N. globifera: the thumb-like process is not so apparent in the female gonads as in the male gonads. Sections of the female gonads show bodies in the ova similar to those described above for N. atlantica.

In both species the mature eggs are white; and in both species the marginal tentacles are laterally compressed except close to the basal bulb, possibly an effect of preservation.

EXPLANATION OF PLATE I

Left: Nausithoë atlantica Broch.

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Right: N. globifera Broch.

Above: exumbrellar and lateral views of freshly preserved specimens, $\times 1.7$.

- Below: sectors of umbrella bleached by Mayer's chlorine method, stained with borax carmine and mounted.
- N.B. In the upper photographs of *N. atlantica* the gonads can be seen in places showing through the jelly. The white objects present on the dome of the umbrella are radiolarians which have become pressed into the jelly.

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Russell. Plate I



(Facing p. 370)

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ON A NEW MEDUSA, AMPHINEMA KRAMPI N.SP.

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The Plymouth Laboratory

(Text-figs. 1 and 2)

In a collection of plankton made by R.V. *Sarsia*, in a 2 m stramin ring trawl at 47° 12' N., 7° 40' W., on 21 July 1955 with 450 fathoms of wire out, there was a small anthomedusa which does not agree with any previously described species.



Fig. 1*a*, *b*. Amphinema krampi n.sp.; the specimen has been drawn from both sides to show it as it actually looks in the preserved state.

The specimen is sufficiently well preserved to show its chief characters, and apparently belongs to the family Pandeidae. Its characters are such that it can be included in the genus *Amphinema*.

I have great pleasure in naming the medusa Amphinema krampi n.sp. in honour of P. L. Kramp, the world's leading authority on medusae.

Amphinema krampi n.sp.

The umbrella is bell shaped and higher than wide; the jelly is much wrinkled and contracted but would in nature have been fairly thick; there is no apical process. The stomach is cross-like in section and about two thirds the length

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of the subumbrellar cavity; it has no peduncle. The mouth is cruciform with four simple lips with a thickened margin and almost no crenulation. The four radial canals and ring canal are fairly broad; they have smooth margins; there are about twelve strands of cellular tissue running from each radial canal to the exumbrella surface, distributed along the length of each canal between the summit of the stomach and the level of the mouth lips. The gonads, which are male, form four simple cushions, one on each interradial surface of the stomach. There are two opposite perradial marginal tentacles with swollen elongated basal bulbs, and eight marginal tentaculae. There are no ocelli. The height of the umbrella is about 6 mm and it is about 4 mm wide. The colour of the stomach and gonads is rich reddish brown, and there is a core of brownish pigment in the ring canal extending into each of the two marginal tentacle basal bulbs; the marginal tentaculae are colourless.

Drawings of the specimen are given in Fig. 1a and b. It can be seen that

the umbrella jelly is shrunken and that the umbrella has been much contorted in the marginal region. Two of the gonads on one side have been squashed so that they are folded down their centres, and the mouth has been torn on that side.

Nevertheless it has been possible to reconstruct the medusa fairly accurately and a drawing of its probable appearance if it had been well preserved is given in Fig. 2.

As there is only one specimen I did not have sections made for microscopic examination. One or two details remain therefore undetermined.

The strands of cellular tissue running from the radial canals to the exumbrella surface are of special interest, and nothing like them has ever been recorded before. They appear as though they might be canals running from the radial canals to the exterior, but microscopic sections would be required to prove whether this were so.



Amphinema krampin.sp.: the medusa reconstructed as it would probably appear if well preserved.

The marginal tentacles appear to be typical of pandeid medusae and it is probable that they are hollow. The marginal tentaculae are uniformly covered with nematocysts. The distribution of the tentaculae around the margin of the umbrella is rather irregular. In one sector at any rate, one tentacula is perradial so that there are two in one interradius and one in the other. The distribution appears to be similar in the other sector, but as the radial canal is damaged on that side it is not possible to say for certain whether one tentacula is perradial. There is no indication that there are any missing tentaculae. Owing to the dark coloration it was not possible to tell the sex except by breaking one of the gonads, when the specimen was found to be a male.

The following characters distinguish *Amphinema krampi* from other species in the genus: no apical process; cellular strands of tissue running from radial canals to exumbrella surface; four simple interradial gonads.

The specimen has been deposited in the British Museum (Natural History) and has been given the registered number B.M. 1956.1.10.1.

My thanks are due to Captain C. A. Hoodless and the crew of R.V. Sarsia, who made the collection in which the specimen was found.

SUMMARY

A single specimen of a new pandeid medusa was caught in deep water off the mouth of the English Channel in July 1955.

A description is given, and the species has been named Amphinema krampi n.sp.

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THE SIZE OF DIATOMS

III. THE CELL WIDTH OF *BIDDULPHIA SINENSIS* GREVILLE FROM THE SOUTHERN NORTH SEA

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(Text-figs. 1-5)

The present contribution deals with the measurements of fifty-two samples of *Biddulphia sinensis* collected by Hensen net hauls from the Ministry of Agriculture and Fisheries research ships *George Bligh* and *Onaway*, working in the southern North Sea between 1932 and 1938. With one exception in which there were only seventy available, the samples consisted of a hundred cells and the unit of measurement was that employed in Part I of this paper (Wimpenny, 1936). The dimension used was the greatest width (apical axis), and care was taken to see that the cells measured were lying flat, to give the true maximum of their elliptical cross-section. For convenience in tabulation and to avoid random fluctuations due to too small grouping of the data, the measurement units have been taken in pairs in the presentation of all the sea results, each arbitrary unit being equivalent to about 8μ . The measurements from cultures, where the samples were sometimes fewer than a hundred, have been 4μ units.

The positions of the stations, the mean widths, the population densities and the temperatures and salinities relating to the samples are given in Table I. The individual measurements from which this table has been compiled have been deposited at the Marine Laboratory, Plymouth, whence they may be obtained for consultation on request.

OBSERVATIONS MADE ON CELL WIDTH

A representative series of size-frequency samples covering the period 1932–38 has been plotted in Fig. 1. This may usefully be compared with Text-fig. 2 in Part II of this work (Wimpenny, 1946). It will be seen at once that the regularly recurring and persistent form of the size distribution shown by *Rhizosolenia styliformis* is absent in *Biddulphia sinensis*, where the width distribution in one year, or indeed on one cruise, may vary as much as it does throughout the whole period.

These big variations within the area of one cruise are, however, more explicable when related to the salinity of the surrounding water, and in Fig. 2 I have shown the surface salinities of two cruises in 1937 in relation to the

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Date	Cruise	Sta- tion	Depth (fathoms)	Latitude N.	Longitude E.	$t^{\circ} C$ at o m	Salinity at 0 m	Mean diameter in arbi- trary units	1000's per m ³
26. x. 32	J	7	15	52° 55'	4° 00′	13.67	34.67	17.6	23.8
28. x. 32	J	17	15	53 45	6 07	12.57	33.40	16.7	30.3
7. x. 33	K	4	13	52 12	3 53	16.70	33.82	16.4	136.5
8. x. 33	K	8	17	53 06	3 02	16.70	34.66	17.4	351.7
8. x. 33	K	IO	18	53 26	2 27	16.46	34.62	10.1	1417.2
19. x. 33	L	15	16	53 19	3 07	14.89	34.85	17.8	375.6
20. x. 33	L	22	17	53 45	2 35	14.32	34.73	17.0	6.1
28. viii. 34	J	35	18	52 03	3 15	18.12	34.60	20.1	0.6
28. viii. 34	J	36	28	52 03	2 11	17.03	35.07	14.5	т.8
27. ix. 34	L	24	27	52 00	2 II	16.80	35.00	14.4	170.1
27. ix. 34	L	26	16	51 48	3 15	17.21	34.81	16.4	146.2
28. ix. 34	L	29	145	53 00	3 12	16.76	34.89	14.8	332.6
20. x. 34	N	2	30	52 20	2 28	15.07	35.10	15.6	300.0
22. X. 34	N	20	15	53 00	3 49	14.17	35.03	14.0	1284.4
1. xi. 34	0	IO	24	54 27	4 40	12.74	34.82	16.7	787.5
3. x. 35	0	4	15	51 45	3 18	15.57	34.65	16.0	2.25.8
4. x. 35	0	II	22	53 54	3 03	14.35	34.62	14.8	1650.0
4. x. 35	0	12	19	53 36	2 21	13.08	34.60	15.6	782.0
25. X. 35	Р	13	29	54 10	4 30	12.87	34.76	17.1	124.0
9. xi. 35	Q	24	25	53 44	4 09	11.73	34.83	16.3	128.6
24. xi. 35	R	6	24	54 54	5 17	10.30	34.81	18.0	221.8
27. ix. 36	N	19	17	53 30	2 57	16.12	24.11	20.6	146.2
27. ix. 36	N	20	14	53 30	3 53	16.47	34.40	10.1	140 2
29. ix. 36	N	29	7	51 31	I 24	15.84	34.50	19 I 18·T	870.0
29. ix. 36	N	30	14	51 29	0 52	15.30	32.56	18.2	400.5
6. x. 36	0	2	19	52 00	2 06	15.84	34.12	18.2	200.0
II. X. 36	0	20	22	53 17	2 25	14.31	34.28	10.1	2106.8
14. x. 37	M	24	32	54 07	2 25	14.37	34.85	15.4	27.5
15. X. 37	M	25	20	53 43	2 53	14.53	24.14	18.5	1224.1
15. X. 37	M	26	18	53 26	2 11	14.38	24.18	10.6	1234 1
27. X. 37	N	4	IO	52 42	4 23	12.11	22.02	20.8	128.0
27. X. 37	N	5	15	53 06	4 21	13.21	32.07	25.2	130 9
28. x. 37	N	12	13	53 35	2 14	13.26	34.84	15.0	16:0
28. x. 37	N	13	17	53 35	2 57	13.48	34.13	10.1	1800.0
14. xi. 37	0	8	16	53 32	3 42	11.35	34.14	20.0	165.0
15. xi. 37	0	12	IO	53 32	2 20	11.47	34.52	20.0	220.0
15. xi. 37	0	16	17	53 57	2 23	11.77	34.83	16.0	107.5
15. xi. 37	0	17	24	53 58	3 06	12.02	24.65	10.1	284.8
15. xi. 37	0	18	19	53 58	3 47	11.77	34.13	20.1	481.0
16. xi. 37	0	19	21	53 58	4 20	11.60	24.00	10.6	20.6
16. xi. 37	0	21	22	54 23	3 32	11.20	34.02	190	547.2
16. xi. 37	0	23	171	54 20	2 08	11.67	34.70	14.0	347 3
28. xi. 37	Р	Ĩ	101	53 32	2 20	0.60	34.18	10.6	284.0
28. xi. 37	Р	2	171	53 32	3 02	0.88	24.66	10.0	22.8
21. x. 38	Р	5	13	52 48	4 01	14.30	34.62	25.5	220.8
21. x. 38	Р	6	17	52 32	3 25	14.57	34.78	10.3	250.0
22. X. 38	Р	7	18	53 14	3 35	14.10	24.88	15.2	28.6
23. x. 38	Р	12	19	53 38	3 00	12.38	34.58	15.6	200
23. x. 38	P	13	35	54 00	2 34	13.10	34.66	17.1	81.9
II. xi. 38	0	7	22	54 48	4 32	12.22	34.68	18.0	77.5
13. xi. 38	õ	19	25	57 12	7 38	11.20	54 00	16.7	120.5
14. xi. 38	Q	20	21	56 08	6 32	12.36	_	19.6	14.9

TABLE I. POSITION OF STATIONS AND OTHER DETAILS REFERRING TO THE DIAMETER MEASUREMENTS OF BIDDULPHIA SINENSIS

CELL WIDTH OF BIDDULPHIA



Fig. 1. *Biddulphia sinensis* width frequencies for various stations in the southern North Sea between 1932 and 1938. The ordinate is marked in 5s.



Fig. 2. Surface salinities on Cruise N, 1937 (above) and on Cruise O, 1937 (below) showing stations at which 100 width measurements of *Biddulphia sinensis* were made (ringed figures) and on the left the actual width frequencies from these stations.

positions from which samples were taken and the corresponding width distributions. The relation between surface salinity and cell width seems close in these cases, and even when all the fifty-two samples available over the period 1932–38 are taken together there is a negative correlation with the surface salinity of -0.43. This would happen by chance less than once in a hundred times. Similar correlations with density of population and with surface temperature (-0.06 and -0.17) were found to be of negligible significance.

Lucas & Stubbings (1948), using material from the Hardy continuous recorder in the southern North Sea between 1931 and 1938, measured samples amounting to 20,000 cells, most of them from 1938 material. From their distribution when compared with the data published in the *Bulletin Hydro-graphique* these workers inferred that the wider cells were found in the water of lower salinity mainly near the continental coast. They distinguish narrow, medium and wide cells in their samples, but on a line from Hull to Bremen in November 1938 they figure (p. 156) what at first appears to be a unimodal population changing abruptly near the Friesian Islands into a bimodal one with subsequent increasing emphasis on the larger mode. This latter appearing in Lucas and Stubbings's results in November seems to correspond with a similar one found by me at Station P 5 in October 1938, 20 miles off the Texel.

Consideration of the facts presented up to this point would make it appear that *B. sinensis* must adjust its width to changes of salinity fairly rapidly so that it would not be possible to follow and identify a population by its size distribution. On the contrary, it is rather more likely to be an index of contemporary salinity, and shows no steady diminution of size over a long period followed by a sudden return to maximum width as a result of the formation of auxospores as happens in *Rhizosolenia styliformis*.

However, when all the samples are grouped together by years (Fig. 3 and Table II), it is seen that there is a sharp rise in the chief mode of the sizefrequencies between 1935 and 1936 which is reminiscent of that shown by the individual samples of Rhizosolenia styliformis taken in these years. There is also a slight rise in the mean size between 1932 and 1933 which, on account of the poor sampling in 1932, might have been thought of as of no significance if I had not been afforded the opportunity of examining some of Dr Lucas's unpublished measurements. With the latter's kind consent I have prepared Fig. 4 from these data. The figure shows the percentage frequency distribution of *Biddulphia sinensis* for the same general area as my material for the years 1932-38. It will be seen that, in addition to the increase in the modal frequency between 1935 and 1936 there are indications of increases from 1932 to 1933 and 1937 to 1938. It is as if, for B. sinensis as for Rhizosolenia styliformis, the same law of diminishing division followed by a sudden increase is being observed-if one adds together for each year all the separate samples which in some way appear adjusted in width to their contemporary salinity.



Fig. 3. Biddulphia sinensis width frequencies for the whole years 1932-38. The ordinate is marked in 10s.

TABLE II. MEASUREMENTS OF BIDDULPHIA SINENSIS DIAMETERS, FOR SEPARATE YEARS 1932-38

Measurement groups (8 μ units)

Year	8	9	IO	II	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	Mean
1932			_	_	2	5	9	25	28	30	35	22	10	23	3	6	_	I	I	_	—	_	_	_	_	_	_	_	_	—			18.2
1933		2	I	8	II	15	31	32	58	71	57	49	43	35	31	18	13	13	4	5	I	I	_		_	_	I		_	—			18.7
1934		5	7	25	48	82	91	104	88	82	60	55	38	22	18	22	II	3	3	2	I	2	_	I							-		16.2
1935	I	Ĩ	4	22	27	57	61	53	63	46	56	42	37	46	26	29	14	IO	2	3	_				-		_					-	17.6
1936					3	10	8	18	40	77	77	97	89	58	49	32	21	7	2	2	5	2	I		Ι		I				-		19.9
1937	I	4	4	13	32	39	80	123	137	146	178	172	175	125	120	83	93	64	37	26	7	8	7	6	4	5	4	5	2	-		Ι	19.4
1938		I	6	18	25	38	41	48	73	72	71	66	79	61	47	44	20	17	21	17	15	14	6		—	—		-	—	—	—	—	19.4

TABLE III. GROWTH OF BIDDULPHIA SINENSIS CULTURES SHOWN BY CELL NUMBERS; AND MEAN SIZE OF CELLS

Cultures set up on 11 August 1950 in a north window. Size expressed as mean widths and lengths of samples of 100 cells taken on 15 and 21 August 1950, in units of 4μ .

Date in	Sea water		with distilled water of percentage												
1950 erdschreiber			10	-	20	30	<u>`</u>								
			Cell	numbers											
12	6.75		5.0 4.75			6	.5								
13	18.75		37.25		22.75	20	.75								
14	53.5		95.25		80.0	73	.5								
15	117.5		178.25	I	53.0	162									
16*	197.75		253.75	2	51.5	299	.25								
17	462.5		650.0	4	87.5	550	0.0								
18	1,187.5		862.5	62.5 1,200.0			1,312.5								
19	1,937.5	2,725.0		2,725.0		2,725.0		2,725.0		2,725.0		25.0 2,162.5		2,500	
21*	5,262.5					8,3	12.5	6,725	.0						
22	12,500.0	9	375.0	25,6	25.0	18,125	•0								
24	37,500.0	51	250.0	54.3	75.0	63,125	•0								
26	96,875.0	96	250.0	101,8	75.0	119,375	•0								
				Cell s	shape										
	Width L	ength	Width	Length	Width	Length	Width	Length							
15	68.5	03.6	70°T	03.0	60.0	02:45	68.3	88.0							
21	67.3	93.3	68.0	93.4	66.5	92.5	66.8	88.9							

* Subcultured.

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Fig. 4. Biddulphia sinensis width frequencies for the whole years 1932–38 in arbitrary units of approximately 12 μ . Lucas and Stubbings's material expressed as percentages along the ordinate.

CELL WIDTH OF BIDDULPHIA

Egusa (1949), who has worked on this species from a coastal bay in Japanese waters from September 1946 to April 1948, found a large and small diameter group alternating, the former dominating in winter and the latter in summer. No auxospore formation is described and there was no horizontal distribution of the samples which would indicate whether the individuals came from an identical stock. If the cells did in fact come from the same stock these observations suggest the annual formation of an auxospore generation in an environment where there is little change in the salinity.

FACTORS AFFECTING SIZE IN BIDDULPHIA SINENSIS

Width adjustment in diatoms is well known to occur downwards by division and upwards and suddenly by auxospore formation, and we may examine how this known method of diminishing growth and auxospore formation could produce the observed situation for *B. sinensis*. First, reference may be made to the work of Schreiber (1931), who figured and observed auxospore formation in *B. sinensis* in material collected off Heligoland on 19 July 1926, and at a time when the salinity—28.6%—had reached a lower value than the preceding and following days and lower than the July average for 15 years—31.5%. Schreiber also quotes Mielck as noting that *B. sinensis* is smaller in the northern than the southern North Sea.

In view of the observations on this species at Heligoland and the fact that he was able to produce abundant auxospore formation in Melosira nummuloides by lowering the salinity, Schreiber was of the opinion that the greater width in North Sea diatoms is due to more auxospore formation in an area of lower salinity. The correspondence of lower salinity with auxospore formation is also pointed out in Part I of this work (Wimpenny, 1936), where the distribution of *Rhizosolenia alata* is examined, and again in Part II (1946), where it was thought worth noting that a commencement in the lowering of salinities in 1935-36 corresponded with the origin of a new auxospore generation of R. styliformis in 1935 and its development in 1936. No auxospore formation has actually been seen in my material, but in a collection taken on the same voyage (Station 23, Cruise P, 1935) as that on which some of the present measurements were collected, what appeared to be newly formed auxospores and detached parent cells were seen. These are reproduced in Fig. 5. They occurred in the same year as did those of R. styliformis and, if we lump all the years' samples together, precede a year in which there was a sudden increase of size. This circumstantial evidence then favours the thesis of an auxospore formation in 1935 following populations which were on the whole diminishing in size and preceding a wider population which had also diminished in size by 1937. There is also the suggestion particularly supported by the width distributions communicated to me by Dr Lucas, that there may have been auxospore formation in 1932 or 1933 and possibly in

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1938. Unfortunately the observations do not go beyond 1938 so that it cannot be said whether an unusually wide population occurring at Station 5 of Cruise P off the Dutch coast in 1938 could have been the precursor of a new auxospore generation.



Fig. 5. Drawings of *Biddulphia sinensis* cells from station 23 of *George Bligh* Cruise P, 1935.

It is very puzzling to account for the big differences of widths in the same voyage or season, but three reasons occur to me as affording a possible mechanism. These are: (a) the frequent origin of auxospore generations in the less saline water; (b) direct and immediate adjustment of cell-size to the salinity of the surrounding water, perhaps by some osmotic action taking place at cell division; and (c) differential survival or growth of cells in water of different character, particularly with reference to changes of salinity.

In an attempt to test explanations (b) and (c), I made some simple experiments in 1950 on a culture of *B. sinensis* which Mr D. Jefferies of the Fisheries Laboratory, Lowestoft, had succeeded in establishing. Unfortunately, the cells of this culture were already similar in width to the wider fraction of those found in the sea, so that the fact that my first series of experiments in which the erdschreiber-enriched sea water was diluted to various degrees (Table III) showed no auxospores may only have meant that auxospore formation is not possible above a certain size. The dilution experiments also showed little or no difference in growth rate over the period of 21 days (about a division a day for most of the time). However, for the first two days it did appear that dilution accelerated the rate of growth, 10% being the most effective and 30% the least. There were no increases in width attributable to osmotic swelling or any other cause. There also appeared to be little or no mortality in this series and the diminishing cell widths suggested that on the average the cell wall might be expected to be about 1.5μ thick. These experiments were carried out in a room with a north light where the day temperature varied between 18° and 20° C.

TABLE IV.	GROWTH OF	BIDDULPHIA	SINENSIS,	IN	Cell	NUMBERS
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Cultures set up on 23. viii. 50

Date	In erdschreiber- enriched seawater at 24° C	In erdschreiber- enriched seawater at 10° C	
23. viii.	II	15	
24. viii.	20	16	
25. viii.	27	22	
26. viii.	33	38	
28. viii.	40	42	
29. viii.	42	54	
30. viii.	55	62	
31. viii.	80	64	
I. ix.	78	72	
2. ix.	75	92	
4. ix.	90	103	
5. ix.	<u> </u>	93	
6. ix.	na na nastro t ere stratel star e	85	
7. ix.	92	90	
8. ix.	91	96	
9. ix.	93	IOI	
11. ix.	98	108	
12. ix.	95	98	
13. ix.	98	IOI	
14. ix.	100	100	

TABLE V. LENGTH AND WIDTH OF *BIDDULPHIA SINENSIS* CELLS AT DIFFERENT TEMPERATURES

Measurements in 4μ units. Light supply 550 Lux

	Parent population 23. viii.	Popu	lation at :	24° C	Population at 10° C					
		29. viii.	2. ix.	12. ix.	29. viii.	2. ix.	12. ix.			
Observations Mean width Mean Length	100 66·4 106·2	29 62·0 93·0	50 60·5 97·8	41 62·4 121·4	27 61·2 112	46 61·0 110·9	33 56·9 134·1			

In the second series two experiments run at 24° and 10° C (Tables IV and V) showed little difference in growth, which stopped after three divisions, but many morbid cells appeared, more at the higher temperature. Cell

measurements indicated that the mortality was selective, the higher temperature culture being left with cells that were wider and shorter than those grown at the lower temperature.

As far as they go, therefore, these experiments do not suggest that immediate swelling or formation of auxospores follows a lowering of salinity where the cells are of the larger size. On the other hand they do suggest that an environmental difference, in this case temperature, can act on cell shape through selective mortality at different values.

SUMMARY

The cell widths of samples of *Biddulphia sinensis* taken from Hensen net hauls made in the southern North Sea between 1932 and 1938 correspond rather closely to the contemporary salinity samples, but not to the density of population or to temperature.

The width distributions of *B. sinensis* do not give a persistent and characteristic guide or mark to populations of this species in the way that is characteristic of *Rhizosolenia styliformis*, but rather give a rough indication of the salinity of the water in which they are found.

There is nevertheless some circumstantial evidence pointing to a 3-year auxospore cycle similar to that shown by *R. styliformis* in the same area. It is, however, much masked and overlaid by other causes of change in cell width.

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STUDIES ON MARINE FLAGELLATES

III. THREE FURTHER SPECIES OF CHRYSOCHROMULINA

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The Plymouth Laboratory

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(With total of 76 Figures in text and on Plates I-IX)

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INTRODUCTION

Two of the new species of Chrysochromulina to be described here are somewhat more like the type species (C. parva Lackey) than were any of those included in our last communication (Part II of this series-Parke, Manton & Clarke, 1955). The diagnostic generic character of the presence of three filiform appendages arising close together is shared by all, and as before two of the appendages are flagella of equal or almost equal length and the third is a special organ to which the name *haptonema* has been given (Gr. $a\pi\tau\omega$ to attach, $v\eta\mu a$ pl. $v\eta\mu a\tau a$, a thread) (1955, p. 581). In our previous species the haptonemata when fully extended were relatively short, being not very different in length from the flagella. When not extended it was coiled in a flat spiral. Our three new species all have much longer haptonemata, of the order of twice the length of the flagella in C. ericina and three to five times the length of the flagella in C. ephippium and C. alifera. In all three species the haptonema is distinctly thinner than the flagella, a character probably connected with the absence of a conspicuous sheath (contrast with C. kappa and C. minor of our previous paper) and when not extended it is coiled in a solenoid. Several of these characters agree fairly closely with those given by Lackey for C. parva, as will be explained in

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connexion with *C. ephippium* (p. 406), though the comparison cannot yet be made in full detail since *C. parva* is an American freshwater species which has only been found once (Lackey, 1939) and it has not yet been available to us for study.

Our principal comparisons are therefore with *C. kappa*, *C. minor* and *C. brevifilum* of our previous paper, and here there is marked agreement in the main features of structure and life-history. As before we are dealing with pigmented flagellates showing many of the metabolic characteristics of the photosynthetic Chrysophyceae combined with the habit of phagotrophic feeding. Ingestion of graphite has been demonstrated with the light microscope in all three new organisms and evidence is included in the plates. As before the body surface is apparently covered by translucent scales without mineral impregnation, which take up cresyl blue. Their details can only be accurately seen with the electron microscope but they provide important criteria for the specific diagnoses. The very long spines of *C. ericina* can, however, with difficulty be seen individually with the light microscope.

Though we are still ignorant of the functional significance and mode of formation of the scales, our three new species all suggest that they may contain two layers of material. All the spineless scales show a characteristic and different pattern on their two surfaces, and since similar patterns occur on the flat parts of the spined scales (with special clarity in *C. ephippium*) we have been able to identify the outer and inner surfaces respectively. These differences were not detectable in our previous species.

Another detail of difference from our previous species, the significance of which cannot yet be wholly evaluated, is that the point of emergence of the three appendages is somewhat asymmetrical in relation to the rest of the cell. In *C. ericina* the point of emergence is no more than slightly 'off centre' and the two flagella seem isodynamic in function as well as equal in length. In the other two species the point of emergence is more definitely ventral under certain conditions, though the capacity for the body to change its shape hampers exact description. We have not been able to detect in these any marked or constant difference in either the length or the structure of the two flagella, but when the organisms are studied alive the flagella are definitely heterodynamic in behaviour. The significance, if any, of this observation will be discussed on a later occasion, but it is perhaps of importance to draw attention to the facts as described for *C. ephippium* (pp. 403–5) and *C. alifera* (p. 412) and to the preliminary discussion on p. 413.

With regard to life history, an advance on our previous work has been the more detailed observation of the emergence of cells of the motile phase from the dormant, walled, cells of the non-motile phase in C.ephippium (pp. 405, 406). In all our other species we have described empty membranes with a circular opening as providing strong suggestive evidence that such a transition takes place and the new observations demonstrate the truth of this supposition.

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In presenting the facts for individual species we have necessarily had to do so in considerable detail, since it cannot yet be known with certainty which characters are limited to, and therefore diagnostic of, single species, and which will be found common to assemblages of species when more are known. We have already evidence that the remarkable spines of *C. ericina*, for example, are not an isolated phenomenon but that they will recur in various ways in the specific descriptions of other organisms which have not yet been fully studied. We have therefore placed on record everything that we have been able to ascertain about the species to be described, as studied in unialgal cultures, apart from certain fundamental characters common to all species of *Chrysochromulina* that have already been discussed (1955).

Our methods of study have been exactly as enumerated before (1955, pp. 281-3).

As before, our grateful thanks are due to Dr J. E. Morton, of Queen Mary College, for translating our specific diagnoses into Latin, and to Miss D. Ballantine for testing these organisms for their possible toxicity to fish.

SPECIFIC DESCRIPTIONS

Chrysochromulina ericina n.sp., Parke & Manton

(Lat. *Ericinus*—like a hedgehog)

Diagnosis

Motile cells usually ovoidal to nearly oblong, very slightly flattened in one plane, showing marked metaboly, 6-10 (exceptionally 5-12) μ in length, 5-8 (exceptionally 4-10) μ in breadth; flagellar pole obliquely truncated with a slight, almost central depression. Two flagella and one haptonema arising close together not quite centrally from the depression: the flagella equal, homodynamic, 2-21 times body length, smooth, gradually attenuated to a small knob (E. M. observation); the haptonema thinner than the flagella, 4-5 times body length when fully extended with a small basal swelling, a club-shaped tip but no clearly marked translucent sheath obvious under the electron microscope. The periplast of a pectic nature covered by very thin transparent, sculptured, dimorphic scales, details visible only under the electron microscope. Scales without spines very numerous, $0.5 \times 0.6 \mu$ to $0.7 \times 0.9 \mu$, with a pattern of radiating ridges on one side and a slightly raised rim surrounding irregular crossed striations on the other. Spined scales, 28-30 in number, the spine abruptly truncated and slightly tapering, 9-12 (exceptionally 15) μ long, 0.2–0.3 μ wide, arising from a circular (or conical?) base, $I-I\cdot 4\mu$ wide, marked with concentric striations on its outer side.

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Cells uninucleate, no stigma. Chromatophores usually 2 or 4, sometimes 6 or 8, deep golden brown; in motile phase saucer-shaped, ellipsoid, or oblong, frequently bifid towards non-flagellar pole, parietal, with a single globular body (pyrenoid?) on inner face placed near margin towards the non-flagellar pole; in non-motile phase deeply lobed or stellate. Oil and leucosin produced. Ejectile muciferous bodies generally distributed in peripheral cytoplasm. Nutrition phototrophic and/or phagotrophic. Non-toxic to fish.

In motile phase asexual reproduction by fission into 2 daughter-cells of equal or unequal size; in non-motile phase reproduction (asexual?) by successive fission of amoeboid cells to produce 4 ovate daughter-cells with walls, walls faintly brownish and slightly rugose on the exterior; motile phase probably liberated from walled daughter-cells through a pore.

Habitat: the sea at position (Plymouth Laboratory Station L4) Lat. N. 50° 15', Long. W. 4° 13' (15 May 1949, type culture) at surface; and at position (International Station E1) Lat. N. 50° 02', Long. W. 04° 22' (13 July 1955) at 20 m. Type culture (Plymouth no. 25) deposited with the Type Culture Collection, Cambridge; preserved material and photographs lodged with the Marine Biological Association, Plymouth, England.

Cellula motili, generaliter ovoidali aut ferme oblongio, paululum planato in uno aspectu, formam conspicue mutanti, longitudine 6–10 μ (rare 5–12 μ), latitudine 5–8 μ , rare 4–10 µ; apice quo inserta flagella oblique truncato, leviter depresso prope centrum. Duobus flagellis et unico haptonemate conjunctim exorientibus e depressione; flagellis aequis, homodynamicis, longioribus 2 ad 2¹/₂ quam cellula, teretibus, paulatim attenuatis et acutis; haptonemate teneriore quam flagellis, longiore 4-5 quam cellula, cum maxime extensus, leviter tumescenti prope originem, clavato extremitate sed nulla tunica externa semidiaphana ut videtur per microscopiam electronicam. Periplasto, pectico natura, induto delicatissimis sculptis squamis diaphanis, sculptura invisibili nisi per microscopiam electronicam, manifestis sub duobis formis: altera forma, sine spinulis, pernumerosis, longis 0.6–0.9 μ , latis 0.5–0.7 μ , ornatis radiantibus striis ad inferiorem aspectum, margine paululum elevata circumdanti irregulares decussatas strias ad superiorem aspectum: altera forma, squamis 28-30 numerosis, spinulis praeditis, quoque spinulo subfastigiato sed et abrupte truncato ad extremum, 9–12 μ (rare 15 μ) longo, 0.2-0.3 μ lato, exoriente e basi circulari aut conica, ornata concentricis striis ad aspectum superiorem.

Nucleo unico, nullo stigmate, chromatophoris ex norma 2 aut 4, nonnunquam 6 aut 8, profunde aureo-brunneis; in statu motili cellulae crateriformibus, ellipsoidalibus aut oblongis, saepe bifidis versus apicem cellulae quo desunt flagella, parietalibus;

Legends to Text-figs. 1-2

Chrysochromulina ericina n.sp. (× 5000)

Fig. 1. Individual with two dividing chromatophores anchored by haptonema which is partly extended; the flagella are in the characteristic position adopted when the species is stationary. c, chromatophore; f, flagellum; h, haptonema; l, leucosin vesicle; m, muciferous body; n, nucleus; p, pyrenoid-like body; s, scale; ss, spined scale.

Fig. 2. Individual anchored by coiled haptonema which is hidden below protruding lobe of flagellar pole; cell contains an ingested *Navicula salinicola* Hust. (d).



unico corpore globulari (? pyrenoidali) in concavo aspectu prope marginem chromatophori posito versus apicem quo desunt flagella; in statu non-motili cellulae chromatophoris profunde lobatis vel stellatis. Cellula oleum leucosinumque parienti; corporibus muciferosis et ejectilibus undique distributis in cytoplasmate superficiali. Nutritione phototrophica necnon phagotrophica. Non toxica piscibus.

Generanti asexualiter in statu motili per fissionem in duas cellulas filiolas vel aequas vel inaequas magnitudine; in statu non-motili generanti (?asexualiter) per fissiones subsequentes cellularum amoeboidalium ad 4 cellulas filiolas ovoidales producendas, parietibus leve brunneis et paulum rugosis externe; maxime potest ut cellulae in statu motili ex cellulis pariete praeditis per foramen liberentur.

Habitat mare prope Plymouth ad locationem Lat. N. 50° 15', Long. W. 4° 13' (15 Mai 1949—cultura typica) ad summum mare; necnon ad locationem Lat. N. 50° 2', Long. W. 4° 22' (13 Jul. 1955).

Description

The form range of the motile cells is illustrated in Figs. 1–5 and in the photographs of Pl. I. The slight flattening of the body can be most easily observed when looking down on the non-flagellar pole (Fig. 3) and the pronounced metaboly is most obvious when individuals are ingesting or have ingested cells of other species (Figs. 2, 4, 5). In an actively growing culture 85% of the cells are from 6 to 10μ in length, while 5% are between 5.0 and 6.0μ . The remaining 10% are incipient fission stages from 10 to 12μ in length.

The flagella and haptonema arise close together slightly to one side of a shallow depression at the obliquely truncated pole (Fig. 13, Pl. I; Figs. 1, 4, 5). The flagella (Figs. 14, 15, Pl. II) are very thin as in *C. kappa* Parke & Manton,

Legends to Text-figs. 3-9

Chrysochromulina ericina n.sp. (× 5000)

- Fig. 3. Characteristic position of an anchored cell when the haptonema is not extended; view is looking down on non-flagellar pole with flagella lying straight out below body; bacteria (b) in vacuole adjacent to pyrenoid-like body.
- Fig. 4. Individual with four chromatophores swimming with flagella and haptonema behind body in the position characteristic for the species during rapid swimming; muciferous organelles exuding contents; recently ingested *Chlorella stigmatophora* cell (*i*) at nonflagellar pole and an empty wall of a *Chlorella* cell immediately after ejection from the end of a colourless tube.
- Fig. 5. Individual swimming with flagella and haptonema in front of the body in characteristic position, haptonema fully extended; a cell of *Oicomonas* (*i*) being ingested and large vacuoles (*v*) containing granules showing Brownian movement adjacent to both pyrenoidlike bodies.
- Fig. 6. Late fission stage just before separation of daughter-cells.
- Fig. 7. Large amoeboid individual with four deeply lobed, pale chromatophores and four pyrenoid-like bodies surrounded by non-refringent material; ingested bacteria (b) dancing in vacuoles.
- Fig. 8. Second fission of a large walled cell almost completed, to give four small, walled daughter-cells.
- Fig. 9. Small rugose walled daughter-cell with two stellate chromatophores and two pyrenoid-like bodies.



Text-figs. 3-9

and difficult to see under the light field, so also is the haptonema which when fully extended is much longer than in the species previously described (approximately twice the length of the flagella, Pl. I; Fig. 5).

Like C. kappa the haptonema has a club-shaped tip (Pl. II) and a swollen base (Fig. 13, Pl. I; Pl. II; Fig. 17, Pl. III) but the base is smaller and more ovoid than in C. kappa; the delicate sheath of the haptonema is very inconspicuous (Fig. 16, Pl. II).

The two types of scales may be seen at low magnifications in Pls. I and II and in greater detail in Pls. III and IV. While the plate-scales can only be separately detected with the electron microscope, the spines are sufficiently large to be visible and even counted with the light microscope if the cells are dried. They are just detectable in Figs. 10 and 11, Pl. I, and they become even clearer if methylene iodide saturated with sulphur at 30° C. is added to dry preparations (Hollande, 1952, p. 472). They are too translucent to be visible without staining on living or undried cells, but their presence is sometimes detectable after addition of graphite to a culture by the adhesion of small masses of graphite to their tips. By this means their length and distribution on the living cell can be assessed and we believe them to be uniformly distributed on the body surface with their bases separated by a distance equivalent to the diameter of 2 or 3 plate-scales. They are very readily displaced after death, and especially by the act of drying.

The chromatophores of the motile phase are parietal and deeply pigmented and frequently appear striated, their shape and position changing with the metaboly of the body. They tend to lie towards the flagellar pole (Figs. 1–6). In the non-motile phase they are paler and deeply lobed (Figs. 7–9). Individuals lacking chromatophores are normally not seen in cultures of this species except rarely after treatment with penicillin and streptomycin.

As in our previous species there is a refringent body, the so-called pyrenoid, present on the inner face of each chromatophore. Its position is eccentric, towards the non-flagellar pole (Figs. 1-6) as in *C. brevifilum* Parke & Manton, but it changes with the metaboly of the body. These pyrenoid-like bodies, 0.5 to 1.0μ in diameter, appear greenish and are fairly conspicuous in some individuals but in others they are hardly visible; after osmic fixation they show up more clearly. Frequently these bodies are surrounded by non-refringent material, sometimes by quite large masses up to 2μ across. The nucleus, placed nearly centrally in the body, is of medium size and can sometimes be seen in the living cells. Leucosin vesicles of various sizes, sometimes as large as 3μ in diameter, are present, usually lying in the body towards the nonflagellar pole; small oil globules are distributed through the cytoplasm.

The muciferous organelles are quite large and appear to be generally distributed in the peripheral cytoplasm of the cell but with the metaboly of the body they can sometimes be seen in rows. When they expel their contents rapidly, straight threads up to 90μ long can be shot out, but when they dis-

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charge slowly, as for instance when kept at a temperature of $22-24^{\circ}$ C or when certain other organisms have been added to the culture, then the contents exude either as small balloons or as thin waving threads (Fig. 4) frequently showing what appears to be a small flat colourless disk sticking to them (Fig. 4). When extremely dilute cresyl blue is added to the living cells one sees almost immediately what appear to be minute disks shot out from the cell surface, which dance about for a time and then disappear. It could not be ascertained whether these disks were caps covering the organelles, as in Hovasse's discobolocysts (Hovasse, 1949), or surface scales pushed off during the discharge, but their capacity to stain a deep blue with cresyl blue suggests that they are probably caps, not scales, as the latter usually stain a pale violet colour. Immediately after the liberation of disks the contents of some of the organelles are discharged, some as small balloons, others as fine threads (Fig. 4).

Some distinct granules, possibly mitochondria, occur generally distributed in the peripheral region of the cell. They stain an intense blue with cresyl blue and under oil immersion can be seen to be connected together by a very fine blue network.

This species moves comparatively slowly with a fairly even rotation and little gyration. There is a marked phototactic reaction in spite of the absence of a stigma. As in the three species already described, swimming is most rapid when the flagella and haptonema are directed backwards and the haptonema is tightly coiled (Fig. 14, Pl. II; Fig. 4).

The rate of movement decreases with an increase of temperature up to $22-24^{\circ}$ C. when movement becomes extremely slow, the individual then generally swimming with the haptonema in front of the body.

When not tightly coiled, the haptonema may be fully extended (Fig. 5), in front of, or behind the body, or only partly extended, the remainder appearing as a blob at the distal end (Fig. 11, Pl. I). When individuals swim with the haptonema foremost the flagella are held as in Fig. 5, but when they swim with the haptonema behind the body the flagella are held as in Fig. 4 with their free ends farther apart than the width of the body. The cells do not swim for long in one direction. They can stop suddenly by bringing the flagella to the position shown in Fig. 1, or they can suddenly change and move in the opposite direction by a flick of the flagella from the position of Fig. 5 to the position of Fig. 4 and vice versa. When moving with the haptonema extended in front of the body (Fig. 5) cells are frequently seen to jump back suddenly as if the haptonema had touched something obnoxious. The haptonema can also be bent over from side to side.

Quite long periods of anchorage are common, but the tip of the haptonema can seldom actually be seen attached to a surface, the cell body usually lying over it. The most characteristic position adopted by attached cells is shown in Fig. 3; the haptonema is tightly coiled below the body while the

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flagella appear as a straight line on either side. The flagella can either remain quite still or vibrate slowly, causing the body to show a slight dancing movement. Individuals can frequently be seen in the act of attaching with the haptonema nearly fully extended (Fig. I). The haptonema may remain fully extended or it may coil up drawing the cell down to the surface of attachment (Fig. 2). In the latter position the haptonema becomes hidden owing to the asymmetry of the body. When the distal end of an attached haptonema can be seen, it is sometimes coiled in a flat spiral appearing as a disk with the point of attachment in the centre (Fig. I). In other cases the haptonema can appear very short (and thicker?), as in *Prymnesium* species, without a visible disk at the attached end (Fig. 6). In these it is perhaps only the distal tip of the haptonema that is extended, the remainder lying coiled and hidden below the body since we have no evidence suggesting that the haptonema can actually contract, as opposed to coiling.

Phagotrophy is of common occurrence, the individuals ingesting bacteria and other organisms, usually up to a size of 3μ but occasionally larger, the maximum ingested size observed being a diatom cell of $9 \times 3\mu$. In addition to graphite (Fig. 12, Pl. I), a number of cultures of different sized organisms were also used with the following results: ingestion of *Oicomonas* sp. $1-2\mu$

Explanation of Plates I-IV

Chrysochromulina ericina n.sp.

I

- Fig. 10. A cell killed with osmic vapour and dried on a glass slide, with some detached scales marked by arrows. Photographed dry without a coverslip. Magnification \times 1000.
- Fig. 11. Two cells of the same.
- Fig. 12. Three cells killed with osmic vapour after graphite feeding and photographed in a liquid mount with oil-immersion lens and visual light. Magnification × 2000.
- Fig. 13. A low-power view of a cell dried and shadowed after vapour killing, on a formvar film, seen with the electron microscope. Micrograph M. 128 \cdot 1, magnification \times 3000.

II

- Fig. 14. A cell showing flagella and a coiled haptonema. Electron micrograph M. 239.26, magnification \times 5000.
- Fig. 15. Tip of left-hand flagellum of Fig. 14, magnification \times 10,000.
- Fig. 16. A haptonema from the cell of Fig. 13 more highly magnified. Electron micrograph M. 128.2, magnification × 50.00.

III

- Fig. 17. The body of the cell of Fig. 13 more highly magnified to show scales and the bases of spines. Electron micrograph M. 128.3, magnification \times 10,000.
- Fig. 18. A group of detached spines and scales. Electron micrograph M. 128.9, magnification \times 5000.

IV

Fig. 19. Part of Fig. 18 more highly magnified to show details of the scales and bases of the spines. Electron micrograph M. 128·13, 40 kV, magnification \times 20,000.

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PARKE, MANTON & CLARKE. PLATE I





(Facing p. 396)
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PARKE, MANTON & CLARKE. PLATE II



J. MAR. BIOL. ASS. U.K., 35 (2) PARKE, MANTON & CLARKE. PLATE III



J. MAR. BIOL. ASS. U.K., 35 (2) PARKE, MANTON & CLARKE. PLATE IV



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(Fig. 5), Stichococcus cylindricus Butcher $3-5 \times 2\mu$, Plymouth no. 55 (possibly a Stichochrysis sp.) $3-10 \times 3\mu$, and Chlorella stigmatophora Butcher $2.5-4.5\mu$ (Fig. 4) was fairly frequent; ingestion of the smaller individuals of Nitzschia gotlandica A. Cleve-Euler 6-10 µ L. and Porphyridium cruentum (Ag.) Näg. $4-12\mu$ diam, was not uncommon, but the ingestion of Navicula salinicola Hust, 9–10.5 μ L, was seen only once (Fig. 2) when a cell 9×3 μ had been ingested by an individual $10 \times 6\mu$. The following species were tested for ingestion with negative results: two Dunaliella spp. 6-12 µ, Phaeodactylum tricornutum Bohlin 8-35 μ and Nannochloris atomus Butcher 2-3 μ . One of the Dunaliella sp. (Plymouth no. 81) and the Nannochloris appeared to have an adverse effect on the Chrvsochromulina ericina, whilst Chrvsochromulina cells which had actually ingested Chlorella cells were believed to disintegrate afterwards, but the evidence is not vet absolutely conclusive. With the addition of certain unialgal cultures (e.g. Dunaliella, Chlorella, Phaeodactylum, Navicula) to the Chrysochromulina, the muciferous organelles of the Chrysochromulina cells were seen to exude their contents (Fig. 4) as they did when the cultures were kept at a temperature of 22-24° C. General exudation from the muciferous organelles was never seen when graphite was added, although a few hours after the addition practically every individual had ingested a certain amount-from minute particles to masses up to 4.5μ (Fig. 12, Pl. I). Small discharges from the organelles were sometimes observed accompanying ejection of the graphite.

The actual ingestion of material occurs always at the non-flagellar pole (Fig. 12, Pl. I; Figs. 4, 5). The ingested material, if sufficiently small, is then moved close to one of the 'pyrenoids'. The whole process was followed in detail in a culture of Chrysochromulina, which had been cleaned by utilizing the phototactic properties of the species (Droop, 1954), until the bacterial contaminants were reduced to one species, in this case a species distinctly bottle-shaped and about 1 µ in length. The Chrysochromulina was then observed to take in bacteria by surrounding them with a clear or slightly granular substance which flowed out from the body enclosing one or more bacteria. Almost immediately afterwards the bacteria could be detected in a vacuole (Fig. 3) close to one of the 'pyrenoids' which were sometimes masked by the vacuole (Fig. 5). The bacteria then began to show dancing movements inside the vacuole and in a matter of 2-3 minutes were broken up into minute granules (Fig. 5) which continued to show Brownian movement for several more minutes. Similar vacuoles, full of minute particles in Brownian movement, were seen by Parke (1949) in Chromulina pleiades, but for Prymnesium parvum and P. minutum, Carter (1937) records the presence of a large number of minute granules in active Brownian movement in 'an illdefined region', not in clearly delimited vacuoles. In this culture, with only one bacterial contaminant, the phagotrophic nature of the large amoeboid non-motile phase of the Chrysochromulina was also demonstrated; a number

of vacuoles containing bacteria could be seen quite clearly lying close to the pyrenoid-like bodies (Fig. 7).

When the motile phase ingests cells with definite walls the cell contents are absorbed but the walls are not; a colourless tube containing the wall flows out, usually from the side of the body, and discards the wall from its tip (Fig. 4); the tube is then withdrawn into the body. Empty walls of *Chlorella*, *Stichococcus*, '*Stichochrysis*', *Porphyridium* and *Nitzschia gotlandica* have been seen thrown out of the body in this manner.

Reproduction follows the same pattern as that described for *Chrysochromulina kappa*, but in the motile phase no double-fission stages have so far been observed. The second haptonema and the two new flagella can be formed before the cell broadens for the actual fission, which can produce daughter-cells of equal or very unequal size (Fig. 6). In the species previously described, the daughter-cells remain attached by a small connexion at the non-flagellar pole when the fission is nearly completed, but in *C. ericina* the connexion was frequently seen to be between the sides of the daughter-cells (Fig. 6) towards the flagellar pole.

At the peak of growth a culture produces $1\frac{1}{2}-2$ million cells per ml. Nonmotile stages, similar to those described in detail for C. kappa, have been observed, forming a dark olive-green to brownish skin on one side of the bottom of the flask after the peak of growth has been passed. The large amoeboid cells, up to $14 \times 9.5 \mu$, with four very finely lobed chromatophores, frequently show large numbers of ingested bacteria (Fig. 7) while the tetrads of walled daughter-cells (Fig. 8), each with 2 stellate or finely lobed chromatophores, were distinguishable by deeper pigmentation. The free, walled daughter-cells (Fig. 9), in which the pyrenoid-like bodies could sometimes be seen, were usually ovoid, measuring from $4 \times 2.5 \mu$ to $7 \times 4 \mu$. They differed only from those previously described in having a slightly thicker wall which appeared faintly brownish and was delicately rugose on the outside, somewhat as described by Carter (1937) for Prymnesium parvum. A thick culture of the motile phase can be obtained from the non-motile phase in 6-9 days after addition of fresh culture medium, the dark skin disappearing from the bottom of the flask.

Chrysochromulina ephippium n.sp., Parke & Manton

(Gr. $\epsilon \phi i \pi \pi \iota o \nu$ —a saddle)

Diagnosis

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Motile cells showing considerable metaboly, approximately saddle-shaped when moving slowly or stationary, bell-shaped to spheroidal when swimming rapidly, 6–10 (exceptionally 4.5-12) μ in size (length of back of saddle). Two flagella and one haptonema arising close together from the ventral concave surface near to one margin in a centre line; flagella equal, smooth, gradually attenuated to a hair point (E. M. observation), usually heterodynamic, occasionally appearing homodynamic, 3 to 4 times cell size in length; the haptonema, thinner than the flagella, 12 to 14 (exceptionally 16) times body size in length when fully extended, a club-shaped tip but no obvious translucent sheath visible with the electron microscope. The periplast, pectic in nature, showing a covering of very thin transparent circular to oval sculptured, dimorphic scales, visible only under the electron miscroscope. Scales without spines $0.5-0.7\mu$, with a pattern of radiating ridges on one side and crossed striations within a wide raised rim on the other. Scales with spines $0.3-0.6\mu$, with a pattern of radiating ridges on the side towards the body and a narrow raised rim surrounding concentric markings on the outer side, the slender tapering spine, approximately equal to scale diameter in length, attached by 4 decurrent ridges extending to scale margin. Distribution of two types of scales on body unknown.

Cells uninucleate, no stigma. Chromatophores appearing striated, I or 2, pale golden brown; in cells of motile phase parietal, saucer-shaped to oblong, with a single inconspicuous globular body (pyrenoid?) placed eccentrically on inner face of each; in cells of non-motile phase coarsely lobed. Oil and leucosin produced. Ejectile muciferous bodies small, localized in groups in peripheral cytoplasm, but their position changing with the metaboly of the body. Nutrition phototrophic and/or phagotrophic. Not toxic to fish.

In motile phase asexual reproduction by fission into two daughter-cells, usually of equal size. In non-motile phase by successive fission of amoeboid cells to produce 4 ovate daughter-cells with very thin walls; motile phase almost certainly liberated from walled daughter-cells through a pore.

Habitat: the sea at position (Plymouth Laboratory Station L4) Lat. N. 50° 15', Long. W. 4° 13' (13 Sept. 1950, type culture) from a townet sample. Type culture (Plymouth no. 31) deposited with the Type Culture Collection, Cambridge; preserved material and photographs lodged with the Marine Biological Association, Plymouth, England.

Cellula motili formam satis mutanti, fere ephippioidea cum lente natat aut restat immotilis, cupuliformi aut sphaeroidali cum natat rapiditer, longitudine $6-10\mu$ (rare $4\cdot5-12\mu$) per dorsum ephippii. Flagellis duobus et unico haptonemate conjunctim exorientibus ex aspectu concavo ventrali, prope lineum medium; flagellis aequis, teretibus, paulatim attenuatis sicut ad capilli extremitatem, ut videtur per microscopiam electronicam, generaliter heterodynamicis, nonnunquam homodynamicis, longioribus 3 vel 4 quam cellula. Haptonemate teneriore quam flagellis, 12-14 (rare 16) longiore quam cellula, cum maxime extensus, apice clavato sed nulla tunica externa semidiaphana ut videtur per microscopiam electronicam. Periplasto, pectico natura, induto delicatissimis squamis diaphanis, circularibus aut ovalibus, sculptis, invisibilibus nisi per microscopiam electronicam; squamis manifestis sub duabus formis: altera forma, sine spinulis, $0.5-0.7\mu$ longis, sculptis radiantibus rugis ad aspectum inferiorem, et striis decussatis circumdatis ab lata margine elevata ad aspectum superiorem; altera forma, praeditis spinulis longis $0.3-0.6\mu$, sculptis rugis radiantibus

ad aspectum inferiorem, et angusta margine elevata circumdanti rugas concentricas ad aspectum superiorem. Spinulis teneribus, longitudine ferme aequis latitudine squamae, affixis per quattuor costas decurrentes, extendentes ad marginem squamae. Ignotum est quomodo duae formae squamarum distributae sint in superficie cellulae.

Nucleo unico, nullo stigmate, chromatophoris striatis ut videntur, I aut 2, pallide aureo-brunneis; in cellula in statu motili, crateriformibus aut oblongis, praeditis unicis corporibus globularibus inconspicuosis (?pyrenoidalibus) locatis ex centro in aspectu concavo; in cellula in statu non-motili rude lobatis. Cellula oleum leucosinumque parienti; corporibus parvis ejectilibus et muciferosis, aggregatis in cytoplasmate superficiali, situ tamen mutanti secundum mutationem formae cellulae. Nutritione phototrophica necnon phagotrophica. Non toxica piscibus.

Generanti asexualiter in statu motili per fissionem in duobus cellulis filiolis, generaliter aequis magnitudine; in statu non-motili per fissiones subsequentes cellularum amoeboidalium ad 4 cellulas filiolas producendas, cum tenerrimis parietibus. Ferme certum est quod cellulae in statu motili ex cellulis filiolis per foramen liberantur.

Habitat mare prope Plymouth ad locationem Lat. N. 50° 15′, Long. W. 4° 13′ (13 Sept. 1950—cultura typica).

Description

The position of the haptonema differs from all those previously described in lying across the body during slow swimming (though not during rapid swimming) instead of projecting out from it. In this condition, or when anchored, the cells are roughly saddle-shaped with smooth curved sides. When seen from above or below the cells appear squarish or oblong with the

Legends to Text-figs. 20-29

Chrysochromulina ephippium n.sp.

(Figs. 20-22 × 1250; Figs. 23-29 × 5000)

- Fig. 20. Cell in shape adopted during rapid swimming; flagella and haptonema behind body in position characteristic for the species in this state.
- Fig. 21. Saddle-shaped cell gliding slowly with haptonema fully extended in front of the body.
- Fig. 22. Similar to Fig. 20 but sides of saddle overlapping differently and flagella in position for slower movement.
- Fig. 23. Ventral view (concave surface) of saddle-shaped cell, haptonema loosely coiled; one flagellum still, the other undulating. c, chromatophore; f, flagellum; g, graphite; h, haptonema; l, leucosin vesicle; m, muciferous body; n, nucleus; p, pyrenoid-like body; s, scale; v, vacuole containing ingested particles in Brownian movement.

Fig. 24. Lateral view of saddle-shaped cell, haptonema fully extended; bacterium in vacuole.

- Fig. 25. Dorsal view (convex surface) of anchored saddle-shaped cell, chromatophore dividing, anchored haptonema bent and partly extended; flagella undulating at different speeds.
- Fig. 26. Individual with sides of saddle overlapping; flagella and haptonema behind body in position characteristic for the species during very rapid swimming; positions A and B, less rapid swimming than in position C; position D, slower movement than in positions A or B.
- Fig. 27. Optical section of large saddle-shaped individual with two chromatophores.

Fig. 28. Walled daughter-cell with contents shrunk away from the wall and with chromatophore similar to those of the motile phase.

Fig. 29. Contents of walled daughter-cell partly released through pore, flagella not detected.



Text-figs. 20-29

flagella and haptonema arising in the median line near one end of the concave ventral surface (Fig. 23). The lateral views (Fig. 24) are somewhat oval, the narrowest dimension being about half that of the dorsal or ventral views (Figs. 23, 25). The optical section through the saddle is bean-shaped (Fig. 27).

When the cell starts to swim rapidly the shape changes to a half-ovoid, or is spheroidal, or somewhat bell-shaped, with the flagella and haptonema directed backwards (Figs. 20, 22, 26). The change in shape is brought about by the rolling in and sometimes overlapping of the curved sides of the saddle. The different shapes during rapid swimming depend on how tightly the curved sides of the saddle are lying over each other. The flagellar end, now at the back of the saddle, sometimes protrudes behind the body as a small lobe (Fig. 20), the insertion of flagella and haptonema being clearly seen.

Using the length of the dorsal surface as an indication of size, in an actively growing culture 80% of the cells are from 6 to 9μ , while 5% are between 4.5 and 6μ . The remaining 15% are incipient fission stages and are from 9 to 12 μ , the largest being ovoid to nearly spheroidal in shape.

The flagella and haptonema (Figs. 30-32, 34, Pl. V; Figs. 35, 36, Pl. VI) are delicate and not very easily seen under the light field; they are also thrown off fairly quickly under both light and dark fields. Measurement of the flagella of a large number of individuals shows that the two flagella are of equal length although their movement is generally heterodynamic; they are 3-4 times the body size in length (Figs. 30-32, Pl. V; Figs. 20, 25, 26). The haptonema (Pl. V) is usually about four times the flagella length when fully extended (Fig. 21), but when very tightly coiled the coil measures $1.5-2.0 \mu$ in length; the regular coiling, when not too tight, can be seen quite clearly under a 2 mm. objective (Fig. 23).

The general shape of the body scales, their surface sculpturing and relative sizes are shown on Pls. VI and VII. The spines are directed outwards (Fig. 35, Pl. VI) and the two differently marked surfaces of the subtending scale can thus be identified. On the inwardly directed surface (i.e. that away from the spine) there is the usual system of radiating ridges extending to the margin that has been encountered in other forms (e.g. C. kappa, C. minor, C. ericina). On the outer surface from which the spine arises there is a raised rim and roughly concentric surface markings upon which four cruciform ridges, extending from rim to centre, support the base of the spine. These two surfaces are separately distinguished in Fig. 39, Pl. VII, and in various parts of Fig. 38. Similar details for the two surfaces of spineless scales are contained in Fig. 40. By analogy with the spined scales it is probable that the rimless ridged surface (right-hand scale of Fig. 40) is that towards the body and that the face with the wide rim and criss-cross marking (left-hand scale of Fig. 40) is outwards. These scales are larger and fewer than the spined scales in this species (cf. Fig. 37, Pl. VI) but their relative distribution is unknown. It is probable that the information regarding the identity of the two surfaces will be found

applicable to other species in which direct evidence has not so far been obtained, notably for the flat scales of *C. ericina*.

The chromatophores, one in smaller individuals, two in larger, are clearly striated and their position changes very considerably with the metaboly of the body. When the cell is saddle-shaped the chromatophores lie close to the dorsal surface (Figs. 23, 25) and curve round on to the ventral surface (Figs. 23, 27). They sometimes appear ribbon-shaped, the two edges nearly meeting ventrally if there is one chromatophore, or both dorsally and ventrally if there are two. When the cell changes shape for rapid swimming, the chromatophores tend to elongate, also becoming narrower (Fig. 26).

Completely colourless cells have not yet been detected in this species, but some peculiar small orange-brown chromatophores borne singly in a few otherwise unpigmented small cells are suspected to have been ingested fragments of degenerating cells. It is therefore probable that specimens lacking chromatophores are occasionally formed.

In the motile phase the pyrenoid-like bodies are very inconspicuous, measuring only about 0.5μ in diameter. In many individuals they could not be seen at all, but when observed each one appeared to lie on the inner face of a chromatophore towards one margin and slightly towards the non-flagellar end of the cell (Fig. 23); they sometimes appeared to be surrounded by a small mass of non-refringent material. The medium-sized nucleus is occasionally visible in the living cells lying in the body towards the ventral surface near the point of insertion of flagella and haptonema. In this species fairly small vesicles of leucosin are produced, generally one to three in each cell, and they lie in the body towards the dorsal surface away from the flagellar end (Figs. 23–25). Small oil globules could also be detected distributed throughout the cytoplasm. The refringent ejectile muciferous bodies are not very conspicuous and are localized in groups of 5 to 7, scattered over the body in the peripheral cytoplasm (Figs. 23–26). Their contents are generally exuded quickly as short threads, but sometimes slowly as small globules.

Movement is generally extremely rapid, the individuals swimming in straight lines for long periods. In spite of the absence of a stigma there is a marked phototactic reaction.

Figs. 20, 22 and 26 illustrate the body shape and the position of the flagella and haptonema during the most rapid swimming. The body rotates very quickly as the cell moves forward in the water, showing only slight gyration. One flagellum trails behind the body showing little movement except possibly near the tip, which appears to beat from side to side, though this appearance is probably due to the rotation of the body. The other flagellum adopts the various attitudes labelled A to D in Fig. 26, the position C being that of the most rapid motion, A and B being less rapid and D still slower. During very rapid swimming the haptonema is coiled. The various degrees of uncoiling exhibited by Figs. 30–32, Pl. V, are probably fixation

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effects but the attitudes of the flagella shown in these figures are highly characteristic of the normal slow swimming in the directions indicated by the arrows.

By putting the flagella straight out stiffly from the body, a cell can stop abruptly from rapid swimming. It then usually reassumes the saddle shape and becomes anchored by the end of the haptonema. Under dark field the uncoiling of the haptonema can be followed quite easily. It unrolls, sometimes quite slowly, the unrolling starting from the body until it lies out stiffly like a rod: it then attaches. Alternatively the haptonema can anchor at any stage of the uncoiling or when not uncoiled at all. If the haptonema does not uncoil when the cell anchors, the cell rotates very rapidly with the flagella either lying out from the body or curved inwards at their distal ends and under dark field recalling a catherine wheel firework. If the haptonema uncoils partly or completely the body is seen usually with the dorsal (convex) surface uppermost, the flagella projecting in the opposite direction to the haptonema (Fig. 25). When the cell is attached with the haptonema extended both

Explanation of Plates V-VII

Chrysochromulina ephippium n.sp.

V

- Fig. 30. A cell killed with iodine in KI and dried on a glass slide; photograph of the dry specimen taken without a coverslip. Magnification \times 1000.
- Fig. 31. Another cell, as Fig. 30.
- Fig. 32. Another cell as Fig. 30 after transfer from glass to a quartz slide, examined in a liquid mount (water, with a trace of iodine) and photographed on the ultraviolet microscope with a glycerine-immersion monochromet (wave length 2750 A) Exposure no. UV 256·3*b*. Magnification \times 3000.
- Fig. 33. A cell killed with osmic vapour after graphite feeding, photographed in the cultur fluid with an oil-immersion lens. Magnification \times 2000.
- Fig. 34. A cell killed on a formvar film with osmic vapour, shadowed, and examined with the electron microscope; the appendages more disarranged than in Figs. 30–32 but visible. Electron micrograph M 115.20, magnification × 3000.

VI

- Fig. 35. Central portion of the cell of Fig. 34, Pl. V, more highly magnified to show scales in position on the body. Electron micrograph M. 115.21, magnification × 10,000.
- Fig. 36. Tip of a flagellum. Electron micrograph M. 273.11, magnification × 10,000.
- Fig. 37. Scales near the body of another cell. Electron micrograph M. 251.15, magnification × 20,000.

VII

- Fig. 38. Scales near the body of another cell showing details of both surfaces of plate scales and spined scales; for further description see text p. 402. Electron micrograph M. 251.4, magnification × 30,000.
- Fig. 39. Details of two spined scales from the field of Fig. 37, Pl. VI, to show the two different faces, left-hand scale showing inner face, right-hand scale showing outer face. Electron micrograph M. 251.15, reversed print, magnification × 30,000.
- Fig. 40. Details of two plate scales from another cell showing the two faces, left-hand scale showing outer face, right-hand scale showing inner face. Electron micrograph M. 251.8, reversed print, magnification × 30,000.

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(Facing p. 404)

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PARKE, MANTON & CLARKE. PLATE VI



J. MAR. BIOL. ASS. U.K., 35 (2) PARKE, MANTON & CLARKE. PLATE VII



STUDIES ON MARINE FLAGELLATES

flagella can undulate at the same rate, or appear to do so, or one can undulate more slowly than the other with undulations of larger amplitude (Fig. 25). In the extreme case, which is quite common, one flagellum can undulate and the other remain still or move stiffly in a short back and forward dithering stroke. When attached with the haptonema extended the body can sway about on the attached haptonema and the haptonema itself can bend over (Fig. 25) so that sometimes the body is near the point of attachment of the haptonema.

Saddle-shaped cells are frequently seen gliding through the water and rotating very slowly with the haptonema fully extended forwards and lying across the body in the direction of motion (Figs. 21, 24). The flagella thus project backwards and both can either undulate slowly, usually at a slightly different rate, or one can remain stiff while the other undulates (Fig. 21). If another cell is encountered, or for no apparent reason, the haptonema may be withdrawn with a sudden jerk and coiled up so quickly that the act cannot be followed. The body then resumes the shape and characteristics of rapid swimming.

Phagotrophy is of common occurrence, the cells ingesting graphite, bacteria and other organisms up to a size of $2 \cdot 5 \mu$. Ingested material lies at the nonflagellar end towards the dorsal surface (Figs. 23, 24). In a few instances small vacuoles containing either bacteria or graphite have been seen lying close to the pyrenoid-like bodies (Fig. 23). As in *C. ericina*, Brownian movement can be seen inside the vacuoles which, after a short time, suddenly disappear.

Before fission the motile cells become more ovoid to spheroidal in shape, the incipient fission stages being from $9-12 \mu$ in diameter. The second pair of flagella, frequently seen as very short ones, and the second haptonema develop before the actual fission which passes from dorsal to ventral surface, giving usually daughter-cells of equal size but occasionally ones of unequal size.

In culture, this species produces from 1 to 2 million cells per ml. at the peak of growth, after which, as in the other species, non-motile stages are produced. The large naked phagotrophic amoeboid cells, up to $16 \times 9 \mu$, have lobed chromatophores but they are rather coarsely lobed in this species. The four daughter-cells with stellate chromatophores, product of the fission of the large walled cells up to $14 \times 10 \mu$, are generally ovoidal with a very thin smooth wall, and range in size from 5×3.5 to $8 \times 6 \mu$. In a four-month-old culture many of these small, walled, cells were present and in some of them the contents had shrunk quite considerably leaving a clear area inside the wall. The cells with the shrunk contents (Fig. 28) were more deeply pigmented than the others and therefore conspicuous. On examination it was found that the chromatophores although striated were no longer lobed but had resumed the appearance of those of the motile phase (Figs. 28, 29); the pyrenoid-like body and small leucosin vesicles could also be seen in some of these cells. Only the part-release of the contents of a number of these daughter-cells has

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been seen so far; in one, the cell was seen to come partly out of the wall through the pore and what was almost certainly the haptonema could be seen on that part of the body still inside the wall, but no flagella could be detected. Numerous empty walls with circular pores were found on the bottom of the flask containing the four-month-old culture.

In shape this species is very similar to the type species of the genus, C. parva Lackey, but it is larger, has a relatively longer haptonema which is thinner instead of thicker than the flagella. It also lacks a contractile vacuole and, when saddle-shaped, has the flagella and haptonema projecting in the opposite direction to that shown by Lackey for C. parva.

Chrysochromulina alifera n.sp., Parke & Manton

(Lat. Ala—a wing+fero—I bear)

Diagnosis

Motile cells showing extreme metaboly, approximately saddle-shaped with large lateral curved wings when moving slowly or stationary; bell-shaped, oblong, ovoid or spheroidal when swimming rapidly; 6-10 (exceptionally $(4-12)\mu$ in length of back of saddle. Two flagella and one haptonema arising close together from ventral concave surface near to one margin in a centre line; flagella smooth, of equal length or subequal, gradually attenuated to a hair point (E. M. observation), usually heterodynamic, occasionally appearing homodynamic, $2-2\frac{1}{2}$ times cell size in length; the haptonema thinner than the flagella, 10 to 12 (exceptionally 14) times body size in length when fully extended, with a swollen tip but no obvious translucent sheath visible under the electron microscope. The periplast, pectic in nature, showing a covering of very thin transparent circular to oval sculptured, dimorphic scales, visible only under the electron microscope; scales without spines 0.25 to 0.45 μ , sculpturing similar to those of C. ephippium; scales with spines 0.28 to 0.45 μ , the spine slightly less than scale diameter in length attached centrally by 2-4 short decurrent ridges not extending to the margin. Distribution of the two types of scales on body unknown.

Cells uninucleate, no stigma. Chromatophores striated, 2 or 4, occasionally one or none, intense golden brown; in cells of motile phase saucer-shaped to square or oblong, with single inconspicuous globular body (pyrenoid?) placed near the margin towards the non-flagellar end; in non-motile phase finely lobed. Oil and leucosin produced. Ejectile muciferous bodies small, localized in groups mainly towards the non-flagellar end of the cell. Nutrition phototrophic and/or phagotrophic. Not toxic to fish.

In motile phase asexual reproduction by fission into two daughter-cells of equal or unequal size; in non-motile phase by successive fission of amoeboid cells to produce 4 ovate daughter-cells with exceptionally thin walls; motile

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phase probably liberated from walled daughter-cells through a pore. Habitat: the sea at position (Plymouth Laboratory Station L4) Lat. N. 50° 15', Long. W. 4° 13' (4 May, 1950, type culture) at surface. Type Culture (Plymouth no. 34) deposited with the Type Culture Collection, Cambridge; preserved material and photographs lodged with the Marine Biological Association, Plymouth, England.

Cellula motili, maxime formam mutanti, fere ephippioidea, praedita magnis alis lateralibus curvatis cum lente motilis aut immotilis, cupuliformi, oblonga, ovoidali aut sphaeroidali cum natat rapiditer; longi $6-10 \mu$ (rare $4-12 \mu$) per dorsum ephippii. Flagellis duobus et haptonemate unico conjunctim exorientibus e concavo aspectu ventrali prope marginem in medio lineo; flagellis teretibus, longitudine aequis aut subaequis inter se, paulatim attenuatis sicut ad capilli extremitatem ut videtur per microscopiam electronicam; generaliter heterodynamicis, nonnunquam homodynamicis, ut videtur, longioribus 2-21 quam cellula; haptonemate teneriore quam flagellis, longiore 10-12 (rare 14) quam cellula, cum maxime extensus, apice tumescenti sed nulla tunica externa semi-diaphana apparente, ut videtur per microscopiam electronicam. Periplasto, pectica natura, induto delicatissimis diaphanis squamis circularibus aut ovalibus, sculptis, manifestis sub duabus formis, invisibilibus nisi per microscopiam electronicam; altera forma, squamis sine spinulis, $0.25-0.45 \mu$ longis, sculptis simili modo squamis C. ephippii; altera forma, squamis praeditis spinulis, longis $0.28-0.45 \,\mu$ quoque spinulo longo minusquam squamae latitudo, affixo ad centrum squamae per 2-4 breves costas decurrentes, non extendentes usque ad marginem squamae. Ignotum est quomodo duae formae squamarum distributae sint in superficie cellulae.

Nucleo unico, nullo stigmate. Chromatophoris striatis, 2 aut 4, rare unico aut absente, profunde aureo-brunneo; in cellulis in statu motili, crateriformibus, rectangularibus aut oblongis, unico corpore inconspicuoso globulari (?pyrenoidali) locato prope marginem cellulae, versus apicem quo desunt flagella; in cellulis in statu non-motili chromatophoris delicate lobatis. Corporibus ejectilibus muciferosis parvis, locatis versus apicem cellulae quo desunt flagella. Nutritione phototrophica necnon phagotrophica. Non toxica piscibus.

Generanti asexualiter in statu motili per fissionem in duas cellulas filiolas magnitudine aequas aut inaequales; generanti in statu non-motili per fissiones subsequentes cellularum amoeboidalium ad 4 ovatas cellulas filiolas producendas, parietibus extreme delicatissimis. Fere certum est quod cellulae in statu motili liberantur per foramen.

Habitat mare prope Plymouth ad locationem Lat. N. 50° 15', Long. W. 4° 13' (4 Mai 1950—cultura typica) ad summum maris.

Description

The details which distinguish this species from the preceding include body shape, the relatively shorter flagella and haptonema, some details of the swimming movements, the position of the pyrenoid, the greater average number of chromatophores and the smaller and slightly simpler scales.

The exceptional form-range is illustrated in Figs. 41-59. In general character this species is somewhat similar to *C. ephippium*, though the form range is greater, the body thinner (Fig. 65) and the wings larger and more curved (Figs. 46, 60, 61). It was impossible to get an exact measurement of the thickness of the body, but it is not more than $1.5-2.0 \mu$.

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When a cell glides slowly through the water without rotating and with the haptonema extended, or when it is anchored by the extended haptonema, the body shape is characteristically as in Fig. 60 (see also Fig. 70, Pl. VIII). When the cell moves fairly slowly with the haptonema extended and the body rotating the sides curl in slightly and frequently overlap (Figs. 41, 42). Sometimes the sides fold in, one above the other, as in Fig. 49. When the cells are swimming rapidly (Figs. 55–57, 62, 63) all shapes from spheroidal, ovoidal, half an ovoid, oblong, bell-shaped to umbrella-shaped can be seen, depending on how much and at what angle the wings are overlapping.

The flagella (Pls. VIII, IX) are comparatively shorter and a little sturdier than in *C. ephippium*, but even so neither the flagella nor the haptonema are easily seen under the light field, particularly when the cells are moving rapidly; the flagella are also thrown off very quickly under both light and dark fields. Measurement of the flagella of a large number of cells showed that in the majority they were of equal length, as in the previous species, but in a few, one flagellum was slightly longer $(1-3 \mu)$ than the other; their movement is generally heterodynamic as in *C. ephippium*. The haptonema is usually

Legends to Text-figs. 41-59

Chrysochromulina alifera n.sp. (×1250)

- Fig. 41. Saddle-shaped cell moving slowly with haptonema fully extended, one flagellum slowly undulating, the other stiff or gently vibrating; wings incurved, one slightly overlapping the other.
- Fig. 42. As Fig. 41 but wings incurved and not overlapping, body rotating slowly.
- Fig. 43. As Fig. 41 but wings straight, body not rotating and haptonema lying close to ventral surface of body.
- Fig. 44. As Fig. 41 but wings lying close together but straight not incurved, haptonema lying away from body.
- Fig. 45. Anchored cell with haptonema coiled and flagella lying out from body, two new flagella developing, wings of body curved in and one slightly overlapping the other; body rotating very rapidly giving the impression of a catherine wheel firework when looking down on it under dark field.
- Fig. 46. Stationary cell with wings straight out and haptonema slowly uncoiling.
- Figs. 47-48. Cells anchored by partly extended haptonemata.
- Fig. 49. Cell swimming with flagella and haptonema in front of the body, body elongated and wings rolled in one above the other.
- Figs. 50-51. Stationary cells with incurved wings.
- Fig. 52. Early fission stage with overlapping wings and with four flagella and two haptonemata behind body, characteristic position for rapid swimming.
- Fig. 53. Early fission stage with four flagella and two haptonemata, body anchored by one haptonema, the other coiled up close to body.
- Fig. 54. Cell in process of overlapping wings to produce shape seen in Fig. 56 looking down on ventral surface which is folded inside in Fig. 56.
- Figs. 55–57. Variously shaped cells with flagella and haptonemata behind body in positions characteristic for the species during rapid swimming.
- Fig. 58. Cell swimming with flagella and coiled haptonema in front of the body.
- Fig. 59. Same cell as Fig. 58 just stopped swimming, body shape slightly changed and haptonema extended. It then started gliding with the extended haptonema in front of the body.



Text-figs. 41-59

about five times the length of the flagella when fully extended (Figs. 41-44) and shows the same regular coiling (Figs. 61-64) as in *C. ephippium*, and is again thinner than the flagella (Fig. 70, Pl. VIII; Fig. 73, Pl. IX).

The scales (Pl. IX) are very much like those of *C. ephippium* but smaller, and their markings, especially those of the outer face, less distinct (Fig. 76, Pl. IX). The struts at the base of the spine are also less massive on the spined scales and they do not extend to the rim of the scale (Figs. 74, 76, Pl. IX).

The chromatophores, two in smaller individuals (Fig. 61), four in larger (Fig. 60), are striated, but not as clearly as in *C. ephippium*. Occasional cells, usually small, lacking chromatophores have been seen in stock cultures of this species and they were found to be not uncommon in cultures which had been treated with penicillin and streptomycin. When two chromatophores are present they lie mainly in the wings (Fig. 61), filling them completely and leaving most of the back as a clear area (Figs. 65, 66); when four are present (Fig. 60) two are then situated in this part and no clear area is visible but their shape and position changes with the metaboly of the body. Occasionally cells possessing extremely small chromatophores are seen, the chromatophores filling only about one quarter of the wings.

As in *C. ephippium* the pyrenoid-like bodies are small (Figs. 60, 63), $0.5-0.75 \mu$ diameter, and cannot always be seen; their position is on the margin of the chromatophore towards the non-flagellar end of the cell (Fig. 66); they sometimes appear to lie on the margin in the centre line, but if the chromatophore is squarish or oblong they appear to be at one corner. The nucleus is of medium size and lies in the body close to the point of the insertion of the flagella and haptonema (Figs. 60, 63). As in *C. ephippium* a number of small, sometimes very small, vesicles of leucosin are produced, up to 5 in a cell, but no large vesicles have been observed. The leucosin lies in the central clear area

Legends to Text-figs. 60-67

Chrysochromulina alifera n.sp. (× 5000)

- Fig. 60. Saddle-shaped cell with straight wings and with the haptonema fully extended, the shape characteristic of gliding motion without rotation: four chromatophores and four pyrenoid-like bodies, ingested graphite at non-flagellar end of back of saddle.
- Fig. 61. Saddle-shaped cell with two chromatophores and coiled haptonema.
- Fig. 62. Cell in the shape adopted for rapid swimming, wings in the front, incurved and slightly overlapping; two chromatophores, one in each wing.
- Fig. 63. Early fission stage with four chromatophores, four flagella, two haptonemata, and two nuclei; wings curved in and overlapping behind; ingested graphite at non-flagellar end of back of saddle. c, chromatophore; f, flagellum; g, graphite; h, haptonema; l, leucosin vesicle; m, muciferous body; n, nucleus; p, pyrenoid-like body; s, scale.
- Fig. 64. Late fission stage.
- Fig. 65. Optical section of saddle-shaped cell.
- Fig. 66. Anchored cell viewed from convex dorsal surface, ingested graphite at non-flagellar end.
- Fig. 67. Small thin-walled daughter-cell with two stellate chromatophores and two pyrenoid-like bodies.





of the cell at the end opposite to that at which the flagella and haptonema are inserted (Figs. 63, 66); leucosin vesicles have not been detected in the lateral wings. Small oil globules are generally distributed throughout the cytoplasm. Inconspicuous muciferous bodies are present in small groups in the peripheral cytoplasm, and appear more numerous in that part of the body in which the leucosin is situated (Figs. 63, 66).

Movement is very rapid but the cells do not move quite so quickly as in *C. ephippium*, neither do they swim for such long periods in one direction; they do, however, show a marked phototactic reaction in spite of the absence of an obvious stigma. The behaviour of the flagella and their position during rapid (Figs. 55-57) and slow (Figs. 41-44, 49, 58, 59) movement is similar to that already described for *C. ephippium*; that is, the flagella nearly always behave heterodynamically, though sometimes appearing to be homodynamic.

The haptonema is sometimes seen partly extended behind the body (Fig. 57) during fast swimming, with the cells rotating very rapidly, sometimes showing considerable gyration and often changing their shape whilst in motion. Swimming with the flagella and haptonema in front of the body (Figs. 49, 58, 59) is more frequent than in *C. ephippium* but the movement is much slower than when the flagella are behind the body. The uncoiling of the haptonema (Fig. 46) and the method of anchorage of the cell by it (Figs. 47, 48) is as described for *C. ephippium*. The rapid rotation of the anchored body (Fig. 45), recalling under dark field the motion of a catherine wheel, occurs also in this species, but the rotation does not last for such long

Explanation of Plates VIII-IX

Chrysochromulina alifera n.sp.

VIII

- Fig. 68. A cell killed with osmic vapour and dried on glass, photographed without a coverslip. Magnification \times 1000.
- Fig. 69. A cell after graphite feeding, killed with osmic vapour and photographed in a liquid mount under oil immersion. Magnification × 2000.
- Fig. 70. The cell of Fig. 68 stripped from glass and remounted for electron microscopy. Electron micrograph M. 162.1, magnification × approx. 2300.
- Fig. 71. Another cell killed directly on the formvar film. Electron micrograph M. 179.7, magnification × 3000.

IX

- Fig. 72. Tip of a flagellum. Electron micrograph M. 273.11, magnification × 10,000.
- Fig. 73. A body showing haptonema and scales. Electron micrograph M. 179.8, magnification × 10,000.
- Fig. 74. Part of the field of Fig. 73 to show details of scales. Electron micrograph M. 179.12, magnification \times 20,000.
- Fig. 75. Group of scales more highly magnified showing spined and spineless scales, most viewed from the body side. Electron micrograph M. 277·12, reversed print, magnification × 30,000.
- Fig. 76. Another part of the field of Fig. 75; an isolated spined scale showing the outer face on the right; both views visible in the group on the left. Electron micrograph M. 277.12, reversed print, magnification × 30,000.



(Facing p. 412)

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PARKE, MANTON & CLARKE. PLATE IX



periods as in *C. ephippium*. Cells are commonly seen stationary, or gliding through the water with their haptonemata extended for longer periods than in *C. ephippium*, and, as in that species, the cells always give a sudden backward jerk when the haptonemata are coiled up rapidly.

Phagotrophy has been demonstrated (Fig. 69, Pl. VIII; Figs. 60, 63, 66). Cells containing ingested material are frequently but not commonly seen, the maximum size of ingested material being $2 \times I \mu$. Ingestion of material takes place at the back end of the saddle (Fig. 60), that is the part of the body foremost (Fig. 63) when the cell is swimming rapidly with the flagella and haptonema behind. No vacuoles containing granules in Brownian movement have so far been seen.

Before fission the back of the saddle widens (Fig. 63), not lengthens, and cells showing two very short flagella and two long flagella (Fig. 45), are sometimes seen. The second haptonema, as well as the two new flagella, are formed before the actual fission starts (Figs. 52, 53, 63). In this species incipient fission stages are frequently seen anchored by one haptonema whilst the second remains coiled (Fig. 53). Fission down through the back of the saddle starting at the non-flagellar edge gives two daughter-cells (Fig. 64), which can be from equal to very unequal in size.

In culture from $\frac{1}{2}$ to 1 million cells per ml. are produced at the peak of growth. Non-motile stages similar to those already described for the other species are then produced. The large amoeboid and walled cells, with chromatophores more finely lobed than in *C. ephippium*, measure from 14 × 10 to 16 × 12 μ . The four ovate daughter-cells produced by the large walled cell have exceptionally thin walls and fairly finely lobed or stellate chromatophores and measure from 4 × 3 to 7 × 5 μ in size (Fig. 67). The shrinkage of the contents of these cells away from the walls has not so far been seen in old cultures, nor has the liberation of the contents been observed.

DISCUSSION

The only point which at this stage perhaps merits further discussion is our treatment of the facts for heterodynamic flagellar motion in *C. ephippium* and *C. alifera*. We are well aware that, on some systems of classification, this character would at once remove these species not only from the same genus but even from the same order as that containing the other species with which we have been concerned. That we have not, at this stage, chosen to do this is partly due to the striking similarity of all these species in other respects, which in this particular group are perhaps as important taxonomically, but in part also to our inability to find any structural differences between the two flagella of the kind which normally accompanies the truly heterokont condition, cf. *Symura* (Manton, 1955); when fixed therefore they cannot be distinguished from isokonts. There is the further difficulty caused by our present ignorance

of the relevant facts for the type species *C. parva* Lackey. We do not yet know whether the apparent resemblance between this species and our *C. ephippium* extends to the motion of their flagella, and without this knowledge we should be in grave danger of misapplying the generic name were we to attempt to split the assemblage of species at present included under *Chryso-chromulina* on a character as elusive as flagellar motion.

This negative attitude does not, however, preclude the possibility that subdivision may have to be carried out at a later stage. The six species which we have now described fall into three or perhaps four distinct assemblages, namely *C. ericina*; *C. ephippium* and *C. alifera*; *C. kappa* and *C. minor*; and *C. brevifilum*. We are not, however, yet prepared to say whether these ought to be thought of as subgenera or as genera, and since we have additional groups still undescribed, further discussion of the larger topic must necessarily be deferred.

SUMMARY

Diagnoses and descriptions are given of three new species of marine plankton flagellates in the class Chrysophyceae: Chrysochromulina ericina, C. ephippium and C. alifera. All possess two equal or subequal flagella and a long haptonema. In two of the species flagellar movement is heterodynamic and in one homodynamic. Phagotrophic feeding has been demonstrated in all. The descriptions include structural details of scale characters visible only with the electron microscope as well as observations on behaviour and life-history visible only in living material. The reasons for temporarily placing the three organisms in the genus Chrysochromulina Lackey are given.

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OBSERVATIONS ON THE SHOALING BEHAVIOUR OF COD (*GADUS CALLARIAS*) IN DEEP WATER RELATIVE TO DAYLIGHT

By G. H. Ellis

[Kelvin and Hughes Ltd]

(Plates I and II)

It is well known that vision is the main physical factor governing the formation and maintenance of fish shoals, and that, in general, shoals break up when the light intensity falls below a certain level. Breder (1929, 1942), Newman (1876), Parr (1927, 1931), and others, have shown this by laboratory experiment.

During a commercial fishing voyage to the Barents Sea it became possible, by means of a recording echo-sounder, to study the shoaling behaviour of cod in deep water relative to light intensity. The observations were made aboard the Hull trawler *Lancella* whilst fishing in a depth of 110 fathoms at Skolpen Bank in September 1955. For this a Kelvin and Hughes recording echosounder type MS. 24J was used, the depth range across the chart being 55 fathoms. The scale was phased so that the region between 80 and 135 fathoms deep was displayed.

The trawler was, for the period of 19 h, towing over substantially the same ground on consecutive trawling tows, position and direction of tow being maintained by the use of radar equipment in conjunction with two anchored dan buoys. The duration of each tow was approximately 2 h. The fishing gear used was a standard deep sea trawl, and the towing speed of the vessel was 4 knots.

The charts (Pls. I, II) show the results obtained on seven consecutive trawling tows made between 13.10 G.M.T. on 17 September 1955, and 08.15 G.M.T. on 18 September 1955, for which particulars are given in Table I. It will be noticed that all recorded echoes have serrated edges, and that there is occasional 'missing' and 'lining' on the charts. These effects are caused by the vertical movement of the vessel due to heavy swell which persisted throughout the tows. All fish caught whilst these charts were recorded were cod, the length of which lay between 40 and 90 cm. From the catches it is assumed that the recorded fish traces were due to cod of sizes within this range.

The charts show clearly that the cod were mainly in compact shoals during daylight hours, and that during darkness they were distributed fairly evenly over the whole area of the tow. The process of dispersal started just before

TABLE I. DESCRIPTION OF CHARTS

Pls. I, II	Times of tow, G.M.T.	hour (baskets)	Description of traces	Weather and sea	Remarks
Chart (a)	13.10–14.55 h, 17. ix. 55	70	Dense 'Thumbprint' record- ings throughout the whole tow. Few crescent traces due to single fish	Overcast, fairly heavy swell	Tow made in daylight ending shortly before sunset. The fish are mainly in discrete shoals forming a composite target. Average height of fish from sea-bed 10 fm
Chart (b)	15.45–17.45 h, 17. ix. 55	60	Fairly dense traces at the beginning of the recording, thinning out into less distinct single crescent echoes	No moon, overcast, fairly heavy swell	Tow made during and after sunset. The shoals have split up at sunset and the fish have dispersed evenly over the whole of the tow between the sea-bed and 30 fm above
Chart (c)	18.30–20.30 h, 17. ix. 55	75	Single crescent echoes through- out the tow	No moon, overcast, fairly heavy swell	Tow made during darkness. The fish are spread out over the whole tow area between the sea-bed and 30 fm above
Chart (d)	21.10–23.30 h, 17. ix. 55	50	As (c)	As (c)	As (c)
Chart (e)	00.10–02.30 h, 18. ix. 55	50	As (c) and (d)	As (c) and (d)	As (c) and (d)
Chart (f)	04.00–06.00 h, 18. ix. 55	35	Dense 'Thumbprint' traces throughout recording with some single crescents	Hazy, fairly heavy swell	Tow made after sunrise. The fish have re-formed into compact shoals; average height of fish from sea-bed 10 fm
Chart (g)	06.25–08.15 h, 18. ix. 55	35	As recording (<i>f</i>)	Bright and clear, fairly heavy swell	Tow made in daylight. The fish are mainly in discrete shoals as on the previous daylight recordings (Charts (a) and (f)). Average height of fish from sea-bed 10 fm

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⁽Facing p. 416)



the sunset at 16.12 G.M.T., presumably when the light intensity fell below the threshold of vision of the cod. Conversely, there is evidence to show that the re-forming of the shoals took place at sunrise (02.55 G.M.T.).

The average height of the fish above the sea-bed remained at about the same level (10-15 fm) irrespective of the formation of the fish. Unlike sprats and herring, which have been shown by Richardson (1952) to exhibit diurnal vertical migration, the cod maintained the same average level throughout day-light and darkness, although the maximum height above the sea-bed was greatest in darkness.

The maximum possible vertical movement of the fish on dispersal at night, i.e. 30 fm (about 25 % change in level), was well within the theoretical limits imposed by the swim-bladder as deduced by Jones (1952).

The catches did not vary significantly with the change in formation of the fish.

SUMMARY

During a commercial fishing voyage to the Barents Sea continuous observations were made on the shoaling behaviour of cod in deep water over a period of 19 h.

The cod were studied by the use of a Kelvin and Hughes MS. 24 J recording echo-sounder.

Compact cod shoals recorded in 100 fm during daylight dispersed at sunset and re-formed at sunrise.

The maximum possible vertical movement of the fish during observation was 30 fm.

The catches did not vary significantly with the formation of the cod.

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THE USE OF TRAWL, GRAB AND CAMERA IN ESTIMATING MARINE BENTHOS

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(With Plates I–IV and Text-fig. 1)

Certain animals of the epifauna, because of their distribution over the bottom, are often difficult to sample quantitatively. They may occur as individuals widely dispersed over a large area, or they may be present in dense aggregations which themselves have a patchy distribution. In the past, workers have tried to estimate the numbers of such animals by the combined use of trawls and grabs of various types. The post-war development of underwater photography suggests that the camera will be a useful additional tool (e.g. Vevers, 1951, 1952). During the testing of an underwater camera from Aberdeen an opportunity was taken to compare the estimates of some of the larger epifauna from grab and trawl hauls with estimates derived from underwater photographs. The results are described in this paper.

THE GEAR

A $\frac{1}{10}$ m² Van Veen type grab, weighted to 72 lb. (33 kg) and fitted with the endless warp rig, was used. The trawl was a standard Agassiz with a 6 ft. (182 cm) beam. The underwater equipment for the camera was designed by Mr R. E. Craig. The unit was a Royal Air Force F-24 camera using $5\frac{1}{2}$ in. aerofilm giving negatives of roughly 13 × 11 cm. Light was provided by an electronic flash apparatus, and a yellow filter was used. Technical details of this equipment are not discussed here.

METHODS

The work was carried out in Loch Creran, and in the Lynn of Lorne, near Oban in Argyllshire. Dans were set out marking five stretches varying in length from 417 to 1174 m. The positions of these stretches are shown in Text-fig. I. On each stretch a similar procedure was followed. First the ship was allowed to drift between the two dahns while a series of photographs was taken. At the beginning of the run the camera was lowered to the bottom, and was raised a few feet after each exposure to allow the equipment to recharge. Recharging generally took about 30 sec, so that a continuous series of photographs was taken over the ground at a rate of one exposure per minute. The ship was then allowed to drift over the same ground while a series of grab

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hauls was made. Finally, the Agassiz trawl was towed between the two dans. Since the distance between the dahns was so short, it was fairly certain that between any two sets the three gears covered the same ground, and this was confirmed by an examination of traces from the ship's echo-sounder, which was run continuously.



Text-fig. I. Chart of the area studied, showing the positions of the five stations. From Admiralty Chart No. 2814A.

All the larger animals of the epifauna caught by trawl and grab were counted and identified. The nomenclature used is that in the *Plymouth Marine Fauna* (Marine Biological Association, 1931). In dealing with photographic data, series of approximately 21×17 cm prints were made. Each print represented almost 1 m² of bottom, but since the focus often deteriorated towards the edges the prints were masked, and animals on a $\frac{7}{10}$ m² area were counted.

RESULTS

Details of the estimates by the three gears are given below for each ground separately. The Agassiz trawl catches are summarized in Table 1.

Stretch A (Pl. IA)

This was in the Lynn of Lorne in 22–28 m. The dans were 1174 m apart, and the ground was covered by seventy-two photographs and twenty-one grab hauls, as well as the Agassiz haul. The total area of bottom considered, i.e. the area swept by the trawl, was 2147 m².

ESTIMATING MARINE BENTHOS

	Stretch number				
Animal	A	В	С	D	Е
Ophiothrix fragilis	1093	1992	215	524	290
Asterias rubens	2	5	2	in - an	IO
Other Asteroidea	3	5	2		7
Echinoidea	24	36	20	I	18
Chlamys opercularis	23	4	27	12	118
Lima		83	35	8	5
Other Mollusca	_	2	3	2	42
Decapoda reptantia	17	29	20	29	84
Decapoda natantia		5	38	38	14
Ascidians		45	21	6	14
Fish	8	2	I	4	ıĠ

TABLE I. NUMBERS OF ANIMALS TAKEN IN EACH STRETCH BY THE Agassiz Trawl

As shown by the photographs, the north end of the ground was of uniform sand, which merged about half-way along the stretch into a short area of coarser sand and gravel. This gave place to mud (Pl. IB) which covered most of the second half of the stretch, with the exception of a few patches here and there where shells, mostly of *Cyprina islandica*, were mixed with the mud. The main animals of the epifauna are considered below.

Ophiothrix fragilis was the most abundant animal encountered, but photographs showed it to be confined to the stretch of sand and gravel, occurring in the mud area only on the shell patches. Even on the hard ground, however, the distribution of Ophiothrix was by no means uniform. It occurred on each of the first thirty prints, ranging from one to sixty individuals per frame, with an average of thirty-three. The following nine prints, although over apparently similar ground, showed no Ophiothrix, but just before the beginning of the muddy ground they again appeared, with an average of eighteen per print. Knowing the number of photographs taken, it is possible to calculate that the sandy stretch was 650 m long, so that the Agassiz on this part swept an area of 1190 m². Eleven of the grab samples came from this area, and all except two contained Ophiothrix, the mean number being 1.6 per sample. From the photographs the estimated number of Ophiothrix in the sand was 39,542, from grabs, 19,418, and the total number taken in the trawl was 1093. The trawl value may be an overestimate for the sandy area alone, since it is assumed that all the Ophiothrix in the trawl were taken on this part.

On this stretch, as well as inside Loch Creran, small numbers of other ophiuroids (e.g. *Ophiocomina nigra* and *Ophiopholis aculeata*) were found mixed with the *Ophiothrix* populations.

Ophiura texturata, although slightly more abundant on the hard ground than on the soft, occurred over the whole stretch, and was seen on fifty-four of the seventy-two prints in numbers ranging from I to 7 per print. Single specimens were found in four grab samples, but none was taken by trawl.

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From the photographs we can calculate that the total number of *Ophiura* present on the area swept by the trawl was 5325, while the comparable value from the grab data is 4090.

The seventeen kinds of decapoda reptantia found in the trawl consisted of four *Munida bamffica*, one small *Galathea*, nine small spider crabs (mostly *Inachus*) and three *Eupagurus prideauxi*. These same types were also seen on the photographs—a total of eight decapods on seven prints distributed over both the sand and the mud. The grab took one *Eupagurus*. Since the numbers are small it would be misleading to compare estimates for the whole stretch without taking into account the different areas sampled by each gear. The comparison is shown below:

Gear	Area sampled	Estimate for stretch
Grab	2 m^2	1074 decapods
Camera	50 m ²	341 decapods
Trawl	2147 m ²	17 decapods

Twenty-three small specimens of *Chlamys opercularis* were taken in the trawl and none in the grabs. On the photographs only two individuals could be distinguished, but small specimens could easily have been obscured by the overlying brittle-stars. This, together with the fact that a *Chlamys* was usually counted only if both valves could be seen makes it probable that the photographic count is an underestimate.

Among other animals, a flatfish was seen on one print, but no fish were taken by the grabs. In general, however, the fish which the trawl showed to be present in small numbers—codling and *Gadus minutus*—would be difficult to see in photographs. On the soft ground the grab took two *Cyprina islandica* and one *Aphrodite aculeata*. Neither of these was found in the trawl, but although they could not be seen on photographs, numerous tracks were noticed on the mud (e.g. Pl. IB), and many small holes, probably breathing apertures. Lastly, the following echinoderms were 'taken' by the three gears:

	Totals observed			
the mean mus	Trawl	Grab	Prints	
Echinoids	24	I	4	
Solaster papposus	3	0	0	
Palmipes membranacea	I	0	0	

EXPLANATIONS OF PLATES I AND II

Underwater photographs, each covering approximately $\frac{2}{3}$ m² of the sea bottom. Each represents one print used in counting, except that trimming has reduced it by about 5%. The weight for operating the trigger mechanism can be seen on each print. This was 7 cm in diameter.

Pl. I. Lynn of Lorne, stretch A: A, showing the sandy area of this stretch and the typical distribution of brittle-stars found in it; B, showing the muddy area, with tracks.

Pl. II. Loch Creran: A, stretch B, showing the epifauna mainly of brittle-stars and ascidians; B, stretch C, coarse deposit where grabbing was difficult, showing *Chlamys opercularis*, starfish and a spider crab.

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MCINTYRE. PLATE I




J. MAR. BIOL. ASS. U.K., 35 (2)

MCINTYRE. PLATE II



Stretch B (Pl. IIA)

This was across the entrance to Loch Creran in 15–22 m. The dans were 464 m apart, and the area swept by the trawl (848 m²) was covered by sixteen photographs and eighteen grab samples. The photographs showed a fairly uniform stretch of coarse material—sand mixed with stones and shells, with an epifauna of brittle-stars and ascidians.

Ophiothrix fragilis occurred on all the photographs from this stretch, ranging in number from four to seventy-two per print, with a mean of twenty-seven. In the grabs, *Ophiothrix* was found in eleven of the eighteen samples, ranging from one to seventeen per sample, with a mean of 4.9 individuals. The calculated numbers for the whole stretch are 32,702 for the camera and 41,919 for the grab, while the trawl caught 1992.

Lima hians, a lamellibranch which builds a nest among stones and shells, was abundant. Eighty-three were found in the trawl and seven were taken in four grab samples. A nesting animal such as this is difficult to detect on photographs, and only one could be distinguished.

The only natantian decapods found were five *Pandalus* taken in the trawl. The remaining decapods in the trawl consisted of six *Eupagurus bernhardus*, eight *Hyas araneus* and fifteen small spider crabs, mostly *Inachus*. The camera showed four decapods in four prints. Three were spider crabs and the fourth a *Eupagurus*.

Other animals occurring in smaller numbers were as follows:

	Totals observed						
	Trawl	Grab	Prints				
Asterias rubens	5	0	8				
Henricia	5	I	I				
Echinoidea	36	3	0				
Holothuroidea	0	I	0				
Chlamys opercularis	4	0	6				
Buccinum undatum	2	0	2				
Lamellibranchs	0	2	0				
Goby	2	0	0				

Stretch C (Pl. IIB)

The dans were placed in 11-28 m depth along the south shore of the loch, and were 579 m apart. The area covered by the Agassiz was 1059 m², and was represented by twenty-four photographs and fifteen grabs. The stretch consisted of coarse gravel and stones of various sizes, with some large boulders here and there. Only three of the grab hauls produced fauna—eight *Ophiothrix* three *Lima* and one ascidian. At all the other attempts either the jaws were held open by stones, or the grab was empty, presumably having landed on large boulders. After several further attempts, grab sampling on this stretch was abandoned. On such ground the trawl sampling also is probably far from optimum, and the camera is the one instrument which can operate satisfactorily. The trawl and camera results are considered below.

Ophiothrix fragilis was absent from the first seven prints, although the ground here, except for the presence of a few fragments of algae, appeared to be similar to that of the remainder of the stretch. All the other prints showed *Ophiothrix* in numbers varying from one to forty-two, the mean for all prints being ten. This gives an estimate of 15,577 for the whole area, compared with the trawl catch of 215.

Chlamys opercularis was distributed over the whole area. Twenty-eight individuals were observed on eleven prints in numbers varying from one to ten per print. The estimate for the whole area is 1766 compared with the trawl catch of twenty-seven.

Of the decapods taken in the trawl, thirty-eight were *Pandalus montagui*, and none of these was seen on photographs. Natantian decapods in general probably merge with their surroundings so well that they would be difficult to distinguish on prints. It should be noted that the gear described here is triggered when a weight hits the bottom. The slight interval between the landing of the weight and the taking of the photograph might allow a rapidly moving animal to leave the field. Modification of the camera release would obviate this. The remaining trawl-caught decapods consisted of three *Eupagurus bernhardus*, eleven large *Hyas araneus* and six small spider crabs (*Inachus* and *Macropodia*). Twelve decapods could be seen on ten photographs—one *Eupagurus* and eleven spider crabs, mostly *Hyas*. These spider crabs were distributed fairly evenly over the ground, and the calculated population for the whole area is 694.

Twenty specimens of echinoids were taken in the trawl, and twelve were seen in five photographs. These five photographs were all from a small area at the beginning of the stretch, and on any one print the echinoids usually occurred together and in association with pieces of *Laminaria*.

Other animals are as follows:

	Totals	observed		Totals	observed
	Trawl	Camera		Trawl	Camera
Lima	35	—	Henricia	2	I
Buccinum	I	2	Sabellids		9
Pecten	2		Ascidians	21	6
Asterias	2	2	Flatfish	I	

The nine sabellids all occurred in one small isolated patch of soft ground seen on one print. A number of *Pecten* shells were seen on prints, but since these appeared to be flat on the bottom they were not counted as being living animals.

Stretch D (Pl. IIIA)

This extended from the entrance along the north shore of Loch Creran, at a depth of 20-28 m. The dans were 417 m apart, giving 763 m² as the area

trawled, and this area was covered by twenty-six photographs and twenty grabs. The stretch had a fairly uniform bottom of sandy gravel and small stones, with a more or less continuous covering of mussel shells. The most abundant animals were brittle-stars and decapod crustaceans.

Ophiothrix fragilis was fairly evenly dispersed over the ground. It was present on all prints in numbers between twenty-one and seventy-six, with a mean of fifty-six per print. It was also present in all the grab samples, varying from two to thirty-six per sample, with a mean of 10.5. The camera and grab estimates for the whole stretch are 61,330 and 79,686 respectively, compared with 524 individuals taken by the trawl.

Again natantian decapods could not be seen in photographs, although thirtyeight *Pandalus* were found in the trawl and two in the grab samples. The trawl took five large *Hyas araneus* and twenty-one other small spider crabs, and three *Eupagurus*, while three *Hyas* were caught in the grab. Two *Eupagurus* were seen on the photographs and nineteen spider crabs, mostly *Hyas*. The spider crabs were distributed fairly evenly over the stretch occurring on sixteen of the twenty-six prints, giving an estimate of 796 individuals for the whole stretch.

Ascidians were mostly species of *Ascidiella* and *Ciona* and thirty-seven were seen in fifteen prints, in numbers ranging from one to five per print. They were also found in thirteen of the twenty grabs, the total number being twenty-three. Estimates for the whole area amount to 1550 individuals for the camera, and 8769 for the grab. The trawl took six specimens.

Thirty-one *Lima hians* were taken in thirteen grab samples, ranging from one to five per sample. Only eight specimens were taken in the trawl. Trawl catches of *Lima* are likely to be very variable, depending on the extent to which the trawl bites into the bottom. No *Lima* were seen on the prints.

Seven mussels were taken in the trawl and thirteen in nine grabs. On the photographs almost every print showed mussel shells, and in several prints two closed valves could be seen. These lay singly or in small groups, not in a continuous bed. It was, however, difficult to decide if these animals were alive, and mussels were therefore not counted.

The following other animals were found in the three gears:

	Totals observed					
	Trawl	Grab	Prints			
Chlamys	12	2				
Buccinum	I	I	2			
Echinoids	I	5	4			
Asterias rubens		4	8			
Solaster	<u> </u>		I			
Fish	4	5	I			

Stretch E (Pl. III B)

This was a continuation of stretch D along the north shore of the loch in 26–31 m. The distance between dans was 834 m, and the area swept by the

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trawl 1525 m². This area was covered by fifty-seven prints and twenty grabs. Two distinct types of bottom were encountered. About a third of the stretch consisted of sandy gravel with large stones here and there. This merged into mud which covered the remainder of the stretch, except for a few small patches of muddy sand. The prints showed that most of the epifauna occurred on the gravel.

Ophiothrix fragilis occurred only on the area of sand and gravel, which was covered by the first twenty prints, and the numbers were lower than on any of the other stretches. They were seen on fifteen of the twenty prints in numbers varying from two to forty per print, with a mean of eight. Five of the grabs were on the sandy area, and took a total of twelve *Ophiothrix*. The estimates for the whole gravel area for camera and grab are 4916 and 10,455 respectively. The trawl took 290 *Ophiothrix*.

Chlamys opercularis was distributed over the whole area but was more numerous on the gravel than on the mud. No *Chlamys* were taken by the grab. Photographs showed twenty-five individuals in fifteen prints, varying in number from one to four per print, and giving an estimate for the whole area of 956 *Chlamys*. The number taken by the trawl was 118.

Eleven Pandalus and three Crangon were taken by the trawl, but no natantian decapods were recorded from grabs or photographs. The Reptantia, however, were numerous. Forty-eight spider crabs, mostly small, thirty-five eupagurids and one Munida were taken in the trawl. In the grab samples only one Eupagurus and one Galathea were taken. Twelve crabs were noted in ten prints—five spider crabs and seven Eupagurus. The spider crabs were mostly large Hyas, and the population of small spider crabs sampled by the trawl could not be estimated from photographs.

Other animals which occurred in smaller numbers were as follows:

	To	otals observ	7ed
	Trawl	Grabs	Prints
Pennatulacea			I
Pecten	I	- <u>-</u>	2
Mussel	13		+
Cockle	2	I	
Asterias rubens	IO		I
Solaster endica	3		I
Solaster papposus	2		4
Henricia	I		I
Palmipes	I		
Ascidians	_	8	3
Fish	16	_	I

The ascidians in the grabs were taken in two clumps in two consecutive hauls, and those in photographs were on consecutive prints, suggesting that these animals were localized in a small part of the stretch, which could account for their absence from the trawl. The fish consisted mainly of gobies and flatfish.

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DISCUSSION

In considering three gears as different as trawl, grab and camera it is obvious that direct comparisons cannot be made. Each gear has its own peculiarities which give it advantages and limitations not possessed by the others. In dealing with the epifauna one of the important factors is the area of bottom which can be conveniently sampled. Thus between two dans in the present work, the trawl in half an hour could cover 2000 m² of bottom, the camera in the same time photographed 50 m² and the grab in half an hour generally sampled about 2 m².

Since the trawl covers a large area it is useful in sampling organisms which are few in number and widely dispersed. Further, it can take large animals, and also active ones such as natantian decapods. But the trawl gives no indication of the distribution of the animals within the limits of the comparatively extensive ground covered in any one haul. A series of grab samples can give information on distribution, but since each sample covers so small an area, an impossibly large number of samples would be required before grab results for less numerous animals could be applied to a wide area. The camera is intermediate between the trawl and grab in that it can cover a fairly wide area yet indicate in considerable detail the distribution of the animals. On stretch C, for example, the trawl showed merely the presence of *Chlamys opercularis* and of Echinoidea. The camera, however, established that while the former species was distributed fairly evenly over the whole stretch, the latter group was confined to a small area, and even there occurred only in association with *Laminaria*.

In practice, the relative effectiveness of the three gears will vary with the numerical density of any particular species, and with its distribution over the whole area studied. The most abundant animal in the present work was *Ophiothrix fragilis*, and the various estimates of the numbers of this species on the five stretches are given in Table II.

TABLE II. NUMBERS OF O. FRAGILIS PRESENT ON EACH STRETCH AS ESTIMATED BY THE THREE GEARS

Stretch	Trawl	Camera	Grab
А	1093	39,542	19,418
В	1992	32,702	41,919
С	215	15,577	(No samples)
D	524	61,330	79,686
E	290	4,916	10,455

The trawl always gave the lowest estimate. The camera values are from 16 to 117 times greater, and the grab values from 18 to 152 times greater than those of the trawl. Comparing the camera and the grab, it can be seen that on stretch A the camera estimate is higher, while on the other four stretches the grab gives a rather greater value. The difference between stretch A and the

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other grounds with regard to the relative estimates of camera and grab is connected with a difference in the distribution of the animals (cf. Pls. IA and IV). In the Lynn of Lorne generally (where stretch A is located), the brittle-stars are found not in dense masses but either as single individuals (Pl. IA), or in small clumps of up to five or six individuals. With such a distribution there are large patches of bare ground and the grab will tend to underestimate the number present. The camera, on the other hand, covering a larger area, gives a better estimate. In Loch Creran, however, the brittle-stars occurred in dense masses (Pl. IV) or at least as a fairly even covering over the ground (Pl. IIIA). For such distributions the grab gave rather higher estimates than the camera, probably partly because in counting brittle-stars in prints the general practice was to count an animal only when the disc could be seen. Thus when the animals are aggregated, often several individuals thick, the discs of animals in the lower layers tend to be obscured and an underestimate results. It should be noted, however, that although in these conditions the camera may give a slightly lower estimate than the grab, it is a much less variable, and therefore more reliable estimate. On stretch D, for example, where the densest population of brittle-stars was found, the coefficient of variation of the grab counts was 85 %, while the corresponding value for the camera was only 25%.

The other animals of the epifauna were all considerably less abundant than Ophiothrix, and usually occurred as single individuals often widely separated from each other. For animals distributed in this way the grab is generally the least efficient of the three gears, since, covering such a small area, it takes too few individuals to allow valid estimates to be made for the whole ground. The trawl is better, mainly because it covers considerably more ground. The best results were usually from the camera. For example, in stretch D, only three of the twenty grab samples contained spider crabs, while sixteen of the twentysix photographs showed these animals, giving an estimate of 796 individuals for the whole area, compared with the trawl catch of twenty-six. Another species on which the camera gave useful information was Chlamys opercularis, and the estimated numbers of this species on each stretch are shown in Table III. The camera not only most often gave higher estimates, but also gave information not obtained from the other gears. It showed on stretch E, for example, that Chlamys was distributed over the whole stretch; that it was more abundant on the gravel than on the mud, and that its density varied from one to four individuals per square metre.

EXPLANATION OF PLATES III AND IV

Underwater photographs, those on Pl. III covering approximately $\frac{2}{3}$ m² of the sea bottom, as in Pls. I and II; that on Pl. IV about $\frac{7}{10}$ m². The weight for operating the trigger mechanism, seen on each print, was 7 cm in diameter.

Pl. III. Loch Creran: A, stretch D, showing the covering of mussel shells; B, stretch E, showing the coarse deposit with *Chlamys opercularis*.

Pl. IV. Example of the aggregation of brittle-stars found on several stretches in Loch Creran.

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MCINTYRE. PLATE III



J. MAR. BIOL. ASS. U.K., 35 (2)

MCINTYRE. PLATE IV





ESTIMATING MARINE BENTHOS

TABLE III. NUMBERS OF *CHLAMYS OPERCULARIS* ON EACH STRETCH AS ESTIMATED BY THE THREE GEARS

Stretch	Trawl	Camera	Grab
A	23	85	0
В	4	454	0
C	27	1766	No samples
D	12	0	763
E	118	956	0

Finally, it should be noted that the use of the camera is limited to areas of fairly clear water. It is difficult to obtain clear pictures, for example, in the turbid water of Aberdeen Bay, and off some parts of the south-west Scottish coast.

SUMMARY

Agassiz trawl and Van Veen grab catches of certain animals of the epifauna are compared with numbers of these animals estimated from underwater photographs.

In sampling brittle-stars, which occurred in large numbers, the Agassiz trawl was the least efficient of the three gears. When the brittle-stars were distributed singly or in small patches the camera gave better results than the grab. When the patches were large, or when the distribution was more or less continuous, the grab gave slightly higher estimates, but its estimates were considerably more variable than those of the camera.

For the less common animals of the epifauna the grab was generally a poor sampling instrument. The trawl was rather better, but within fairly wide limits it can give no indication of distribution. The camera gave more acceptable estimates and also indicated the distribution of the animals over the ground.

For certain areas of hard bottom the camera is probably the only instrument which can give adequate results.

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THE ATTENUATION OF LIGHT IN SEA AND ESTUARINE WATERS IN RELATION TO THE CONCENTRATION OF SUSPENDED SOLID MATTER

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(Text-figs. 1-8)

Experiments have been reported recently (Atkins, Jenkins & Warren, 1954) in which the relative concentration of suspended matter at different depths in the sea was determined by filtering samples of water through collodion membranes and measuring the relative albedos. Also reported in the same paper are the results of a series of observations of the visual range of a Secchi disc at station E I in relation to the concentration of phytoplankton.

Experiments are now described which were designed to investigate the relation between the Secchi disc reading, the concentration of suspended matter, and the attenuation coefficient of tungsten light in sea water.

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MEASUREMENT OF ATTENUATION COEFFICIENT

It is well known that the optical properties of a sample of natural water may be affected during collection and removal to a laboratory (Hulbert, 1945; Jenkins & Bowen, 1946; Jerlov, 1951). Such measurements should therefore be made as far as possible *in situ*. The Admiralty Research Laboratory hydrophotometer is an instrument which may be lowered into water at any desired position, and measures the attenuation of an approximately parallel beam of light from a tungsten filament lamp traversing a path of length 50 cm. in the water. It is somewhat similar to that developed by Pettersson (1934), the main difference being that the A.R.L. hydrophotometer has been designed to prevent as far as possible scattered light falling on the photocell. The instrument consists of a lamp-housing and a photocell-housing rigidly connected together by three tubes and may be seen in the photograph of Fig. I. A diagram of the optical system and the electrical circuit is given in Fig. 2. Light from the bulb B is rendered parallel by the lens L_1 and passes through the $\frac{3}{8}$ in. plate glass window W_1 into the turbid water T. After traversing a path



Fig. 1. The A.R.L. hydrophotometer.





of length 50 cm. the light enters the photocell-housing through the window W_2 , and is brought to a focus near the plane of the stop S_2 . Although the image is formed in a slightly different position according to whether the instrument is in water or in air, all the light still passes through S_2 . It finally falls on a Weston barrier layer photocell C_2 which incorporates a green filter producing a spectral response approximating to that of the eye. The stop S. effectively prevents daylight reaching the photocell C_2 , and so the instrument can be used equally well in daylight. A similar photocell C_1 is located inside the lamp-housing and a portion of the light from B passes through the adjustable stop S_1 and falls on C_1 . A heat-absorbing glass H is necessary to minimize heating of C_1 by the lamp with consequent change of sensitivity. The two cells C_1 and C_2 are connected in opposition as shown. In the laboratory, with the instrument in air, S_1 is adjusted so that the outputs from the two cells balance. This method of design compensates for variations in intensity of the light source. Just before the instrument is used in water the light-beam is blocked from C_2 and the meter M is set to full-scale deflexion (100 divisions) by means of the variable resistance R. When the instrument is immersed in water, the light transmitted increases by a factor of approximately 1.08 since two airglass reflexions are eliminated. Thus the meter reading obtained when the instrument is immersed has to be corrected, and the percentage light transmission per half metre t is given in terms of the meter reading M by the formula

$$t = (100 - M) 0.92.$$
 (1)

It is well established that the absorption and scattering of light in a turbid medium obey an exponential law, and thus an attenuation coefficient μ (metre)⁻¹ can be introduced given by the formula

$$t = 100 \exp(-0.5\mu).$$
 (2)

It should be emphasized that this coefficient is not the same as the vertical extinction coefficient (μ_v) as found from the variation with depth in the sea of the daylight falling on an upturned horizontal surface which is defined (Poole & Atkins, 1928) by

$$\mu_v = \frac{2 \cdot 3}{d} \{ \log_{10} V_1 - \log_{10} V_2 \}, \tag{3}$$

where V_1 and V_2 are the simultaneous values of the illumination at two points differing in depth by d metres. This is because illumination on a horizontal surface at any depth in water is partly due to light that has been scattered by the water, whereas the attenuation coefficient refers only to a parallel beam (the instrument being designed to eliminate as far as possible the effect of scattered light). It should be mentioned, however, that owing to certain unavoidable limitations a little forward scattered light will always be collected by such an instrument; the error introduced as a consequence of this factor is discussed in the Appendix to this paper.

The current generated by a barrier-layer photocell is no longer proportional to the light intensity when the resistance in series with the cell is too high. It was therefore necessary to test the linearity of response of the instrument. This was done by introducing into the beam (in air) a number of thin glass plates, and measuring the change in galvanometer deflexion as each plate was added. Allowance was made for multiple reflexions between the surfaces of the plates when calculating the attenuation produced by a given number of plates. With the electrical circuit used the response was accurately linear.

MEASUREMENTS WITH SUSPENSIONS MADE UP IN THE LABORATORY

Preliminary experiments were carried out in the laboratory using suspensions of kaolin or Thames mud in tap water. The hydrophotometer was placed in a tank containing about 15 l. of water. Known amounts of a concentrated suspension of kaolin (1000 p.p.m.) or Thames mud (200 p.p.m.) were stirred into the tank and the light transmission was measured at each value. In Fig. 3 is shown a graph of the attenuation coefficient per metre (μ) plotted against the concentration in mg/l. for the kaolin and Thames-mud suspensions.

EXPERIMENTS AT SEA

Method of Obtaining Samples and Measurements

In the measurements on the water at sea one end of a length of clean $\frac{1}{2}$ in. rubber hose pipe was lashed to the hydrophotometer which was then lowered into the sea from a boat. The other end of the pipe was connected to a carefully cleaned 2 l. glass bottle which could be evacuated by means of an electrically driven pump running from a 24 V accumulator. Water was drawn up the pipe into the sample bottle and at the same time the light transmission was measured. The bottle was filled and emptied overboard at least three times before the final sample was taken.

Measurements were made at various depths down to 12 m, and the Secchi disc visibility was also observed using a white disc of 20 cm diameter. The observations were made at various positions in the Thames Estuary between Gravesend and the Nore, and in the sea and estuarine waters near Plymouth. Altogether thirty-four samples of water were filtered, covering a range of light transmission from 5 to 90% per half metre. Details of the observations are given in the table of results (Table I), including light transmission measurements for some positions where no water sample was taken. The positions of the stations are shown on the maps in Figs. 4 and 5.





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ATTENUATION OF LIGHT IN SEA

TABLE I. RESULTS

AHW, after high water; BHW, before high water; c, concentration in mg/l.; D, Secchi disc visibility (metres); S, salinity in g/kg; w, ash weight in mg/l.; μ , attenuation coefficient per metre; $\bar{\mu}$, average attenuation coefficient between surface and depth D; *, indicates two independent determinations of weight of suspended solid. Only the observed values, μ and $\bar{\mu}$ are given in the table, and the correction discussed in the Appendix has not been made. Thus the values are likely to be up to 30 % too small.

Date	Station	Time	Depth (m)	ц	S	c	71)	D	<i>ū</i>
6	Δ	al h provi	()	0.079	24.9				~~~~~
0. v. 53	A	15 II BHW	0.3	0.188	34.0	0.6	_	21	0.211
	в	11 h BHW	0.3	0.472	34.0	1.8		15	0.304
	C	h BHW	_			_		8	0.56
	D	1 h BHW	0.3	0.80	32.7	2.2		6.5	0.68
	E	HW	-	-	—	—	—	II	0.445
	F	2 h AHW	-	-	-			5	0.89
	G	$2\frac{1}{4}$ h AHW	0.3	1.32	33.0	2·7* 4·7	0·99* 1·25	3	1.34
	H	$2\frac{3}{4}$ h AHW		_	-	—	-	10.2	0.472
	Ĩ	$3\frac{1}{2}$ h AHW	0.3	1.83	28.6	3.9	1.4	2.5	1.20
	J	4 h AHW	4.2	1.00	30.0	3.0	0.9	2	1.80
	K	44 n AHW	10.5	1.00	32.1	2.9	-	3	1.24
	L	5 h AHW	3.0	0.522	34.0	2.1	0.0	9	0.48
	IVI	5 II AHW	12.0	0.440	34.7	1.0	0.5	5	0.92
11. v. 53	Eı	5 h bhw	12.0	0.576	_	3.2	0.3	7	0.535
13. v. 53	N	$3\frac{3}{4}$ h ahw	9.0	0.472	34.8	1.9* 1.8		8.5	0.224
	I	5 h ahw	9.0	4.42	31.0	23·6* 24·9	_	I	5.20
	Р	$5\frac{1}{4}$ h ahw	6.0	3.44	32.1	12·9* 11·1	—	1.2	3.63
	Q	$5\frac{1}{2}$ h ahw	12.0	2.48	33.1	9·7* 9·2		1.72	2.20
	С	$5\frac{3}{4}$ h AHW	6.0	1.94	33.6	6.1	-	2.25	2.19
	R	6 h ahw	3.0	1.31	33.8	3·0* 4·1	_	3	1.31
	N	4 h внw	1.2	0.80	34.2	1·5* 1·4		6	0.80
	S	$3\frac{3}{4}$ h bhw	6.0	0.498	35.1	1·3* 0·8	_	8	0.498
18. v. 53	S	$\frac{1}{2}$ h AHW	-	-/	/-			6	0.67
	N	4 n AHW	_	.70	_			5	0.71
	IVI	14 II AHW	_	17-		_		4	0.97
19. v. 53	C	3½ h AHW	-	/				2.5	2.26
	1 D	4 n AHW	72	_		_		1.2	2.97
	I	$4\frac{1}{2}$ h AHW	77	_	=	_	_	0.75	4.00 6.41
9. vii. 53	TA	$1\frac{1}{4}$ h AHW	3.0	1.69	_	9.6		-	
	IB	í∱n AHW	3.0	2.04		7.0			_
	TC	2 h AHW	7.5	2.40		10.4			
	TD	3 h AHW	3.0	4.2		27.3		_	
	TE	3 ¹ / ₂ h AHW	6.0	3.7		21.2			

Determination of Suspended Solid Matter

The water samples were taken to the laboratory and filtered within 48 h through 'Gradocol' nitro-cellulose membranes, as described by Armstrong & Atkins (1950), of average pore diameter 1.3 to 1.6 microns, using an Elford



Fig. 4. Plymouth Sound and Hamoaze.



Fig. 5. Mouth of the River Thames.

filtering equipment. The samples were kept in the dark before being filtered to prevent the growth of algae. One of the filtrates was filtered a second time through a 0.6 micron membrane. Less than 0.05 mg was obtained from 2 l. of filtrate, indicating that the weight of solid matter passing through the 1.6 micron pores was negligible.

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The technique used to determine the weight of dry solid matter was as follows. The membranes which were supplied immersed in water were first dried to constant weight (a) on porcelain dishes at 50° C. According to the Wright-Fleming Institute this does not materially alter the pore size of the membranes used. A measured volume of I or 2 l. of the water was then filtered through the membrane under a reduced pressure of about 15 in. of mercury. A portion of the filtrate was used to remove the last traces of solid matter from the sample bottle and filtering apparatus. The membrane was weighed wet (b), and then dried on the same dish at 50° C, and finally it was weighed again (c). The wet weighing was needed in connexion with the method of allowing for the small amount of sea salts remaining in the membrane after drying. It was considered safer to determine this weight accurately rather than to try and wash away the salts with distilled water. To make this correction a known weight of the filtrate (d) was evaporated at 50° C and the weight of residual salt determined (e). In some of the later determinations a clean dry membrane of the same kind was soaked in the filtrate and dried, so as to make sure that the drying conditions with and without the suspended matter were identical. Let the weight of salt present with the suspended matter =x. The loss of weight on drying was in each case proportional to the weight of salt present and hence x/(b-c) = e/(d-e). Thus the salt correction x was calculated and the corrected weight of suspended matter was c - a - x. In addition to correcting for the salts this method also allows for any water combined with the salts which was not driven off at 50° C.

Some ash weight determinations were also made by the following method. After being weighed dry the membrane was put back into the filtering apparatus and washed with a filtered dilute solution (approximately N/2) of ammonium nitrate to dissolve out the salts. It was then transferred to a weighed platinum crucible and ignited in a muffle at 550° C for 30 min, and finally cooled in a desiccator and weighed. The ash weight of the membrane itself was negligible (less than 0.05 mg). The ash weights are also given in Table I.

DISCUSSION OF RESULTS

Relation between the Attenuation Coefficient and the Concentration of Suspended Matter

In Fig. 3 the experimental results are shown plotted in the form of the attenuation coefficient μ against the concentration of suspended matter in mg/l., approximately equal to parts per million (p.p.m.). The attenuation coefficient was deduced from the hydrophotometer readings by the use of equation (2).

For the suspensions of kaolin and mud in tap water the attenuation is seen to be a linear function of concentration apart from a slight unexplained curvature near the origin. For sea water the points are much more scattered, as might be expected in view of the variations in the nature of the suspended material from place to place, and the experimental errors involved in filtering and weighing. The curve in the figure has been drawn so as to represent, as nearly as possible, the average properties of the different samples investigated. It is clear from the results that the attenuation coefficient is approximately proportional to the concentration only for the lower concentrations and rises less steeply than for the freshwater suspensions, and less and less steeply as the turbidity increases. These results may doubtless be attributed to variations in the nature or particle size distribution of the suspended material. As regards the effect of variations of particle size, the total projected area of the particles for a given amount of material decreases as the particle size increases, i.e. as flocculation proceeds. It is to be expected that the suspended matter present in salt water is in a more flocculated state than suspensions made up in fresh water.



Fig. 6. Relation between attenuation coefficient per metre and Secchi disc visibility.

The point marked E I in Fig. 3 was for an observation made at Hydrographic Station E I, *ca.* 10 miles south-west of the Eddystone, when there happened to be an exceptionally large growth of plankton containing much *Phaeocystis*. The light transmission was 75% per half metre, and the concentration of dry matter came out to be 3.5 mg/l. The usual concentration for this value of light transmission was about 2 mg/l. near the land in the neighbourhood of Plymouth. The weight of the EI material after ignition was only 0.3 mg/l, showing that little material apart from the organic matter was present, as would be expected so far from land.

Relation between the Attenuation Coefficient and Visibility of a Secchi Disc

For the positions where the Secchi disc reading D metres was observed the mean attenuation coefficient $\bar{\mu}$ between the sea surface and depth D was calculated. The results covered the range D=21 m to 0.75 m, corresponding to



Fig. 7. Relation between Secchi disc visibility and the concentration of suspended matter.



Fig. 8. Limiting cases of collected scattered light.

 $\bar{\mu} = 0.2 \text{ m}^{-1}$ to 6.4 m^{-1} and the best relation to fit them all was found to be $\bar{\mu} = (4.75 \pm 0.08)/D^{(1.04 \pm 0.02)}$. If the few results for the very turbid water $(\bar{\mu} > 3)$ were excluded, a satisfactory agreement was obtained with the simple formula $\bar{\mu}D = K$ (a constant) with the value $K = 4.38 \pm 0.1$. Fig. 6 shows $\bar{\mu}$ plotted against I/D together with the straight line $\bar{\mu} = 4.38/D$.

For Station E1, where the turbidity was mainly due to plankton, the observed Secchi visibility was somewhat less than that predicted from a hydrophotometer reading using the above formula. The actual Secchi disc reading was 7 m, whereas the value deduced from the hydrophotometer reading was 8 m. However, this difference may not be significant in view of the rather large experimental errors associated with a single observation.

In Fig. 7 is shown the relation between Secchi disc visibility and the concentration of suspended matter, deduced by combining the results of Figs. 3 and 6.

SUMMARY

For suspensions of kaolin or Thames mud in fresh water the attenuation coefficient per metre of an approximately parallel beam of light from a tungsten filament lamp was found to be a linear function of the concentration of suspended matter. It reached the value 5 m^{-1} for approximately 10 mg/l. of suspended matter. For sea and estuarine waters near Plymouth and in the Thames Estuary the attenuation coefficient, measured *in situ*, was only about $2 \cdot 5 \text{ m}^{-1}$ for 10 mg/l. and it increased still less rapidly for higher concentrations, reaching only $4 \cdot 5 \text{ m}^{-1}$ at about 28 mg/l. The concentration of suspended matter was determined by filtering water samples through 'Gradocol' membranes, drying the membranes at 50° C, and correcting for the quantity of inorganic salts present with the suspended matter.

The Secchi disc visibility was inversely proportional to the attenuation coefficient over the range 1.5 to 21 metres.

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APPENDIX

THE EFFECT OF FORWARD SCATTERED LIGHT ON THE READINGS OF A LIGHT TRANSMISSION METER

This appendix refers to any light transmission meter having an optical system similar to that shown in Fig. 2 (such as the A.R.L. hydrophotometer).

Owing to the finite size of the stop S_2 which cannot be reduced without loss of sensitivity a certain amount of light scattered by the particles of the turbid medium in forward directions (i.e. in nearly the same direction as the incident light) reaches the detector, and thus the measured light transmission is higher than it would be if the hole were negligibly small.

An accurate theoretical calculation of the effect for a given instrument would involve a long computation for each particle size and would have very little value in practice as a method of correcting the reading because the particle size distribution in the turbid medium is very rarely known. It is, however, desirable to know the order of magnitude of the error, and it is now shown how to determine limits within which the error lies for a given particle size. An experimental determination of the effect in a given turbid medium would involve measuring the angular distribution of the scattered light.

Angular Distribution of the Scattered Light

It can readily be shown that if the lens L_2 has no stopping effect the effective semiangle subtended by the photocell C_2 is the same at all points in the absorbing medium, equal to $\theta_0 = s/f$, where s is the radius of the stop S_2 and f the focal length of the lens L_2 .

It has been pointed out by Walton (1947) that the angular distribution of the scattered light may be calculated by the theory of Fraunhofer diffraction and without recourse to electromagnetic theory for the case of opaque particles which are large compared with the wave-length. According to Walton, if the incident parallel beam is of intensity I lumen/cm² and an opaque particle of radius *a* (where *a* is small compared with the diameter of lens L_2 but large compared with the wave-length λ) is placed in front of lens L_2 it will intercept a quantity of light πa^2 lumens and also diffract a quantity of light which will be distributed over the area of S_2 . The total diffracted light is shown to be also equal to πa^2 and the fraction of this lying within a circle of radius *s* is

or
$$I - J_0^2(2\pi as/f\lambda) - J_1^2(2\pi as/f\lambda),$$

where $z_0 = 2\pi a\theta_0/\lambda$ since $\theta_0 = s/f,$

where J_0 is the Bessel function of zero order, and J_1 is the Bessel function of the first order.

The parameter which expresses the proportion of scattered light collected is the ratio per particle:

 $\frac{\text{light intercepted} + \text{light scattered outside the cone of semi-angle } \theta_0}{\text{light intercepted} + \text{total light scattered}}}$

This will be called the factor of merit F. Thus for opaque particles

$$F = \frac{\pi a^2 + \pi a^2 \{J_1^2(z_0) + J_0^2(z_0)\}}{2\pi a^2}$$

= $\frac{1}{2} \{ \mathbf{I} + J_1^2(z_0) + J_0^2(z_0) \}.$ (A I)

It is clear that for a perfect instrument ($\theta_0 = 0$) in which none of the scattered light is collected, F = I. If some of the scattered light is collected F lies between I and 0.5 for opaque particles and may even fall below 0.5 for translucent particles.

Finite Aperture of Lens L_2

The effect of the finite aperture of the lens L_2 will now be considered. If a scattering particle lies near the edge of the beam, or far enough in front of lens L_2 , part of the scattered light within the angle θ_0 may be intercepted by the aperture of the lens. In Fig. 8 W_1 , W_2 represent the windows enclosing the turbid liquid, and R_1 , R_2 are rays defining the width of the light beam. Only particles lying within the cone *CDE* can contribute the full amount of forward scattered light, and particles at other points in the liquid have part of the scattered light intercepted by the aperture of the lens L_2 . The amount of scattered light collected is obviously (a) less than that due to the whole volume of turbid liquid, and (b) greater than that due to the particles in the cone *CDE*. It is therefore possible in a simple way to set limits to the amount of scattered light collected; an exact solution would involve computing the proportion of scattered light collected from each particle outside the cone.

- Let μ_t be the true attenuation coefficient of the turbid medium (as measured with a perfect instrument);
 - μ_a be the attenuation coefficient as measured if all the scattered light were received by the photocell (case *a*);
 - μ_b be the attenuation coefficient as measured if only scattered light from the cone *CDE* were received by the photocell (case *b*);
 - μ be the measured attenuation coefficient with the actual instrument.

Then the value of μ corresponding to a certain value of μ_t will lie between the limits μ_a and μ_b .

Calculation of μ_a and μ_b corresponding to a given value of μ_t

 μ_a is simply related to μ_t . Thus: $\mu_a = F \mu_t$.

(A 2)

To find μ_b consider a typical ray such as R in Fig. 8 which is for part of its path outside the cone CDE and for part inside CDE. The coefficient μ_b is deduced by assuming the attenuation coefficient to be μ_t for the first part of the path and $F\mu_t$ for the latter part.

It is then fairly simple to show that

$$\exp(-X\mu_b) = (\mathbf{I} - r_1^2/R_0^2) \exp(-X\mu_t) + \frac{2\exp[\mu_t \{-X + (\mathbf{I} - F)r_1 \cot \theta_0\}]}{R_0^2 \mu_t^2 (\mathbf{I} - F)^2 \cot^2 \theta_0} \times \{\mathbf{I} - [\mathbf{I} + \mu_t (\mathbf{I} - F)r_1 \cot \theta_0] \exp[-\mu_t (\mathbf{I} - F)r_1 \cot \theta_0]\}, \quad (A 3)$$

where X is the path length of the beam, R_0 is the radius of the beam, and $\theta_0 = s/f$.

Application to the A.R.L. Hydrophotometer

The important dimensions are as follows:

Path length of beam in liquid	X = 50 cm
Radius of beam	$R_0 = 2.25$ cm
Radius of aperture in stop S_2	s = 0.3 cm
Focal length of lens L_2	f = 5.3 cm
	$\theta_0 = 3.2^\circ$

Assume a mean wave-length = 5500Å.

Table II shows the values of μ_a and μ_b calculated from equations (A 2) and (A 3) respectively, corresponding to $\mu_t = 3 \cdot 0 \text{ m}^{-1}$ for opaque particles of different diameters. For a constant size of particle μ_a is proportional to μ_t , equation (A 2), and it has been found by calculation that μ_b is also proportional to μ_t with considerable accuracy.

TABLE]				
Percentage transm				
intercepted by the ag	Particle			
$F \mu_a$	(microns)			
1.000 3.00	0			
0.925 2.78	2.5			
0.585 1.76	IO			
0.200 1.20	00			
0.925 2.78 0.585 1.76 0.500 1.50	2.5 10 ∞			

If $\frac{1}{2}(\mu_a + \mu_b)$ be taken as an approximate measure of μ a factor can be derived which will give some measure of correction for the inclusion of scattered light. This correction factor k is given by $2\mu_t/(\mu_a + \mu_b)$ approximately, and its value for each of the particle sizes computed is shown in Table II. If k be taken as 1.3 the error in k is not likely to exceed $\pm 20\%$ over the size range 5 microns and upwards. For particle sizes much smaller than 5 microns the Fraunhofer diffraction theory does not apply and the electromagnetic theory of scattering must be used to determine the value of the correction factor.

NOTE ON CAPULUS UNGARICUS (L.)

By Margaret Sharman Marine Biological Station, Port Erin

(Text-figs. 1-3)

The marine gastropod *Capulus ungaricus* (L.) is found on rocks and shells, and is known often to associate with filter-feeding lamellibranchs, particularly frequenting beds of *Pecten maximus* (L.), *Chlamys opercularis* (L.) and *Modiolus modiolus* (L.). It has also been found on the shells of living *Turritella communis* Risso (Jones, 1950, unpublished) and on the superior part of the calcareous tubes of *Protula intestinum* Lam. (Lo Bianco, 1888).

Capulus itself is well known to be a ciliary feeder, and its feeding mechanism has been described by Orton (1912) and Yonge (1938). Observation of the site of several specimens on the shells of living lamellibranchs, together with the fact that the gastropod possesses a long mobile proboscis capable of great extension, led Orton (1949, 1950) to suggest that *Capulus* might also be 'semi-parasitic' on lamellibranchs, from which it could collect food by inserting the proboscis inside the bivalve shell and reaching the food in the food-grooves on the gill lamellae or on the recurrent ciliated path along the edge of the mantle. Living material was therefore collected and observed in the hope of obtaining further evidence as to the truth of this suggestion.

Twenty-nine attached specimens were obtained from off the south coast of the Isle of Man, mostly by dredging from the local beds of scallops, queens and horse mussels. Twenty-two were on the shells of living lamellibranchs, one was close to the aperture of a tube of *Pomatoceros* on the shell of a living *Chlamys opercularis*, two were on empty shells, the valves of which were still attached to each other, and four on the outer surface of single valves.

The position on the valve was recorded for twenty-six individuals, of which twenty-three were situated as previously described by Orton (1949). In its characteristic position the gastropod sits at the edge of the valve with the front margin of the shell projecting a little over it and the apex pointing inwards (Fig. 2A, C). Fig. I shows the sites of *Capulus* found on *Chlamys opercularis*. More *Capulus* were on the right valve, which is the flatter of the two and lies undermost when *Chlamys* is living, than on the left. The majority had attached themselves to the anterior half of the margin of the valve, only three out of fifteen being on the posterior side; the smallest of these was that situated by the aperture of a *Pomatoceros* tube, partly on the *Chlamys* and partly on the tube itself, and the other two were on single valves. None have yet been found on the posterior auricle. The numbers are few, but suggest a possible prefer-

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ence for the anterior edge from the auricle and byssal notch round the ventral curve of the margin. Thus almost all the *Capulus* were on that part of the circumference of the valve where the wide inhalant current of *Chlamys* would be operative and away from the powerful exhalant current which goes out posteriorly over a more restricted region. *Capulus* on *Pecten maximus* (Fig. 2C) and *Monia patelliformis* (L.) were similarly placed. On *Modiolus modiolus, Capulus* were on the ventral edge, above or posterior to the emergence of the byssus, again away from the exhalant current (Fig. 2A).



Fig. I. Composite diagram showing positions of *Capulus ungaricus* on *Chlamys opercularis*. e, on empty shell, the valves of which were still attached to each other; s, on single valves. Otherwise on shells of living *Chlamys*. Arrows show direction of outgoing currents of *Chlamys*.

When Capulus is removed from its attachment, the site often displays a scar which may vary from just a cleaner patch, the sculpture of the valve being unaffected, to a well-defined, almost circular mark with a grooved margin within which the sculpture of the valve is destroyed (Fig. 2B). The circumference of the scar corresponds to that of the aperture of the animal's shell, and the grooved margin sometimes found suggests that the edge of the calcareous part of the shell works on the valve and mechanically produces the groove. The shell of Capulus has a fringed periostracum prolonged well beyond the calcareous edge, and this border fits closely on to the undulations of the valve beneath, except at the anterior margin, where the shell projects a little beyond the edge of the valve. In this region there is often a semi-lunar gap in the valve edge, as was first noticed by Orton (1949) in the case of a single specimen on Monia. It is sometimes difficult to assess the genuineness of this gap, as Capulus on a ribbed shell may be so placed that the midanterior margin is opposite a ridge on the outer surface, i.e. opposite a natural inward undulation of the valve, and valves are often chipped. But in some cases the outer layers of the shell are recessed farther back than the inner, which suggests that the Capulus itself was responsible for the gap rather than that it settled, by preference or chance, over such a gap already there. In this

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connexion I have once seen a *Capulus* remove a piece of shell from the edge of a *Pecten* valve by means of its radula.

The majority of those *Capulus* which had been settled sufficiently long to leave a scar had shown no change in position when kept in sea water in aquarium tanks for periods of up to 3 months, but some power of movement



Fig. 2. A: two Capulus ungaricus on the shell of a living Modiolus modiolus, one on each valve: length of Modiolus shell, 62 mm. B: scar left by Capulus ungaricus on shell of Chlamys opercularis: the shell of the Chlamys measures 77 mm from apex to mid-ventral margin. C: Capulus ungaricus on the shell of a living Pecten maximus: the shell of the Pecten measures 120 mm from apex to mid-ventral margin.

is retained; an animal 39 mm in length, the largest found, was able when freed from its attachment to climb up the side of its container for a short distance, and while some of the smaller ones revealed evidence of long settlement others frequently moved off their attachments, leaving no scar, or were brought up free in the dredge. From this it would appear that while after metamorphosis there is a mobile phase during which the animals crawl actively on the substrate, they tend to settle and remain in later life on the shells of ciliary feeders in a position which would give them the opportunity of using the proboscis to collect food as previously suggested.

The so-called proboscis is in fact a prolongation of the lower lips of the animal to form an almost cylindrical structure having a dorsal groove which runs longitudinally from the soft tip to the mouth with the radular apparatus at the base. The proboscis is not eversible, and is often held curled round to left or right and hidden between head and propodium, from the dorsal surface of which it is stated to take up food particles in mucus, brought thither by the animal's own ciliary feeding currents (Yonge, 1938). According to Yonge, the



Fig. 3. Capulus ungaricus attached to shell of living Chlamys opercularis. Right valve of Chlamys removed and corresponding lobe of the mantle and gill reflected. Arrows indicate the directions of the ingoing and outgoing currents of Capulus, and continuous arrows a string of particles passing over the left head lobe to the mouth. e.l.v., edge of left valve of shell of Chlamys; g., gap in the margin of the Chlamys valve; h., head of Capulus; m., mantle of Capulus; m.t., mantle tentacles of Chlamys; per., periostracum of Capulus; t., cephalic tentacle of Capulus.

radula appears to have essentially a conveying function. Peile's observation (1937) that the teeth are slightly blunted in a few of the front rows may possibly be correlated with the formation of the gap mentioned above. On one occasion, when suspended particles of carmine were being used to demonstrate the ciliary currents of a *Capulus* attached to *Chlamys*, the lips diverged and the radula was seen, appearing to grasp a string of particles as does that of *Crepidula fornicata* (L.), but also the string of particles appeared at one time to go smoothly into the mouth, without the emergence of the radula. Fig. 3 shows a sketch made on this occasion; one valve of the *Chlamys* had been removed, and the corresponding lobe of the mantle reflected. The head and cephalic tentacles of the *Capulus* can be seen in the gap between the two shells, over which gap the mantle tentacles of the *Chlamys* partially extend. The

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arrows indicate the directions of the inhalant and exhalant currents of the *Capulus*, as far as they could be seen in this view, and the string of particles passing into the mouth. The current of the *Capulus* also drew down particles from the region of the mantle tentacles of the *Chlamys*.

From such a position the proboscis could be inserted between the valves of a feeding lamellibranch, and in fact has now been observed to be so inserted in the case of a *Capulus* on the shell of a living *Chlamys opercularis*. The proboscis was seen on four occasions to be extended through the gap, over the edge of the *Chlamys* valve, and in between the margins of its velum. It therefore seems clear that *Capulus* may feed on those planktonic constituents already collected by the *Chlamys* on which it sits. The relationship appears, however, to be facultative. Not only have *Capulus* lived for many weeks on single valves in the aquaria at Port Erin and Cullercoats, where their only source of food would be those particles collected by their own ciliary feeding mechanism, but also they have been regularly brought up on rocks and stones in regions off the Northumberland coast where their usual bivalve 'hosts' are scarce (Dr H. O. Bull, personal communication).

As regards the effect on the bivalve, the probable removal of some of its food supply has no obvious detrimental effect, for *Pecten*, *Modiolus* and *Chlamys* bearing *Capulus* have lived for months in aquarium tanks. The velum and velar tentacles of *Chlamys* did not appear to be affected in any way by the insertion of the proboscis, which did not even cause them to retract.

This work was carried out while holding a Herdman Studentship of the University of Liverpool.

SUMMARY

Capulus ungaricus on the shells of living lamellibranchs occupies a characteristic position, at the edge of the valves, away from the exhalant current, and with the anterior margin overlying the valve edge. The valve is scarred by the continued presence of the gastropod and the site of the latter is often associated with a semi-lunar gap in the valve edge.

Insertion of the proboscis of *Capulus* through this gap and between the vela of *Chlamys opercularis* has been observed, thus strongly supporting Orton's suggestion that the gastropod might utilize its position to become semiparasitic. The association appears to be facultative and to have no obvious detrimental effect upon the 'host'.

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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. XXVII (p. 761) and Vol. XXXII (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.

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Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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